LAKE TANGANYIKA CRABS

Evolution, Ecology and Implications for Conservation

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Marijnissen, S.A.E. Lake Tanganyika crabs: evolution, ecology, and implications for conservation. PhD thesis, University of Amsterdam, The Netherlands. xxx pages.

The work presented in this thesis was funded by the Foundation for the Advancement of Tropical Research (WOTRO W84-489). The research was conducted at the Institute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam, and the Tanzanian Institute for Fisheries Research (TAFIRI-Kigoma) in Tanzania.

Cover design: Saskia A.E. Marijnissen and Jan van Arkel
Graphics: Jan van Arkel and Saskia A.E. Marijnissen
Printed by: xxxxx
ISBN: xx-xxxxxxx-xx

Cover: *Platythelphusa armata* var. blue – one of Lake Tanganyika's many endemic mysteries.

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Evolution, Ecology and Implications for Conservation

ACADEMISCH PROEFSCHRIFT

ter verkrijging van de graad van doctor
aan de Universiteit van Amsterdam
op gezag van de Rector Magnificus

prof. dr. J.W. Zwemmer

ten overstaan van een door het college voor promoties
ingestelde commissie,
in het openbaar te verdedigen in de Aula der Universiteit
op woensdag 24 oktober 2007, te 14:00 uur

door

Saskia Antoinette Elisabeth Marijnissen

geboren te Nijmegen

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LAKE TANGANYIKA AS A HOTSPOT OF FRESHWATER CRAB DIVERSITY

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The three great East African Rift Valley lakes Malawi, Tanganyika and Victoria[1] are renowned for their outstanding species richness and high levels of endemicity, representing some of the most diverse aquatic ecosystems in the world (Groombridge & Jenkins 1998; Thieme et al. 2005). The endemic cichlid fish species flocks in these lakes include hundreds of morphologically diverse species that have become famed as textbook examples of rapid speciation and adaptive radiation (e.g. Futuyma 1986). Other fish taxa have also evolved endemic species clusters in these lakes, including bagrids, cyprinids, mastacembelids, and mochokids in Lake Tanganyika (Coulter 1991; Vreven 2005; Day & Wilkinson 2006), and cyprinids in Lake Malawi (Agnèse & Teugels 2001).

Lake Tanganyika (Figure 1) occupies a unique position among the Rift lakes. With an estimated age of 9-12 million years and a maximum depth of 1470 meters (Table 1), it is the oldest and deepest lake in Africa (Cohen et al. 1997a; Scholtz & Rosendahl 1988; Tiercelin & Mondeguer 1991). Although Lake Tanganyika contains fewer cichlid fish species than Lake Malawi and Lake Victoria, its cichlid fauna is phylogenetically, morphologically, and behaviourally more diverse (Meyer 1993). Lake Tanganyika also contains high levels of endemicity across other taxonomic groups, including gastropods, bivalves, ostracods, leeches, sponges, and shrimp (Coulter 1991). Moreover, Lake Tanganyika is the only lake in the world that contains an endemic species flock of freshwater crabs (Groombridge & Jenkins 1998; Cumberlidge et al. 1999).

CAUSES FOR CONCERN

The spectacular diversity of the great African Rift lakes encompasses an invaluable genetic heritage that provides unique opportunities to study evolutionary processes. But similar to other globally important tropical hotspots of biodiversity (Cincotte et al. 2000; Meyers et al. 2000; Brooks et al. 2001), the highly endemic fauna in these lakes is increasingly under threat from environmental changes caused by growing human populations. Tragically, not only do the African Rift lakes include spectacular examples of evolutionary diversification, but they now also include dramatic examples of human-induced extinction. In Lake Victoria, the introduction and proliferation of non-native species in combination with limnological changes has caused the demise of hundreds of endemic cichlid- and other fish species (Barel et al. 1985; Ogutu-Ohwayo 1990; Kaufman, 1992; Goldschmidt et al. 1993; Hecky et al. 1994; Seehausen et al. 1997; Witte et al. 2000; Verschuren et al. 2002; Goudswaard et al. 2002a,b).

The fauna in each of the three great African Rift lakes is currently believed to be at risk from several threats including pollution from municipal, industrial, and

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[1] Lake Victoria is located on an uplifted platform, and strictly speaking this lake does not belong to the Rift Valley system. However, because of its size and biogeographical affinities that closely tie Lake Victoria to Lake Malawi and Lake Tanganyika it is referred to here as one of the three great African Rift Valley Lakes.

agricultural discharges (Meybeck 1985; Coulter 1992; Tweddle 1992; Vandelanoote et al. 1996; Bailey-Watts et al. 2000), overexploitation by fisheries (Turner 1994; Mölsä et al. 1999, 2005), and potentially also climate change (Plisnier 2000; O'Reilly 2003; Verburg et al. 2003; Cohen et al. 2006; but see Sarvala et al. 2006). Another threat arises from increased rates of deforestation. Conversion of forests to agricultural crops causes changes in watershed hydrological regime, which can have a significant effect on lake water levels (Calder et al. 1995). More immediately, there is evidence that deforestation in the catchment basins of the Rift lakes has augmented erosion and sediment discharge (Bizimana & Duchafour 1991; Tweddle 1992; Cohen et al. 1993, 2005; Patterson 1996; Vandelannoote et al. 1996; Alin et al. 1999, 2002; Ribbink et al. 2001; Hecky et al. 2003). Increased discharge of sediment and nutrients can have numerous direct and indirect detrimental effects on aquatic organisms. Evidence from the African Rift lakes has shown that increased sediment discharge negatively affects species assemblages of both benthic invertebrates and fish (Cohen et al. 1993b; Cohen 1995; Alin et al. 1999, 2002; Duponchelle et al. 1999; Wells et al. 1999; Donohue & Irvine 2003, 2004a,b; Donohue et al. 2003; Eggermont & Verschuren 2003; McIntyre et al. 2005; Rusuwa et al. 2006).

Because of the potential combined effects of these threats, there is growing concern about the status of endemic species diversity, as well as the integrity and functioning of the aquatic ecosystems in the Rift Valley lakes (Cohen 1994; West 2001; Duda 2002; Lowe-McConnell 2003; Odada et al. 2003; Darwall et al. 2005; Olago & Odada 2007). It is evident that there is a critical need for conservation and management interventions in these lakes. Several international projects have therefore been initiated since the early 1990's aimed at conservation and sustainable management of their natural resources (reviewed in Lowe-McConnell 2003; also see Duda 2002; Bootsma & Jorgensen 2005; Jorgensen et al. 2005; Mölsä et al. 2005). It is becoming clear that effective conservation and management of biodiversity in the African Rift Valley lakes will largely depend on our ability to predict and mitigate detrimental responses to ecosystem alterations cause by human activities. This requires (i) an understanding of the processes that are causal to the elevated diversity, (ii) knowledge of how species diversity is distributed and how local diversity is maintained, and (iii) an integrated view of the various key components that affect ecosystem functioning (e.g. Moss 2000; Michel et al. 2004; McIntyre et al. 2007)

SPECIATION

The question of what has caused the high levels of diversity and endemicity in the three African Rift lakes Malawi, Tanganyika and Victoria has been a subject of much scientific research and debate (e.g. Boulenger 1898; Moore 1903; Brooks 1950; Fryer & Iles 1972; Greenwood 1974; Mayr 1984; Michel et al. 1992; Meyer 1993; Martens 1997; Sturmbauer 1998; Albertson et al. 1999; Kornfield & Smith 2000: Kocher 2004; Salzburger & Meyer 2004; Seehausen 2006; Genner & Turner 2007). With the emergence of molecular data and increasing knowledge of the ecology of endemic species in these lakes, it is gradually becoming possible to compare patterns across taxa. Examining similarities and differences in evolutionary and ecological patterns among different taxa can help in (i) pinpointing the dominant causes of elevated endemicity; and (ii) understanding how species diversity is maintained.

Molecular analyses indicate that some of the species flocks in these lakes are relatively young on a geological time scale. Using a model based on speciation rates, Seehausen (2002) suggested that the cichlid species flock in Lake Victoria could have diverged in less than 14,600 years. However, this estimate is controversial (Verheyen et al. 2003) and recent analyses using calibrations based on geological and fossil evidence suggest that divergence of cichlids in the Lake Victoria catchment took place approximately 120,000 (± 110.000) or 89,000 (± 74,000) years ago (Genner et al. 2007). The onset of divergence in the Lake Malawi cichlid radiation was dated to 4.63 (± 2.14) or 2.44 (± 1.01) million years ago (Genner et al. 2007). Estimates for divergence times of Lake Tanganyika cichlid clades differ widely (compare Table x and Meyer et al. 1990; Sturmbauer et al. 1994; Duftner et al. 2005; Koblmüller et al. 2005; Won et al. 2005, 2006). Estimates for the onset of marked divergence in Lake Tanganyika *Synodontis* catfish range between 2.6 (± 0.9) and 2.0 (± 0.6) million years ago (Day & Wilkinson 2006). Unfortunately, divergence estimates for other endemic fish taxa and invertebrates are currently lacking (but see Wilson et al. 2004). Irrespective of the focal taxon or the methodology used to arrive at divergence estimates, it is becoming evident that the great African Rift lakes are the cradles of major diversification and speciation episodes.

Factors affecting speciation can be intrinsic and/or extrinsic (e.g. Martens 1997). Examples of intrinsic life-history traits that can make some taxa more prone to lacustrine diversification than others include modes of reproduction, territoriality and homing behaviour (Martens 1994, 1997; Michel 1994). What these traits have in common is that they can limit dispersal capacity. Due to associated levels of gene flow, taxa with high dispersal capacities are less likely to speciate than those with low dispersal capabilities. However, intrinsic traits alone cannot explain the elevated levels of diversity in the lakes Malawi, Tanganyika and Victoria compared to other aquatic habitats (e.g. adjacent rivers, and other East African Rift lakes) and therefore other factors must be invoked as well. In general, it is assumed that intrinsic factors provide the potential, and extrinsic factors provide the opportunity for species to diverge in the African Rift lakes (Sturmbauer 1998).

Two of the most important extrinsic factors impacting the evolution of species diversity in East Africa are the geological processes that are causing the Rift Valley to split, and climate change fluctuations. Both of these forces have lead to numerous changes in the water levels of the Rift lakes. For instance, lake levels have fluctuated markedly since the formation of the Lake Victoria basin approximately 400,000 years ago, and geophysical data indicates that the lake completely dried up approximately 16,000-14,000 years ago and possibly 18,000-17,000 thousand years ago as well (Johnson et al. 1996, 2000; Stager et al. 2002). Lake levels have also showed numerous fluctuations in Lake Malawi (Owen et al. 1990; Nicholson 1998; Johnson et al. 2001, 2002) and in Lake Tanganyika (Table x), although the precise timing and extent of these events remains controversial. As a result of the rifting process and climate change-induced lake level fluctuations, lacustrine habitats are to a high degree isolated from riverine habitats. Furthermore, by dividing larger bodies of water into smaller ones, lake level drops cause temporary geographic isolation between populations of formerly interbreeding individuals. If the period of low lake level stands lasts long enough, this can result in the evolution of reproductive isolation between the geographically separated populations and subsequent allopatric speciation. Analyses of mitochondrial DNA indicate that lake level fluctuations influenced the distribution of genetic variation in several cichlid lineages (Sturmbauer & Meyer 1992; Verheyen et al. 1996; Rüber et al. 1998; Sturmbauer et al. 2001, 2003, 2005; Baric et al. 2003; but see Genner et al. 2007), but these patterns are not consistent across taxa (e.g. Meyer et al. 1996). It is important to realize that in allopatric models, phenotypic divergence is not necessarily coupled to speciation itself. For instance, populations that are separated in sub-basins after a lake level drop might develop phenotypic differentiation before the onset of reproductive isolation. Allopatry itself is unlikely to be the cause of the remarkable variety of functional ecological phenotypes exhibited by African cichlid fish (see below). However, the extrinsic influences of lake level fluctuations have undoubtedly contributed significantly to the generation of faunal diversity.

Repeated lake level fluctuations cause segregated populations to fuse during secondary contact, and possibly stimulate hybridization of sympatric incipient species that have not reached complete reproductive isolation. An increasing number of studies suggests that hybridization has had a major impact on the evolution of fish species diversity in the African Rift lakes (Crapon de Carpona & Fritzsch 1984; Seehausen et al. 2003; Stauffer & Hert 1992; Stauffer et al. 1996; Seehausen et al. 1997; Rüber et al. 2001; Salzburger et al. 2002; Smith et al. 2003; Streelman et al. 2004; Schelly et al. 2006; Day et al. 2007; Koblmüller et al. 2007). It has often been emphasized that hybridization can retard speciation between divergent species, possibly leading to their complete integration (Arnold 1997). However, introgressive hybridization might also contribute to the input of novel genetic variation and it might increase the potential of a population to respond to directional selection (Lewontin & Birch 1966; Grant & Grant 1992). Hybridization is well known to produce novel phenotypes (Arnold 1997), often as a result of transgressive segregation (Rieseberg et al. 1999). Transgressive segregation occurs when phenotypic variation in a hybrid population exceeds the combined variation of both parent populations (Rieseberg et al. 1999), which can be due to segregation variance or reassorting of functional gene complexes (Slatkin & Lande 1994). The origin of a novel male nuptial colour pattern in hybrid Lake Victoria cichlids (Crapon de Carpona & Fritzsch 1984) is probably caused by transgressive segregation (Seehausen 2004). Moreover, it has been shown in cichlid fish that hybridization can result in the origin of novel ecological traits. As a result of transgressive segregation of covarying genes (Albertson et al. 2003; Albertson & Kocher 2005), hybridization in cichlids can result in significant differences between progeny and parental species in a range of functional oral jaw traits (McElroy & Kornfield 1993; Albertson & Kocher 2001). If a transgressive hybrid is sufficiently divergent from both parents and if the environment provides adequate opportunity for the hybrid to establish itself in a new niche, a hybrid species can evolve in coexistence with its parental species. Seehausen (2004) emphasized two important theoretical and empirical points: (i) hybridization is common when populations invade new environments, and (ii) it can predispose colonising populations to rapid ecological diversification and adaptive radiation.

Besides stimulating hybridization by fusing previously segregated populations, lake level fluctuations offer ecological opportunities by providing new, resource-rich environments that are free of competitors and/or predators. It is often argued that the initial colonisers of such environments encounter a vacant adaptive landscape in which ecological diversification and adaptive radiation can take place (Fryer & Iles 1972; Schluter 1996, 2000). Adaptive radiation is defined as the evolution of ecological and phenotypic diversity within a rapidly multiplying lineage (Schluter 2000). Some renowned examples of adaptive radiations of vertebrate taxa include Darwin's finches (Geospizinae) on the Galápagos Islands (Darwin 1841), honeycreepers (Drepanidae) on Hawaiian islands (Amadon 1950), and *Anolis* lizards on Caribbean islands (Underwood 1959). Evidence for adaptive radiation is derived from four criteria: (i) common ancestry; (ii) rapid divergence into multiple lineages;

(iii) divergence in ecologically relevant phenotypic traits, and (iv) ecological utility of these phenotypic traits (Schluter 2000). Although the third criterion remains difficult to demonstrate (see below), there is increasing evidence that ecological differentiation and adaptive speciation have played an important role in facilitating the extraordinary faunal diversity and endemicity in the African Rift lakes.

Evidence for ecological differentiation in African cichlids was initially derived from the observation that species occurring sympatrically in rocky littoral habitats exhibit a wide variety of trophic morphologies (e.g. Figure 2), including specialised traits for scraping algae from rocks, crushing mollusc shells, removing parasites and eating scales from other fish (Fryer & Iles 1972). The presence of a second set of pharyngeal jaws that is functionally decoupled from the oral jaws, allowing rapid modification through a few allometric and genetic changes to adapt quickly to a variety of novel resources appears to be key to the evolutionary success of cichlid fish (Liem 1973, 1980; Liem & Osse 1975; Galis & Drucker 1996; Albertson et al. 2003 REFS). Furthermore, there is evidence of extensive evolutionary parallelism, as similar ecologically relevant traits have evolved independently across cichlid taxa (Figure 3; Fryer & Iles 1972; Kocher et al 1993; Clabaut et al. 2007). Recently, Seehausen (2006) found additional evidence for the plausibility of adaptive radiation as an explanation for the replicate speciation patterns of African lacustrine cichlid fish, by testing two key predictions. One of the predictions of ecological speciation is that after an initial speciation burst, rates of divergence slow down as niche space fills up (Schluter 2000; Dieckmann & Doebeli 1999; Kondrashov & Kondrashov 1999; Gavrilets & Vose 2005). This contrasts with speciation through processes of genetic drift or sexual selection, which are not expected to cause similar temporal trends of declining divergence rates. Another relevant prediction is that larger lakes should be able to generate and sustain more species than smaller ones (Losos & Schluter 2000). Seehausen (2006) demonstrated that these predictions hold true for the African cichlid radiations. Interestingly, it was also shown that the prospensity to undergo adaptive radiation is a derived property that does not necessarily coincide with the appearance of proposed key innovations (Seehausen 2006).

One of the least understood aspects of adaptive radiation is how ecological niche differentiation can result in speciation. According to the classic scenario of sympatric speciation, competition for diverse resources can generate disruptive frequency-dependent natural selection, which might result in the splitting into two or more species. Individuals with intermediate phenotypes are outcompeted by those with extreme phenotypes that are specialised to utilise a particular resource. This can subsequently lead to the evolution of non-random mating, either based on (i) the traits that are under natural selection, or (ii) recruitment of other isolating traits through development of genetic correlations (Dieckmann & Doebeli 1999; Kondrashov & Kondrashov 1999). As such, barriers to gene flow can evolve between populations as a result of divergent ecological selection.

Classic adaptive speciation models predict that sympatric incipient sister species differ primarily in phenotypic traits that are functionally related to competition for ecological resources. However, evidence from cichlid species pairs that this is not always the case (Albertson et al. 1999). Instead, it was demonstrated that ecological differences are often very small among closely related taxa, and increase among more distantly related taxa (Barraclough & Nee 2001). More recent theoretical models suggest that mate choice does play an important role in adaptive radiation, and that ecological differentiation and sexual selection can be mutually reinforcing processes (van Doorn & Weissing 2001; van Doorn et al. 2004). Both experimental and field observations have called attention to the fact that cichlid mating systems are highly conducive to sexual selection, and that mate choice appears to be very important in cichlid species divergence (e.g. Hert 1991; Knight et al. 1998; Van Oppen et al. 1998; Knight & Turner 1999, 2004; Maan et al. 2004; Pauers et al. 2004; Seehausen & Schluter 2004; Dijkstra et al. 2007).

IMPLICATIONS FOR MAINTENANCE OF DIVERSITY

If ecological speciation is a dominant cause of elevated species diversity in the African lakes, it can be predicted that this has resulted in intricate trophic foodwebs comprising many highly derived stenotopic species. Following the competitive exclusion principle, it would then seem logical that coexistence of these species is maintained as a result of ecological niche partitioning by resource specialists (Ribbink et al. 1983). Although there is evidence that corroborates this, patterns differ across taxa and are not always consistent with the expectations.

In Lake Tanganyika, approximately 65% of the endemic cichlid species is restricted to rocky littoral habitats (Hori et al. 1993). Field surveys conducted over a period of ten years in three rocky littoral sites in the north, middle, and south of the lake showed that fish communities in these habitats were in a state of equilibrium, maintained through an intricate network of direct and indirect interactions among and between sympatric species (Yamaoka 1982, 1983; Takamura 1984; Mbomba 1985: Nshombo et al. 1985; Yamaoka et al. 1986; Hori 1983, 1991; Hori et al. 1993). Cluster analyses indicated that fish species were comprised of 12 functional feeding groups within which species shared 50% dietary similarity, and coexistence within those groups appeared to be maintained by divergent morphologies, foraging behaviour, and spatial segregation (Hori et al. 1993; see also Sturmbauer et al. 1992). Trophic niche partitioning has also been demonstrated for rock-dwelling fish in Lake Malawi (Reinthal 1990; Bootsma et al. 1996) and in Lake Victoria (Bouton et al. 1997).

At the same time, several field studies found considerable overlap of ecological niche components between closely related but morphologically distinct fish species in these rocky littoral habitats (Reinthal 1990; Bouton et al. 1997; Genner et al. 1999a,b). Evidently, contemporary coexistence can also occur in the absence of resource partitioning. It was shown that even cichlid species with highly derived feeding morphologies, which are apparently specialised for exploiting distinct food sources, can exhibit extensive versatility in their feeding repertoires (McKaye & Marsh 1983). It might seem like a paradox that species with specialised phenotypes act as ecological generalists. However, using an elegant model based on principles of optimal foraging, Robinson and Wilson (1998) showed that these seemingly counterintuitive results can be explained if specialization is based on non-preferred resources while also allowing exploitation of more preferred common resources. There is also evidence from complex coral reef fish communities that trophic versatility facilitates the maintenance of high local diversity (Bellwood et al. 2006).

Determining the influence of human activities on the stability and functioning of the ecosystems in the African lakes requires not only insight in levels of specialisation and versatility of fish, but also of other key components of lacustrine foodwebs. Unfortunately, little is known about the evolutionary and ecological correlates of species differences in taxa other than fish, with the exception of ostracods (Martens 1994; Cohen 2000; Park & Downing 2000) and gastropods (Michel et al. 1992, 2004; Michel 1994, 2000; West & Michel 2000; Genner & Michel 2003; Genner et al. 2004;

Michel 2004; Wilson et al. 2004; Genner et al. 2007). Given the amount of research effort that has been invested in the African lakes during the past decades, the lack of data on the evolutionary history and ecology of other taxa is remarkable.

FRAMEWORK AND OUTLINE OF THIS THESIS

This thesis is intended to provide a first, fundamental and essential basis of empirical phylogenetic- and ecological data on the endemic freshwater crabs from Lake Tanganyika, and contribute to refining our understanding of the origin and maintenance of life in this aquatic hotspot of biodiversity. After providing a general background here in the introduction, I first discuss some taxonomic issues.

Taxonomy is the practice and science of classification, and it forms the foundation for understanding biodiversity. The classic approach of classifying organisms is based on morphological traits (e.g. Linneaus 1758). The taxonomy of the Lake Tanganyikan crabs has been subject of much scientific debate. The first species that was described from the lake was a single female specimen with juveniles, which was collected by French missionaries in the lake and deposited in the Muséum National d'Histoire Naturelle in Paris. In 1887, this female became the type specimen of a new genus, *Platythelphusa*, when she was described by the renowned French carcinologist Alphonse Milne-Edwards. Undoubtedly inspired by the remarkably large claw and the row of spines on the carapace of this species, he gave it the name *Platythelphusa armata* A. Milne-Edwards, 1887. The description of *P. armata* was soon followed by the discovery of more endemic species from the lake that were described by Cunnington (1899, 1907, 1920), and Capart (1952). Subsequently, the higher and lower level taxonomy of the endemic Lake Tanganyika genus was discussed, rearranged, and revised by a range of authorities (Cumberlidge et al. 1999, 2007, and references therein). After comparing descriptions of species in literature and museum material with newly collected specimens from Lake Tanganyika, I found several discrepancies. This resulted in some comments on the taxonomic position of *Platythelphusa denticulata*, and the description of the new species *P. immaculata* and *P. praelongata* (CHAPTER 1). This chapter furthermore provides a taxonomic key to the species of *Platythelphusa*. With the description of two new species, and removal of *P. denticulata* from synonymy with *P. conculcata*, the total number of platythelphusid species from Lake Tanganyika is nine. Although this might seem like a small number compared to some other taxa, such as cichlids that have evolved hundreds of endemic species in the African lakes, it is relevant to keep in mind that freshwater crabs do not typically exhibit lacustrine divergence. For instance, Lake Kivu contains three endemic species, one of which is shared with Lake Mutanda (Chace 1942, 1953; Bott 1955). Furthermore, one endemic species is found in each of the small East African lakes Chala (Hilgendorf 1897), and Rukwanzi (Corace et al. 2001), but to my knowledge, no endemic species have been described from any of the other African lakes. This raises the question what caused the morphological diversity and elevated endemicity of crabs in Lake Tanganyika.

These questions have intrigued scientists ever since the description of *P. armata*. By noting that "l'abdomen de la femelle est énorme, il forme une poche marsupiale où les jeunes trouvent un abri[2]", Milne-Edwards (1887, p. 146) provided the very first

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[2] The abdomen of this female is enormous, and it forms a marsupial pouch in which the juveniles find shelter. [3] This freshwater crab exhibits great resemblance to certain marine or brackish water species in the Grapsidae, such as the Chinese mitten crab. One might be tempted to assign it to this group, if it was not for the development of the

clue to the evolutionary history of the Lake Tanganyika crabs. In the same paper, he commented that "ce Crabe d'eau douce présente une grande ressemblance avec certaines espèces marines ou d'eau saumâtre du groupe des Grapsidés, telles que l'*Eriochirus sinensis*; on pourrait être tenté de le rapprocher de ces derniers si le développement de l'abdomen et l'absence de métamorphoses chez les jeunes ne le classaient pas de la manière la plus certaine à côté des Thelphuses, des Dilocarcins, des Boscies et des autres genres qui vivent dans les eaux courantes[3]." This comment is critical, because it indicates that the Lake Tanganyika crabs share taxonomic affinities with freshwater crabs rather than marine crabs. In contrast to marine crabs, which produce large quantities of small eggs that hatch into free-swimming larval stages, true freshwater crabs produce relatively small quantities of large eggs that hatch inside the female brood pouch (Figure x). Freshwater hatchlings are truly miniature crabs complete with four pairs of walking legs and two claws. Female freshwater crabs protect these hatchlings in the brood pouch for a number of weeks, during which they undergo several moults until they are released (Cumberlidge 1999). The presence of a brood pouch might thus be taken as evidence that the endemic Lake Tanganyika crabs are derived from freshwater ancestors. However, Moore (1903) questioned this. He emphasised the resemblance with marine taxa, and hypothesised that the Lake Tanganyika crabs "entered the lake more or less directly from the sea, at some time when a connection between them was far more close than present" (Moore 1903, p. 284).

The question whether the 'marine habitus' of the Lake Tanganyika platythelphusids represents the plesiomorphic condition, or whether these characters are the convergent result of long-term isolation in a lacustrine environment was investigated by Richard von Sternberg and Neil Cumberlidge. Based on a total of 77 morphological characters of the carapace, mouthparts, sternum, abdomen, periopods, and gonopods, they conducted a cladistic analyses of the platythelphusid crabs using representatives of six different families as outgroups. Their study did not support the idea that the platythelphusids emerged from a relict population of a grapsid or grapsid-like taxon. Instead, cladistic analyses support the idea that the platythelphusids evolved from freshwater ancestors (von Sternberg & Cumberlidge 1999). However, no consensus was achieved about their closest relative (compare Cumberlidge & von Sternberg 1999; von Sternberg et al. 1999; von Sterberg & Cumberlidge 1999, 2001), and consequently the evolutionary history of the platythelphusids remained enigmatic. Therefore, I examined the phylogenetic relationships of the Lake Tanganyika endemic crabs using sequences of 12S and 16S rRNA mitochondrial DNA (CHAPTER 2). Mitochondrial phylogenies generally provide very reasonable working hypotheses. Assuming that the patterns described in chapter 2 are accurate in the sense that (i) it is likely that the platythelphusids are derived from East African freshwater ancestors (see also Daniels et al. 2006); (ii) the platythelphusids are more closely related to each other than to other African freshwater lineages; (iii) branches within the platythelphusid clade are short, and (iv) platythelphusid species are relatively young, demonstrates that this group shows great potential to serve as an invertebrate model for studies on speciation in Lake Tanganyika.

CHAPTER 3 focuses on two major processes that might have been important in contributing to the divergence of the endemic Lake Tanganyika crabs: ecological

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abdomen and the absence of metamorphosis in the juveniles, which makes it certain that it should be assigned to a freshwater genus.

niche partitioning and sexual selection. The approach that I took in this chapter was to first provide another, more extensive mitochondrial phylogenetic framework based on sequences of 16S rRNA and cytochrome oxidase II mtDNA, and then to use this framework for examining claw functional morphologies. Because of the intimate relationship that exists between the structure of a claw and its ecological performance, comparative claw functional morphology is an excellent method for obtaining insight in patterns of trophic diversification (e.g. Brown et al., 1979; Lawton & Elner, 1985; Freire et al., 1996; Behrens Yamada & Boulding, 1998; Smith, 2004). Kelly West previously demonstrated that *P. armata*'s remarkably enlarged claw is advantageous in crushing the heavily calcified and exceptionally sculptured shells of endemic Lake Tanganyika gastropods (West et al. 1991; West & Cohen 1994). A range of morphological comparisons between the claws of *P. armata* and other freshwater crabs, shell-crushing experiments, and predation experiments provided strong support for the hypothesis that the unusual morphological dervivation of the Lake Tanganyika gastropods is the result of lacustrine coevolutionary interactions (West et al. 1991; West & Cohen 1994, 1996; also see Socci 2001; Rosales 2002). I discuss similarities and differences between *P. armata* and *Potamonautes platynotus*, which is also endemic to Lake Tanganyika (see Cunnington 1907). I then compare claw performance properties of *Platythelphusa tuberculata*, which exhibit strong indications of sexual selection. I subsequently focus on divergence of claw functional morphological traits within the platythelphusid clade as a whole. The results of these analyses indicate that both ecological niche partitioning as well as sexual selection interact in generating diversity in Lake Tanganyika endemic crabs. **CHAPTER 4** discusses the extent to which morphological species are ecologically different based on habitat surveys, gut content analyses, and stable isotope analyses. The patterns observed here are very similar to some of the patterns observed in cichlid communities. Although there is evidence of interspecific segregation in depth, substrate type and mean stable isotope signatures, there is also considerable level of ecological niche overlap among species of *Platythelphusa* that coexist in rocky littoral habitats. I examine the functional role of Lake Tanganyika's endemic crabs in benthic food webs in **CHAPTER 5**, and infer their level of vulnerability to environmental perturbations. Finally, I discuss general implications for activities focusing on conservation of freshwater species diversity.

REFERENCES

Agnèse, J.F. and Teugels, G.G. 2001. The *Bathyclarias-Clarias* species flock: a new model to understand rapid speciation in African Great Lakes. Comptes Rendus de l'Académie des Sciences Paris, Sciences de la Vie 324:683-688.

Airoldi, L. 2003. The effects of sedimentation on rocky coast assemblages. Oceanography and Marine Biology: an Annual Review 41:161-236.

Albertson, R.C. and Kocher, T.D. 2001. Assessing morphological differences in an adaptive trait: a landmark-based morphometric approach. Journal of Experimental Zoology 289:385-403.

Albertson, R.C. and Kocher, T.D. 2005. Genetic architecture sets limits on transgressive segregation in hybrid cichlid fishes. Evolution 59:686-690.

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

Albertson, R.C., Streelman, T.J. and Kocher, T.D. 2003. Directional selection has shaped the oral jaws of Lake Malawi cichlid fishes. Proceedings of the National Academy of Sciences of the United States of America 100:5252-5257.

Alin, S.R., Cohen, A.S., Bills, R., Gashagaza, M.M., Michel, E., Tiercelin, J., Martens, K., Coveliers, P., Mboko, S.K., West, K., Soreghan, M., Kimbadi, S. and Ntakimazi, G. 1999. Effects of landscape disturbance on animal communities in Lake Tanganyika, East Africa. Conservation Biology 13:1017-1033.

Alin, S.R., O'Reilly, C.M., Cohen, A.S., Dettman, D.L., Palacios-Fest, M.R. and McKee, B.A. 2002. Effects of land-use change on aquatic biodiversity: a view from the paleorecord at Lake Tanganyika, East Africa. Geology 30:1143-1146.

Allison, E. H., Paley, R. G., Ntakimazi, G., Cowan, V. J. and West, K., 2000. Biodiversity assessment and conservation in Lake Tanganyika. BIOSS final technical report. Pollution control and other measures to protect biodiversity in Lake Tanganyika. Lake Tanganyika Biodiversity Project (UNDP/GEF/UNOPS, RAF/92/G32), pp 1-166. www.ltbp.org

Amadon, D. 1950. The Hawaiian honeycreepers (Aves, Drepaniidae). Bulletin of the American Museum of Natural History 95:151-262.

Arnold, M.L. 1997. Natural hybridization and evolution. Oxford University Press, New York, NY, USA, pp 1-215.

Bailey-Watts, A. Foxall, C. and West, K. 2000. Pollution control and other measures to protect biodiversity in Lake Tanganyika. Pollution Special Study, Lake Tanganyika Biodiversity Project (UNDP/GEF/UNOPS, RAF/92/G32), pp 1-9. www.ltbp.org

Barel, C.D.N., Dorit, R., Greenwoord, P.H., Fryer, G., Hughes, N., Jackson, P.B.N., Kawanabe, H., Lowe-McConnell, R.H., Nagoshi, M., Ribbink, A.J., Trewavas, E., Witte, F. and Yamaoka, K. 1985. Destruction of fisheries in Africa's lakes. Nature 315:19-20.

Baric, S., Salzburger, W. and Sturmbauer, C. 2003. Phylogeograpgy and evolution of the Tanganyikan cichlid genus *Tropheus* based upon mitochondrial DNA sequences. Journal of Molecular Evolution 56:54-68.

Behrens Yamada, S. and Boulding, E.G. 1998. Claw morphology, prey size selection and foraging efficiency in generalist and specialist shell-breaking crabs. Journal of Experimantal Marine Biology and Ecology 220:191-211.

Bellinger, B.J., Cocquyt, C. and O'Reilly, C.M. 2006. Benthic diatoms as indicators of eutrophication in tropical streams. Hydrobiologia 537:75-87.

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

Berkman, H.E. and Rabeni, C.E 1986. Biomonitors of stream quality in agricultural areas: fish versus invertebrates. Environmental Management 10:413-419.

Berkman, H.E. and Rabeni, C.F. 1987. Effect of siltation on stream fish communities. Environmental Biology of Fishes 18:285-294.

Bizimana, M. and Duchafour, H. 1991. A drainage basin management study: The case of the Ntihangwa River Basin. In: Cohen, A. (Ed.). Report on the first international conference on conservation and biodiversity of Lake Tanganyika. Biodiversity Support Program, Washington D.C., U.S.A., pp 43-45.

Bootsma, H.A. and Hecky, R.E. 1993. Conservation of the African Great Lakes: a limnological perspective. Conservation Biology 7:644-656.

Bootsma, H.A. and Hecky, R.E., Hesslein, R.H. and Turner, G. 1996. Food partitioning among Lake Malawi nearshore fishes as revealed by stable isotopes analyses. Ecology 77:1286-1290.

Bootsma, H.A. and Jorgensen, S.E. 2005. Lake Malawi/Nyasa: experience and lessons learnt brief. In: Managing lakes and their basins for sustainable use: a report for lake basin managers and stakeholders. International Lake Environment Committee Foundation ILEC, Kusatsu, Japan, pp 259-276.

Borgstrom, R., Brabrand, A. and Solheim, T.J. 1992. Effects of siltation on resource utilization and dynamics of allopatric brown trout, *Sulmo trutta,* in a reservoir. Environmental Biology of Fishes 34:247-255.

Boulenger, G.A. 1898. Catalogue of the freshwater fishes of Africa in the British Museum (Natural History), Vol III pp 1-526.

Bouton, N., Seehausen, O. and van Alphen, J.J.M. 1997. Resource partitioning among rock-dwelling haplochromines (Pisces: Cichlidae) from Lake Victoria. Ecology of Freshwater Fish 6:225-240.

Brooks, J.L. 1950. Speciation in ancient lakes. Quarterly Review of Biology 25:30-60, 131-176.

Brooks, T.M., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A.B., Rylands, A.B., Konstant, W.R., Flick, P., Pilgrim, J., Oldfield, S., Magin, G. and Hilton-Taylor, G. 2001. habitat loss and extinction in the hotspots of biodiversity. Conservation Biology 16:909-923.

Brown, S.C., Cassuto S.R. and Loos, R.W. 1979. Biomechanics of chelipeds in some decapod crustaceans. Journal of Zoology London 188:143-159.

Burkhead, N.M. and Jelks, H.L. 2001. Effects of suspended sediment on the reproductive success of the tricolor shiner, a crevice-spawning minnow. Transactions of the American Fisheries Society 130:959-68.

Calder, I.R., Hall, R.L., Bastable, H.G., Gunston, H.M., Shela, O., Chirwa and Kafundu, R. 1995. The impact of land use change on water resources Africa: a modeling study of Lake Malawi. Journal of Hydrology 170:123-135.

Caljon, A.G. 1992. Water quality in the Bay of Bujumbura (Lake Tanganyika) And its influence on phytoplankton composition. Mitteilungen Internationale Vereiningung für Theoretische und Angewandte Limnologie 23:55-65.

Capart, A. 1952. Exploration hydrobiologique du Lac Tanganyika (9146-1947), résultats scientifiques – Crustacés, Décapods, Brachyures. Institute Royal des Sciences Naturelles de Belgique 3:41-67.

Chace, F.A. 1942. Zoological results of a fourth expedition to East Africa. Decapod crustacea. Bulletin of the Museum of Comparative Zoology, Harvard College 91:185-233.

Chace, F.A. 1953. Zoological results of a fifth expedition to East Africa. VI. Decapod crustacea. Bulletin of the Museum of Comparative Zoology, Harvard College 110:427-443.

Cincotta, R.P., Wisnewski, J. and Engelman, R. 2000. Human population in the biodiversity hotspots. Nature 404:990-992.

Clabaut, C., Bunje, P.M.E., Salzburger, W. and Meyer, A. 2007. Geometric morphometric analyses provide evidence for the adaptive character of the Tanganyikan cichlid fish radiations. Evolution

Cohen, A. S. 1994. Extinction in ancient lakes: biodiversity crises and conservation 40 years after J.L. Brooks. In: Martens, K., Goddeeris, B. and Coulter, G.W. (eds.).

Speciation in ancient lakes. Archiv für Hydrobiologie Ergebnisse der Limnologie 44:451-479.

Cohen, A.S. 1995. Paleoecological approaches to the conservation biology of benthos in ancient lakes: a case study from Lake Tanganyika. Journal of the North American Benthological Society 14:654-668.

Cohen, A.S. 2000 Linking spatial and temporal changes in the diversity structure of ancient lakes: examples from the ecology and paleoecology of the Tanganyikan ostracods. In: Rossiter, A. and Kawanabe, H. (eds.). Ancient lakes: biodiversity, ecology and evolution. Advances in Ecological Research 31521-537.

Cohen A.S., Soreghan M. and Scholz C.A. 1993a. Estimating the age of formation of lakes: An example from Lake Tanganyika, East African Rift system. Geology 21:511-514

Cohen A.C., R. Bills, C.Z. Cocquyt, and A.G. Caljon. 1993b. The impact of sediment pollution on biodiversity in Lake Tanganyika. Conservation Biology 7: 667-677.

Cohen A.S., Lezzar K.E., Cole, J., Dettman, D., Ellis, G.S., Eagle Gonneea, M., Plisnier, P.D., Langeberg, V., Blaauw, M. and Zilifi, D. 2006. Late Holocene linkages between decade-century scale climate variability and productivity at Lake Tanganyika, Africa. Journal of Paleolimnology 36:189-209.

Cohen A.S., Lezzar K.E., Tiercelin J.J. and Soreghan M. 1997a. New paleogeographic and lake level reconstructions of Lake Tanganyika: implications for tectonic, climatic, and biological evolution in a rift lake. Basin Research 9/2:107-132.

Cohen A.S., Talbot M.R., Awramik S.M., Dettman D.L. and Abell P. 1997b. Lake level and paleoenvironmental history of Lake Tanganyika. Geological Society of America Bulletin 109:444-460.

Cohen, A.S., Palacios-Fest, M.R. Msaky, E.S., Alin, S.A., McKee, B., O'Reilly, C.M. Dettman, D.L., Nkotagu, H. and Lezzar, K. 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.

Cooper, C.M. 1987. Benthos in Bear Creek, Mississippi: effects of habitat variation and agricultural sediments. Journal of Freshwater Ecology 4:101-113.

Corace, R.G., Cumberlidge, N. and Garms, R. 2001. A new species of freshwater crab from Rukwanzi, East Africa. Proceedings of the Biological Society of Washington 114:178-187.

Coulter, G.W. 1991. Lake Tanganyika and its life. Oxford University Press, London, UK, pp 1-354.

Coulter, G.W. 1992. Vulnerability of Lake Tanganyika to pollution, with comments on social aspects. Mitteilungen Internationale Vereiningung für Theoretische und Angewandte Limnologie 23:67-70.

Crapon de Carpona, M.D. and Fritzsch, B. 1984. Interspecific fertile hybrids of haplochromine Cichlidae (Teleostei) and their possible importance for speciation. Netherlands Journal of Zoology 34:503-538.

Cumberlidge, N. 1999. The freshwater crabs of West Africa, family Potamonautidae. Éditions de l'IRD Institut de Recherche pour le Développement Collection Faune et Flore Tropicales, n°35, Paris, France, pp 1-382.

Cumberlidge, N. and von Sternberg, R. 1998. Phylogenetic relationships of the freshwater crabs of Lake Tanganyika (Decapoda: Brachyura). In: Schram, F.R. and von Vaupel Klein, J.C. (eds.). Crustaceans and the Biodiversity Crisis. Proceedings of the Fourth International Crustacean Congress. Koninklijke Brill, NV Leiden, The Netherlands, pp 405-422.

Cumberlidge, N., von Sternberg, R., Bills, I.R. and Martin, H. 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.

Cumberlidge, N., von Sternberg, R. and Daniels, S.R. 2007. A revision of the higher taxonomy of the Afrortopical freshwater crabs (Decapoda: Brachyura) with a discussion of their biogeography. Biological Journal of the Linnean Society xxx:xxx-xxx.

Cunnington, W.A. 1899 On a new brachyurous crustacean from Lake Tanganyika. Proceedings of the Royal Society 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.

Cunnington, W.A. 1920. The fauna of the African Lakes: A study in comparative limnology with special reference to Lake Tanganyika. Proceedings of the Zoological Society, London 3:507-622.

Daniels, S.R., Cumberlidge, N., Pérez-Losada, M., Marijnissen, S.A.E. and Crandall, K.A. 2006. Evolution of Afrotropical freshwater crab lineages obscured by morphological convergence. Molecular Phylogenetics and Evolution 40:227-23

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

Darwin, C R. The zoology of the voyage of H.M.S. Beagle, under the command of Captain Fitzroy, R.N., during the years 1832-1836: part III, birds. London: Smith Elder, London, UK, pp 99-103.

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

Day, J.J., Santini, S. and Garcia Moreno, J. 2007. Phylogenetic relationships of the Lake Tanganyika cichlid tribe Lamprologini: The story from mitochondrial DNA. Molecular Phylogenetics and Evolution xxx:xxx-xxx.

Dieckmann, U. and Doebeli, M. 1999. On the origin of species by sympatric speciation. Nature 400:354-357.

Dijkstra, P., Seehausen, O., Pierotti, M. and Groothuis, J.G.G. 2007. Male-male competition and speciation: aggression bias towards differently coloured rivals varies between stages of speciation in a Lake Victoria cichlid species complex. Journal of Evolutionary Biology xxx:xxx-xxx.

Donohue, I. and Irvine, K. 2003. Effects of sediment particle size composition on survivorship of benthic invertebrates from Lake Tanganyika. Archiv für Hydrobiologie 157:131-144.

Donohue, I. and Irvine, K. 2004a. Seasonal patterns of sediment loading and benthic invertebrate community dynamics in Lake Tanganyika, Africa. Freshwater Biology 49:3320-331.

Donohue, I. and Irvine, K. 2004b. Size-specific effects of increased sediement loads on gastropod communities in Lake Tanganyika, Africa. Hydrobiologia 522:337-342.

Donohue, I., Verheyen, E. and Irvine. K. 2003. In situ experiments on the effects of increased sediment loads on littoral rocky shore communities in Lake Tanganyika, East Africa. Freshwater Biology 48:1603-161.

Duda, A.M. 2002. Restoring and protecting the African Great Lake basin ecosystems – lessons from the North American Great Lakes and the GEF. In: Odada, E.O. and Olago, D.O. (eds.). The East African Great Lakes: Limnology, Paleolimnology and Biodiversity. Advances in Global Change Research 12:537-556.

Duftner, N., Koblmüller, S. and Sturmbauer, C. 2005. Evolutionary relationships of the Limnochromini, a tribe of benthic deep water cichlid fishes endemic to Lake Tanganyika, East Africa. Journal of Molecular Evolution 60:277-289.

Duponchelle, F., Ribbink, A.J., Msukwa, A., Mafuka, J. and Mandere, D. 2000. The potential influence of fluvial sediments on rock-dwelling fish communities. In: Duponchelle, F., and Ribbink, A.J. (eds.). Fish ecology report, Lake Malawi/Nyasa/Niassa Biodiversity Conservation Project. SADC/GEF report, pp 227-264.

Eggermont, H. and Verschuren, D. 2003. Impact of soil erosion in disturbed tributary drainages on the benthic invertebrate fauna of Lake Tanganyika, East Africa. Biological Conservation 113:99-109.

Ellis, M.M. 1936. Erosion silt as a factor in aquatic environments. Ecology 17:29-42.

Freire, J., Paz Sampedro, M. and Gonzáles-Gurriarán, E. 1996. Influence of morphometry and biomechanics on diet selection in three portunid crabs. Marine Ecology Progress Series 137:111-121.

Fryer, G. and Iles, T.D. 1972. The cichlid fishes of the Great Lakes of Africa: their biology and evolution. Oliver and Boyd, Edinburgh, UK, pp 1-641.

Futuyma, D.J. 1986. Evolutionary Biology. Sinauer Associates, Sunderland, MA, USA, pp 245-246.

Galis, F. and Drucker, E.G. 1996. Pharyngeal biting mechanisms in Centrarchids and cichlids: insights into a key evolutionary innovation. Journal of Evolutionary Biology 9:641-670.

Gasse, F. 2000. Hydrological changes in the African tropics since the Last Glacial Maximum. Quaternary Science Reviews 19:189-211.

Gasse, F., Ledee, V., Massault, M. and Fontes, J.-C. 1989. Water-level fluctuations in-phase with oceanic changes during the last glaciation and deglaciation. Nature 342:57-59.

Gavrilets, S. and Vose, A. 2005. Dynamic patterns of adaptive radiation. Proceedings of the National Academy of Sciences of the United States of America 102:18040-18045.

Genner, M.J. and Michel, E. 2003. Fine-scale habitat associations of soft-sediment gastropods at Cape Maclear, Lake Malawi. Journal of Molluscan Studies 69:325-328.

Genner, M.J., Michel, E., Erpenbeck, D., De Voogd, N.J., Witte, F. and Pointier, J.P. 2004. Camouflaged invasion of Lake Malawi by an oriental gastropod. Molecular Ecology 13:2135-2141.

Genner, M.J., Todd, J.A., Michel, E., Erpenbeck, D., Jimoh, A., Joyce, D.A., Piechocki, A. and Pointier, J.P. 2007. Amassing diversity in an ancient lake:

evolution of a morphologically diverse parthenogenic gastropod assemblage in Lake Malawi. Molecular Ecology 16:517-530.

Genner, M.J., and Turner, G.F. 2005. The mbuna cichlids of Lake Malawi: a model for rapid speciation and adaptive radiation. Fish and Fisheries 6:1-34.

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

Genner, M.J., Turner, G.F. and Hawkins, S.J. 1999b. Foraging of rocky habitat cichlid fishes in Lake Malawi: coexistence through niche partitioning? Oecologia 121:283-292.

Genner, M.J., Seehausen, O., Hunt, D.H., Joyce, D.A., Shaw, P.W., Carvalho, G.R. and Turner, G.F. 2007. Age of cichlids: new dates for ancient lake fish radiations. Molecular Biology and Evolution xxx-xxx-xxx.

Goldschmidt, T., Witte, F. and Wanink, J. 1993 Cascading effects of the introduced Nile perch on the detritivorous/phytoplanktivorous species in the sublittoral area of Lake Victoria. Conservation Biology 7:686-700.

Goudswaard, T., Witte, F. and Chapman, L.J. 2002a. Decline of the African lungfish (Protopterus aethiopicus) in Lake Victoria (East Africa). African Journal of Ecology 40:42-52.

Goudswaard, P.V.C., Witte, F. and Katunzi, E.F.B. 2002b. The tilapiine fish stock of Lake Victoria before and after the Nile perch upsurge. Journal of Fish Biology 60:838-856.

Grant, P.R. and Grant, B.R. 1992. Hybridization of bird species. Science 256:193-197.

Greenwood, P.H. 1974. Cichlid fishes of Lake Victoria, East Africa: the biology and evolution of a species flock. Bulletin of the British Museum of Natural History, Zoology Supplement 6:1-134.

Grobbelaar, J. 1985. Phytoplankton productivity in turbid waters. Journal of Plankton Research 7:653-663.

Groombridge, B. and Jenkins, M. 1998. Freshwater Biodiversity: a preliminary global assessment. World Conservation Monitoring Centre (WCMC), World Conservation Press, Cambridge, UK, pp 1-104. www.wcmc.org.uk

Guiot, J. and Tiercelin, J-J. 1993. Pollen-derived rainfall and temperature estimates from Lake Tanganyika and their implication for Late Pleistocene water levels. Quaternary Research 40:343-350.

Hecky, R.E. 1993. The eutrophication of Lake Victoria. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 25:39-48.

Hecky, R.E., Bootsma, H.A. and Kingdon, M.L. 2003. Impact of land use on sediment and nutrient yields to Lake Malawi/Nyasa (Africa). Journal of Great Lakes Research 29: 139-158.

Hecky, R.E., Bugenyi, F.W.B., Ochumba, P., Gophen, M., Mugidde, R. and Kaufman, L. 1994. Deoxygenation of the deep water of Lake Victoria. Limnology and Oceanography 38:7090-724.

Hecky R.E., Kling, H.J., Johnson, T.C., Bootsma, H.A. and Wilkinson, P. 1999 Algal and sedimentary evidence for recent changes in the water quality and limnology of Lake Malawi/Nyasa. Pages 191-214 In: Bootsma, H.A., and Hecky, R.E. (eds.) Water Quality Report, Lake Malawi/Nyasa/Niassa Biodiversity Conservation Project. SADC/GEF.

Henley, W.W., Patterson, M.A., Neves, R.J. and Lemly, A.D. 2000. Effects of sedimentation and turbidity on lotic food webs: a consice review for natural resource managers. Reviews in Fisheries Science 8:125-139.

Hert, E. 1991. Female choice based on egg-spots in *Pseudotropheus aurora* Burgess 1976, a rock dwelling cichlid of Lake Malawi, Africa. Journal of Fish Biology 38:951-953.

Hilgendorf, F. 1897. Eine neue Landkrabe (*Telphusa platycentron*) aus Ostafrika. Sitzungs-Bericht der Gesellschaft Naturforschender Freunde zu Berlin 1897:81-85.

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

Hori, M. 1991. Feeding relationships among cichlid fishes in Lake Tanganyika: Effects of intra- and interspectfic variations of feeding behavior on their coexistence. Ecology International Bulletin 19:89-101.

Hori, M., Yamaoka, I. and Takamur, K. 1983. Abundance andmicro-distribution of cichlid fishes on a rocky shore of Lake Tanganyika. African Studies Monographs 3:25-38.

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

Johnson, T.C. 1996. Sedimentary processes and signals of past climate change in the lakes of the East African Rift Valley. In: Johnson T.C. and Odada E. (eds). The Limnology, Climatology, and Paleoclimatology of the East African Lakes. Gordon and Breach, Amsterdam, The Netherlands, pp. 367-412.

Johnson, T.C., Barry, S.L., Chan, Y. and Wilkinson, P. 2001. Decadal record of climate variability spanning the past 700 years in the Southern Tropics of East Africa. Geology 29:83-86.

Johnson, T.C., Brown, E.T., McManus, J., Barry, S., Barker, P. and Gasse, F. 2002. A high-resolution paleoclimate record spanning the past 25 000 years in southern East Africa. Science 296:113-114.

Johnson, T.C., Kelts, K. and Odada, E. 2000. The Holocene history of Lake Victoria. Ambio 29:2-11.

Johnson, T.C., Scholtz, C.A., Talbot, M/R., Kelts, K., Ricketts, R.D., Ngobi, G., Beunig, K. Ssemmanda, I. and McGill, J.W. 1996. Late Pleistocene desiccation of Lake Victoria and rapid evolution of cichlid fishes. Science 273:1091-1093.

Kaufman, L. 1992. Catastrophic loss in species-rich freshwater ecosystems: The lessons of Lake Victoria. BioScience 42:846-858.

Knight, M.E. and Turner, G.F. 1999. Reproductive isolation among closely related Lake Malawi cichlids: can males recognise conspecific females by visual cues? Animal Behaviour 58:761-768.

Knight, M.E. and Turner, G.F. 2004. Laboratory mating trials indicate incipient speciation by sexual selection among populations of the cichild fish Pseudotropheus zebra from Lake Malawi. Proceedings of the Royal Society of London Series B, Biological Sciences 271:675-680.

Knight, M.E., Turner, G.F., Rico, C., van Oppen, M.J.H. and Hewitt, G.M. 1998. Microsatellite paternity analysis on captive Lake Malawi cichlids supports reproductive isolation by direct mate choice. Molecular Ecology 7:1605-1610.

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

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

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

Kocher, T.D. 2004. Adaptive evolution and explosive speciation: the cichlid fish model. Nature Reviews Genetics 5:288-298.

Kocher, T.D., Conroy, J.A., McKaye, K.R. and Stauffer, J.P. 1993. Similar morphologies of cichlid fish in Lakes Tanganyika and Malawi are due to convergence. Molecular Phylogenetics and Evolution 2:158-165.

Kondrashov, A.S. and Kondrashov, F.A. 1999. Interactions among quantitative traits in the course of sympatric speciation. Nature 400:351-354.

Kornfield, I. and Smith, P.F. 2000. African cichlid fishes: model systems for evolutionary biology. Annual Review of Ecology, Evolution and Systematics 31:163-196.

Lawton, P. and Elner, R.W. 1985. Feeding in relation to morphometrics within the genus *Cancer*: evolutionary and ecological considerations. In: Metleff, B. R (ed.). Proceedings of the symposium on Dungeness crab biology and management University of Alaska, Fairbanks, Alaska, pp. 357-379.

Lewontin, R.C. and Birch, L.C. 1966. Hybridization as a source of adaptive variation for adaptation to new environments. Evolution 20:315-336.

Lezzar, K.E., Tiercelin, J.-J., De Baptist, M., Cohen, A.S., Bandora, T.,Van Rensbergen, P., Le Turdu, C., Mifundu, W. and Klerx J. 1996.New seismic stratigraphy and late-Tertiary history of the northTanganyika basin, East African Rift system, deduced from multichannel and high-resolution reflection seismic data and piston core evidence. Basin Research 8:1-28.

Liem, K.F. 1973. Evolutionary strategies and morphological innovations: cichlid pharyngeal jaws. Systematic Zoology 22: 425-441.

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

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

Linneaus, C. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata. Holmiæ (Laurentii Salvii), pp. 1-824.

Losos, J.B. and Schluter, D. 2000. Analysis of an evolutionary species-area relationship. Nature 408:847-850.

Lowe-McConnell, R. 2003 Recent research in the African Great Lakes: fisheries, biodiversity and cichlid evolution. Freshwater Forum 20:1-64.

Maan, M.E., Seehausen, O., Soderberg, L., Johnson, L. Ripmeester, A.P., Mrosso, H.D.J., Taylor, M.I., Van Doorn, T.J.M. and Van Alphen, J.J.M. 2004. Intraspecific sexual selection on a speciation trait, male coloration, in the Lake Victoria cichlid Pundamilia nyererei. Proceedings of the Royal Society London Series B. Biological Sciences 271:2445-2452.

Martens, K. 1994. Ostracod speciation in ancient lakes: a review. In: Martens, K., Goddeeris, B. and Coulter, G.W. (eds.). Speciation in ancient lakes. Archiv für Hydrobiologie Ergebnisse der Limnologie 44:203-222.

Martens, K. 1997. Speciation in ancient lakes. Trends in Ecology and Evolution 12:177-182.

Mayr, E. Evolution of fish species flocks; a commentary. In: Echelle, A.A. and Kornfield, I. (eds.). Evolution of fish species flocks, pp 3-11.

Mbomba, N.B. 1985. Comparative feeding ecology of 11 sympatric species of cichlid algal feeders in Lake Tanganyika. Verhandlungen der Internationale Vereinigung fiir theoretische und angewandte Limnologie 22:26-62.

McElroy, D.M. and Kornfield, I. 1993. Novel jaw morphology in hybrids between *Metriaclima zebra* and *Labeotropheus fuelleborni* (Teleostei: Cichlidae) from Lake Malawi, Africa. Copeia 1993:933-945.

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

McIntyre, P.B., Jones, L.E., Fecker, A.S. and Vanni, M.J. 2007. Fish extinctions alter nutrient recycling in tropical waters. Proceedings of the National Academy of Sciences of the United States of America 104:4461-4466.

McKaye, K.R. and Marsh, a. 1983. Food switching by two specialized algae-scraping cichlid fishes from Lake Malawi, Africa. Oecologia 56:245-248.

Meybeck, M. 1985. Evaluation préliminaire de la pollution du Lac Tanganyika. United Nations Educational, Scientific, and Cultural Organisation (UNESCO) Rapport de mission, PNUD, Paris, France, pp 1-46.

Meyer, A. 1993. Phylogenetic relationships and evolutionary processes in East African cichlid fishes. Trends in Ecology and Evolution 8:279-284.

Meyer, A., Kocher, T.D., Basasibwaki, P. and Wilson, A.C. 1990. Monophyletic origin of Lake Victoria cichlid fishes suggested by mitochondrial DNA sequences. Nature 347:550-553.

Meyer, A., Knowles, L.L. and Verheyen, E. 1996. Widespread geographical distribution of mitochondrial haplotypes in rock-dwelling cichlid fishes from Lake Tanganyika. Molecular Ecology 5:341-350.

Meyers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca G.A.B. and Kent, J. 2000. Biodiversity hotspots for conservation priorities. Nature 403:853-858.

Michel, E. 1994. Why snails radiate: a review of gastropod evolution in long-lived lakes, both recent and fossil. In: Martens, K., Goddeeris, B. and Coulter, G.W. (eds.). Speciation in ancient lakes. Archiv für Hydrobiologie Ergebnisse der Limnologie 44:285-317.

Michel, E. 2000. Phylogeny of a gastropod species flock: exploring speciation in Lake Tanganyika in a molecular framework. In: Rossiter, A. and Kawanabe, H. (eds.). Ancient lakes: biodiversity, ecology and evolution. Advances in Ecological Research 31:275-302.

Michel, E. 2004. *Vinundu*, a new genus of gastropod (Cerithioidea: 'Thiaridae') with two species from Lake Tanganyika, East Africa, and its molecular phylogenetic relationships. Journal of Molluscan Studies 70:1-19.

Michel, E., Cohen, A.S., West, K., Johnston, M.R. and Kat, P.W. 1992. Large African lakes as natural laboratories for evolution: examples from the endemic gastropod fauna of Lake Tanganyika. Mitteilungen Internationale Vereinigung für Theoretische und Angewandte Limnologie 23:85-99.

Michel, E., Todd, J.A., Cleary, D.F.R., Kingma, I., Cohen, A.S., and Genner, M.J. 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, Paris 7:161-191.

Mölsä, H., Reynolds, E.J., Coenen, E.J. and Lindqvist, O.V. 1999. Fisheries research towards resource management in Lake Tanganyika. Hydrobiologia 407:1-24.

Mölsä, H., Sarvala, J., Huttula, T., Salonen, K. and Lindqvist, O.V. 2005. Management of an African Great Lake fishery: Challenges to research and community. In: Hietanen, O. (Ed.) University partnerships for international development. Finland Futures Research Centre (FFRC) Publication 6/2005, Helsinki, Finland, pp. 115-142.

Moore, J.E.S. 1903. The Tanganyika problem: an account of the researches undertaken concerning the existence of marine animals in Central Africa.

Moss, B. 2000. Biodiversity in fresh waters – an issue of species preservation or system functioning? Environmental conservation 27:1-4.

Mugidde, R. 1993. The increase in phytoplankton productivity and biomass in Lake Victoria. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 25:846-849.

Nicholson, S.E. 1999. Historical and modern fluctuations of lakes Tanganyika and Rukwa and their relationship to rainfall variability. Climate Change 41:53-71.

Nicholson, S.E. (1998) Fluctuations of rift valley lakes Malawi and Chilwa during historical times: a synthesis of geological, archaeological and historical information. In: Lehman, J.T. (ed.). Environmental Change and Response in East African Lakes. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 207–231.

Nshombo, M., Yanaglsawa, Y. and Nagoshi, M. 1985. Scale eating in *Perissodus microlepis* (Cichlidae) and change of its food habits with growth. Japanese Journal of Ichthyology 32:66-73.

Odada, E.O., Olago, D.O., Bugenyi, F., Kulindwa, K., Karimumuryango, J., West, K., Ntiba, M., Wandiga, S., Aloo-Obudho, P. and Achola, P. 2003. Environmental assessment of the East African Rift Valley lakes. Aquatic Sciences 65:254-271.

Ogutu-Ohwayo, R. 1990. The decline of the native fishes of Lake Victoria and Kyoga (East Africa) and the impact of introduced species, especially the Nile perch, *Lates niloticus* and the Nile tilapia, *Oreochromis niloticus*. Environmental Biology of Fishes 27:81-90.

Olago, D.O. and Odada, E.O. 2007. Sediment impacts in Africa's transboundary lake/river basins: case study of the East African Great Lakes. Aquatic Ecosystem Health and Management 10:23-32.

O'Reilly, C.M., Alin, S. R., Plisnier, P.-D., Cohen, A. S. and McKee, B. A. 2003. Climate change decreases aquatic ecosystem productivity in Lake Tanganyika, Africa. Nature 424:766-768.

Owen, R.B., Crossley, R., Johnson, T.C., Tweddle, D., Kornfield, I., Davison, S., Eccles, D.H. and Engstrom, D.E. 1990. Major low levels of Lake Malawi and their implications for speciation rates in cichlid fishes. Proceedings of the Royal Society London, B. 240:519-553.

Park, L.E. and Downing, K.F. 2000. Implications of phylogeny reconstruction for ostracod speciation modes in Lake Tanganyika. In: Rossiter, A. and Kawanabe, H. (eds.). Ancient lakes: biodiversity, ecology and evolution. Advances in Ecological Research 31:303-330.

Patterson, G. 1996. Sediment discharge and its consequences: baseline review. Pollution control and other measures to protect biodiversity in Lake Tanganyika.

Lake Tanganyika Biodiversity Project RAF/92/G32. Natural Resources Institute, UK. www.ltbp.org

Pauers, M.J., McKinnon, J.S. and Ehlinger, T.J. 2004. Directional sexual selection on chroma and within pattern colour contrast in *Labeotropheus fuelleborni*. Proceedings of the Royal Society of London Series B. Biological Sciences 271:5444-5447.

Plisnier, P.D. 2000. Recent climate change and limnology changes in Lake Tanganyika. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 27:2670-2673.

Reinthal, P.N. 1990. The feeding habits of a group of tropical, herbivorous, rock-dwelling cichlid fishes (Cichlidae: Perciformes) from Lake Malawi, Africa. Environmental Biology of Fishes 27:215-233.

Ribbink, A.J. 1994. Lake Malawi. In: Martens, K., Goddeeris, B. and Coulter, G.W. (eds.). Speciation in ancient lakes. Archiv für Hydrobiologie Ergebnisse der Limnologie 44:27-33.

Ribbink, A.J., Berber, D.G., Bootsma, H.A., Brook, R.G., Cooley, P.M., Hecky, R.E., Kidd, K.A., Kling, H.J., McCullough, G.K. and Mkanda, F.X. 2001. The Lake Malawi/Niassa/Nyasa biodiversity conservation programme: science in a socio-economic context. Annales Museé Royal de l'Afrique Centrale, Tervuren, Science Zoologique 275:28-59.

Ribbink, A.J., Marsh, B.J., Marsh, A.C., Ribbink, A.C. and Sharp, B.J. 1983. A preliminary survey of the cichlid fishes of the rocky habitats of Lake Malawi. South African Journal of Zoology 18:155-309.

Riesenberg, L.H., Archer, M.A. and Wayne, R.K. 1999 Transgressive segregation, adaptation and speciation. Heredity 83:363-372.

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

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

Rüber, L., Meyer, A., Sturmbauer, C. and Verheyen, E. 2001. Population structure in two sympatric species in the Lake Tanganyika cichlid tribe Eretmodini: evidence for introgression. Molecular Ecology 10:1207-1225.

Rüber, L., Verheyen, E., Sturmbauer, C. and Meyer, A. 1998. Lake level fluctuations and speciation in a rock-dwelling cichlid tribe endemic to Lake Tanganyika. In: Grant, P. and Clarke, B. (eds.). Evolution on Islands, Oxford University Press, Oxford, UK, pp 225-240.

Rusuwa, B., Maruyama, A. and Yuma, M. 2006. Deterioration of cichlid habitat by increased sedimentation in the rocky littoral zone of Lake Malawi. Ichtyological Research 53:431-434.

Salzburger, W. and Meyer, A. 2004. The species flocks of East African cichlid fishes: recent advances in molecular phylogenetics and population genetics. Naturwissenschaften 91:277-290.

Salzburger, W., Baric, S. and Sturmbauer, C. 2002. Speciation via introgressive hybridization in African cichlids? Molecular Ecology 11:619-625.

Sarvala, J., Langeberg, V. T., Salonen, K., Chitamwebwa, D., Coulter, G. W., Huttula, T., Kanyaru, R., Kotilainen, P., Makasa, L., Mulimbwa, N. and Mölsä, H. 2006. Fish catches from Lake Tanganyika mainly reflect changes in fishery practices, not climate. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 29:1-7.

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

Schluter, D. 1996. Ecological causes of adaptive radiation. American Naturalist 148:S40-S64.

Schluter, D. 2000. The ecology of adaptive radiation. Oxford University Press, Oxford, NY, USA, pp 1-288.

Scholz, C.A., King, J.W., Ellis, G.S., Swart, P.K., Stager, J.C. and Colman, S.M. 2003. Paleolimnology of Lake Tanganyika, East Africa, over the past 100 k yr. Journal of Paleolimnology 30:139-150.

Scholz, C.A. and Rosendahl, B. 1988. Low lake stands in Lakes Malawi and Tanganyika, delineated with multifold seismic data. Science 240:1645-1648.

Seehausen, O. 2002. Patterns in fish radiation are compatible with Pleistocene desiccation of Lake Victoria and 14600 year history for its cichlid species flock. Proceedings Royal Society London, B. 269:491-497.

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

Seehausen, O. 2006. African cichlid fish: a model system in adaptive radiation research. Proceedings Royal Society London, B. 273:1987-1998.

Seehausen, O., van Alphen, J.J.M. and Witte, F. 1997 Cichlid fish diversity by eutrophication that curbs sexual selection. Science 277:1808-1811.

Seehausen, O., Koetsier, E., Schneider, M.V., Chapman, L.J., Chapman, C.A., Knight, M.E., Turner, G.F., van Alphen, J.J.M. and Bills, R. 2002. Nuclear markers reveal unexpected genetic variation and a Conolese-Nilotic origin of the Lake Victoria cichlid species flock. Proceedings Royal Society London, B. 270:129-137.

Seehausen, O. and Schluter, D. 2004. Male-male competition and nuptial-colour displacement as a diversifying force in Lake Victoria cichlid fishes. Proceedings Royal Society London, B. 271:1345-1553.

Slatkin, M. and Lande, R. 1994. Segregation variance after hybridization of isolated populations. Genetical Research 64:51-56.

Smith, L.D. 2004. Biogeographic differences in claw size and performance in an introduced crab predator *Carcinus maenas*. Marine Ecology Progress Series 276:209-222.

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

Socci, A.M. 2001. Interspecific differences in snail susceptibility to crab predation at Jakobsen's Beach, Lake Tanganyika. Nyanza Project Report 2001, pp 1-7. www.geo.arizona.edu/nyanza

Stager, J.C., Mayewski, P.A. and Meeker, L.D. 2002. Cooling cycles, Heinrich event 1, and the desiccation of Lake Victoria. Palaeogeography Palaeoclimatology Palaeoecology 183:169-178.

Stauffer, J.R. and Hert, E. 1992. Pseudotropheus callanois, a new species of mbuna (Cichlidae), with analyses of changes associated with two intra-lacustrine transplantations in Lake Malawi. Ichthyologocal Explorations of Freshwaters 3:253-264.

Stauffer, J.R, Bowers, N.J., Kocher, T.D. and McKaye, K.R. 1996. Evidence of hybridization between *Cyanotilapia afra* and *Pseudotropheus zebra* (Teleostei: Cichlidae) following an intralacustrine translocation in Lake Malawi. Copeia 1996:203-208.

Streelman, J.T., Gmyrek, S.L., Kidd, M.R., Kidd, C., Robinson, R.L., Hert, E., Ambali, A.J. and Kocher, T.D. 2004. Hybridization and contemporary evolution in an introduced cichlid fish from Lake Malawi National Park. Molecular Ecology 13:2471-2479.

Sturmbauer, C. 1998. Explosive speciation in cichlid fishes of the African Great Lakes: a dynamic model of adaptive radiation. Journal of Fish Biology 53:18-36.

Sturmbauer, C. and Meyer, A. 1992, Genetic divergence, speciation and morphological stasis in a linage of African cichlid fish. Nature 358:578-581.

Sturmbauer, C. and Meyer, A. 1993. Mitochondrial phylogeny of the endemic mouthbrooding lineages of cichlid fishes from Lake Tanganyika in Eastern Africa. Molecular Biology and Evolution 10:751-768.

Sturmbauer, C., Baric, S., Salzburger, W., Rüber, L., and Verheyen, E., 2001. Lake level fluctuations synchronize genetic divergences of cichlid fishes in African lakes. Molecular Biology and Evolution 18:144-154.

Sturmbauer, C., Hainz, U., Baric, S., Verheyen, E. and Salzburger, W. 2003. Evolution of the tribe Tropheini from Lake Tanganyika: synchronized explosive speciation producing multiple evolutionary parallelism. Hydrobiologia 500:51-64.

Sturmbauer, C., Koblmüller, S., Sefc, K.M. and Duftner, N. 2005. Phylogeographic history of the genus Tropheus, a lineage of rock-dwelling cichlid fishes endemic to Lake Tanganyika. Hydrobiologia 542:335-366.

Sturmbauer, C., Mark, W. and Dallinger, R. 1992. Ecophysiology of Aufwuchs-eating cichlids in Lake Tanganyika: niche separation by trophic specialization. Environmental Biology of Fishes 35:283-290.

Sturmbauer, C., Verheyen, E. and Meyer, A. 1994. Molecular phylogeny of the Lamprologini, the major substrate breeding lineage of cichlid fishes from Lake Tanganyika, eastern Africa. Molecular Biology and Evolution 11:691-703.

Takamura, K. 1984. Interspecific relationships of Aufwuchs eating fishes in Lake Tanganyika. Environmental Biology of Fishes 10:225-241.

Tiercelin, J.J. and Mondeguer, A. 1991. The geology of the Tanganyika Trough. In: Coulter, G. (ed.) Lake Tanganyika and its life. Oxford University Press, London, UK, pp. 7-48

Thieme, M.L., Abell, R., Stiassney, M.L.J., Skelton, P., Lehner, B., Teugels, G.G., Dinerstein, E., Kamden Toham, A., Burgess, N. and Olson, D. 2005. Freshwater ecoregions of Africa and Madagascar: A conservation assessment. Island Press, Washington D.C., U.S.A, pp 1-430.

Turner, G. 1994. Fishing and the conservation of the endemic fishes of Lake Malawi. Archiv für Hydrobiologie 44:481-494.

Tweddle, D. 1992. Conservation and threats to the resources of Lake Malawi. Mitteilungen-Internationale Vereinigung fur Theoretische und Angewandte Limnologie 23:17-24

Underwood, G. and Williams, E. 1959. The anoline lizards of Jamaica. Bulletin of the Institute of Jamaica Science Series 9:1-48.

Vandelannoote, A., Robberecht, H., Deelstra, H., Vyumvohore, F., Bitetera, X and Ollevier, F. 1996. The impact of the River Ntahanga, the most polluted Burundian affluent of Lake Tanganyika, on the water quality of the lake. Hydrobiologia 328:161-171.

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

Van Doorn, G.S., Dieckman, U. and Weissing, F.J. 2004 Sympatric speciation by sexual selection: a critical reevaluation. American Naturalist 163:709-725.

Van Oppen, M.J.H., Turner, G.F., Rico, C., Robinson, R.L., Deutsch, J.C., Genner, M.J. andHewitt, G.M. 1998. Assortative mating among rock-dwelling cichlid fishes supports high estimates of species richness from Lake Malawi. Molecular Ecology 7:991-1001.

Verburg, P., Hecky, R. E. and Kling, H. 2003. Ecological consequences of a century of warming in Lake Tanganyika. Science 302:505-507.

Verheijen, E., Salzburger, W., Snoeks, J. and Meyer, A. 2003. Origin of the superflock of cichlid fishes from Lake Victoria, East Africa. Science 300:325.

Verheijen, E., Rüber, L., Snoeks, J. and Meyer, A. 1996. Mitochondrial phylogeny of rock-dwelling cichlid fishes reveals evolutionary influence of historical lake level fluctuations of Lake Tanganyika, Africa. Philosophical Transactions of the Royal Society London, B. 351:797-805.

Verschuren, D., Johnson, T.C., Kling, H.J., Edgington, D.N., Leavitt, P.R., Brown, E.T., Talbot, M.R. and Hecky, R.E. 2002. History and timing of human impact in Lake Victoria, East Africa. Proceedings of the Royal Society of London Series B. Biological Sciences 269:289-294.

Vreven, E.J. 2005. Redescription of *Mastacembelus ophidium* Günther, 1893 (Synbranchiformes: Mastacembelidae) and description of a new spiny eel from Lake Tanganyika. Journal of Natural History 39:1539-1560.

Von Sternberg, R. and Cumberlidge, N. 1999. A cladistic analysis of *Platythelphusa* A. Milne-Edwards, 1887, form Lake Tanganyika, East Africa (Decapoda: Potamoidea: Platythelphusidae) with comments on the phylogenetic position of the group. Journal of Natural History 33:493-511.

Von Sternberg, R. and Cumberlidge, N. 2001. Notes on the position of the true freshwater crabs within the brachyrhynchan Eubrachyura (Crustacea: Decapoda: Brachyura). Hydrobiologia 449:21-39.

Von Sternberg, R., Cumberlidge, N. and Rodriguez G. 1999. On the marine sister groups of the freshwater crabs (Crustacea: Decapoda: Brachyura). Journal of Zoological Systematics and Evolutionary Research 37:19-38.

Wells, T.M., Cohen, A.S., Park, L.E., Detmann, D.L. and McKee, B.M. 1999. Ostracode stratigraphy and paleoecology from surficial sediments of Lake Tanganyika, Africa. Journal of Paleolimnology 22:259-276.

West, K. 2001. Lake Tanganyika: Results and experiences of the UNDP/GEF conservation initiative (RAF/92/G32) in Burundi, D. R. Congo, Tanzania, and Zambia. Lake Tanganyika Biodiversity Project (UNDP/GEF/UNOPS, RAF/92/G32), pp 1-137. www.ltbp.org

West, K. and Michel, E. 2000. The dynamics of endemic diversification: molecular phylogeny suggests an explosive origin of the thiarid gastropods in Lake Tanganyika. In: Martens, K., Goddeeris, B. and Coulter, G.W. (eds.). Speciation in ancient lakes. Archiv für Hydrobiologie Ergebnisse der Limnologie 44:331-354.

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

West, K. and Cohen, A. 1996. Shell microstructure of gastropods from Lake Tanganyika, Africa: Adaptation, convergent evolution, and escalation. Evolution 50:672-681.

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

Wilson, A.B., Glaubrecht, M. and Meyer, A. 2004. Ancient lakes as evolutionary reservoirs: evidence from the thalassoid gastropods of Lake Tanganyika. Proceedings of the Royal Society London, B. 271:529-536.

Witte, F., Msuku, B.S., Wanink, J.H., Seehausen, O., Katunzi, E.F.B., Goudsward, P.C. and Goldschmidt, T. 2000 Recovery of cichlid species in Lake Victoria: an examination of factors leading to differential extinction. Reviews in Fish Biology and Fisheries 10:233-241.

Wood, P.J, and Armitage, P.D. 1997. Biological effects of fine sediment in the lotic environment. Environmental Management 21:203-17.

Won, Y.J., Sivasundar, A., Wang, Y. and Hey, J. 2005. On the origin of Lake Malawi cichlid species: a population genetic analysis of divergence. Proceedings of the National Academy of Sciences of the United States of America 102:6581-6586.

Won, Y.J., Wang, Y., Sivasundar, A., Raincrow, J., and Hey, J. 2006. Nuclear gene variation and molecular dating of the cichlid species flock of Lake Malawi. Molecular Biology and Evolution 23:828-837.

Yamaoka, I.C. 1982. Morphology and feeding behaviour of five species in genus *Petrochromts* (Cichlidae). Physiology and Ecology Japan 19:57-75.

Yamaoka, K. 1983. Feeding behaviour and dental morphology of algae-scraping cichlids (Pisces: Cichlidae) in Lake Tanganyika. African Studies Monographs 4:77-89.

Yamaoka, K. 1991. Feeding relationships. In: Keenleyside, H.A. (ed.). Cichlid fishes behaviour, ecology and evolution. Chapman and Hall, London, UK, pp 151-172.

Yamaoka, I., Hori, M. and Kuratani, S. 1986. Ecomorphology of feeding in "goby-like" cichlid fishes in Lake Tanganyika. Physiology and Ecology Japan 23:17-29.

Zweig, L.D. and Rabeni. C.F. 2001. Biomonitoring for deposited sediment using benthic invertebrates: a test on 4 Missouri streams. Journal of the North American Benthological Society 20:643-657.

Table 1. Features of the three great East African Rift Lakes.

	Lake Tanganyika	Lake Malawi	Lake Victoria
Age (million years)	9-12	4.5-8.6	0.25-0.75
Maximum depth (m)	1 470	706	80
Mean depth (m)	570	264	40
Surface area (km^2)	32 600	29 500	68 870
Volume (km^3)	18 880	7 775	2 760
Oxygen cline (m)	100-200	200-250	—
Water residence time (years)	440	114	23
Length of the lake (km)	670	569	412
Length of the shoreline (km)	1 900	1 500	3 460
Catchment drainage area (km^2)	223 000	100 500	193 000
Population in catchment area	> 10 million	> 10 million	> 30 million
Population growth rates	2.0-3.2%	2.0-4.7%	~ 6%

Adapted from Odada et al. (2004), Bootsma and Jorgensen (2005), Jorgensen et al. (2005), Kayombo and Jorgensen (2005).

Table x. Geological history of the Tanganyika Trough.

Epoch	Event	Date*	Reference
Miocene 5.3-23	Formation of a flat basin with slowly meandering proto-Malagarassi river. Connection to the Congo basin hydrological system. NB: some estimates indicate that formation of the lake was initiated between ~25-15 Mya.	20-12 Ma	Tiercelin and Mondeguer (1991), Cohen et al. (1993) and references therein.
	Transformation of proto-Malagarassi-Congo River in swampy area with mosaic of shallow, and mostly isolated lakes.	12-8	Tiercelin and Mondeguer (1991), Cohen et al. (1993).
	Initiation of tectonic activity in northern Lake Tanganyika region (~7.8-5 Ma). Formation of northern basin	8-7	Lezzar et al. (1996), Cohen et al. (1997).
	Establishment of truly lacustrine habitat. Subsidence of graben produces progressively deeper lakes. Closing of drainage system at Lukuga outlet to the Congo river.	6-5	Tiercelin and Mondeguer (1991).
	Formation of southern basin. Pliocene regional aridification in East and Central Africa (~3-2 Ma).	4-2	Cohen et al. (1997) and references therein.
	Strrong tectonic activity on Kivu-Rusisi Volcanic Dome (~1.9 Ma). Major lake level decline (~650-700 m bpl). Separation of northern, middle and southern basin. Small and probably saline lakes in northern basin.	1.1	Lezzar et al. (1996), Cohen et al. (1997), Scholz and Rosendahl (1988)**.
Pleistocene 0.01-1.8	Rise of lake levels in northern basin, evidence of sedimentation from Proto-Rusisi river basin drainage.	670-550 ka	Cohen et al, (1997).
	Formation of Burton's Bay.Tectonically driven, and/or climatic driven low lake levels (~350 m bpl).	360-390	Cohen et al. (1997).
	Low lake level (~350 m bpl), followed by transgression in the northern basin between ~260-190 ka.	290-260	Cohen et al. (1997).
	Low lake level (>400 m bpl***), followed by transgression in the northern basin between ~170-40 ka.	190-170	Cohen et al. (1997), Scholz et al. (2003).
	Low lake level (~350 m bpl).	55	Scholz et al. (2003).
	Period of repeated fluctuations. Probably dry intervals at 42, 29, and 23 ka, causing intermediately low lake levels (~160 m bpl). Insufficient to separate the northern, middle and southern basin, but low enough to cause near-total desiccation of Burton's Bay in the north.	45-20	Cohen et al. (1997), Scholz et al. (2003).
Pliocene 1.8-5.3	Continued lowering of lake levels, probably associated with a cooler and drier climate resulting from Late Pleistocene glaciation events. Minimum (~350 m bpl) around 18 ka. Possibly increase of precipitation and temperature from ~18-17 ka to ~15-14.5 ka.	19-14	Gasse et al. (1989), Johnson (1996), Guiot and Tiercelin (1993), Cohen et al. (1997), Scholz et al. (2003), Gasse (2000)
	Rising water levels. Increase of water flows through Ruzizi river caused by upfolding of Virunga volcanoes north from Lake Kivu. Establishment of post-glacial climatic conditions by ~12 ka, with increasing temperatures and humidity.	12-9	Gasse et al. (1989), Tiercelin and Mondeguer (1990), Guiot and Tiercelin (1993), Johnson (1996) and references therein.
Holocene Present-0.01	Intermittent closing and opening of Rusisi connection and intermittent establishment of open drainage via Lukuga river. Highest known water levels (784 asl) were presumably reached around 1878, re-establishing Lukuga outlet and causing flood in the Congo river. Regression (~40 m) between 1880 and 1890. Minor regressions during late 1920's,and 1950's. High lake levels after 1960's El Niño event. Minor regressions during mid-1970's and mid-1980's.	5-present	Tiercelin and Mondeguer (1990), Nicholson (1999)

*NB: Note that these are all approximate numbers that are subject to discussion and must be interpreted with caution. **Scholz and Rosendahl (1988) estimated an age of 25,000 ya for a 600 m lake level decline in Lake Tanganyika, based on sedimentation rates of 1mm/year that were calculated for Lake Malawi. Tiercelin and Mondeguer (1991) estimated a minimum of 200,000 years on the basis of a 0.5 mm/year sedimentation rate calculated for marine sediments. ***Scholz et al. (2003) estimated an age of between ~130-190 ya for a lake level drop of at least 400 m, probably as a response to the cool and arid tropical climate during the penultimate Pleistocene glaciation. Ma=million years ago; ka=thousand years ago; bpl=below present lake level (present=1990's); asl=above sea level.

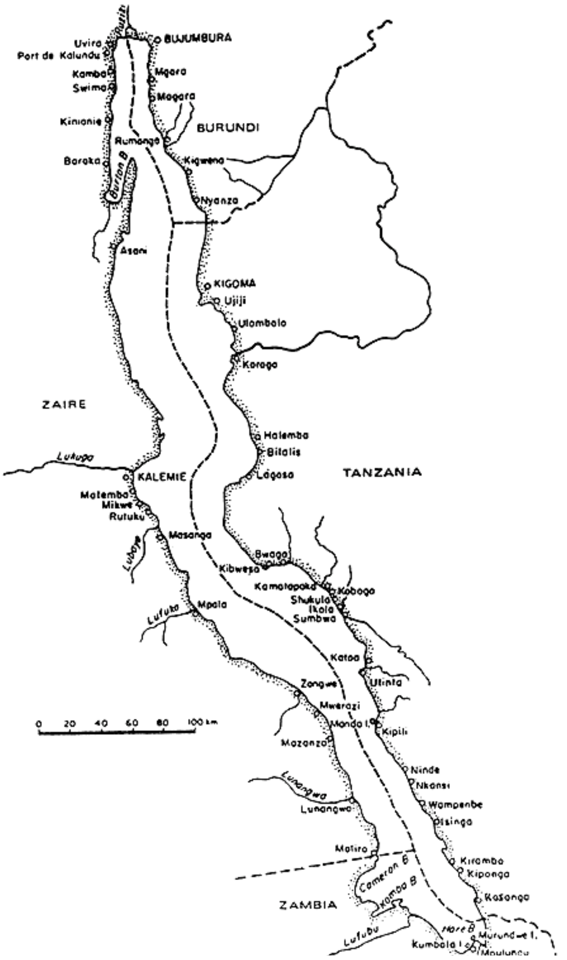

Figure 1. Lake Tanganyika (NB: this figure will be adapted in the final version).

Figure 2. Diversity in trophic morphologies among cichlids (adapted from Fryer & Illes; Futuyma 1986). (will be added)

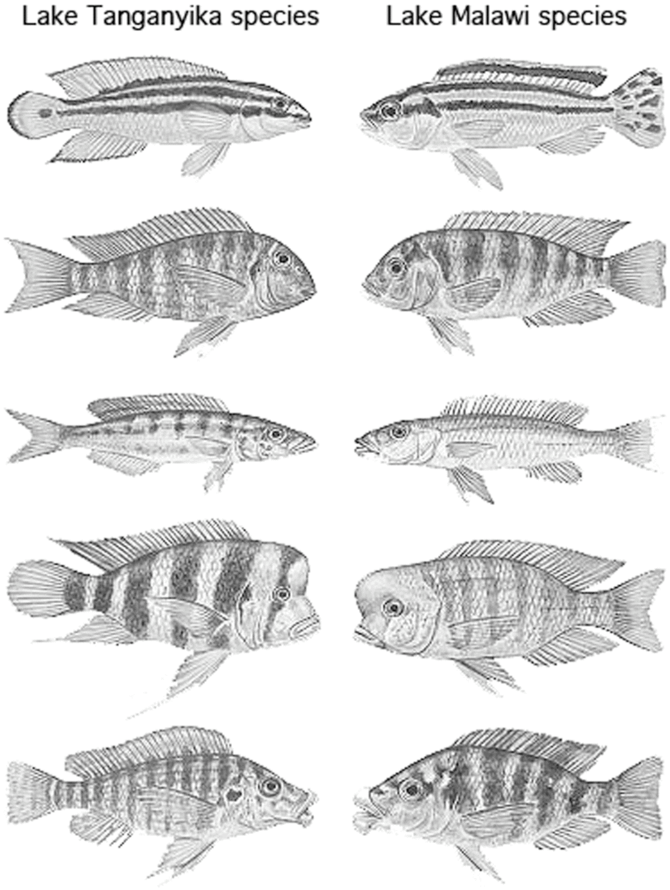

Figure 3. Convergence of body shapes in cichlid fish from Lake Malawi and Tanganyika (adapted from Stiassney & Meyer 1999). (NB: Final figure will include species names).

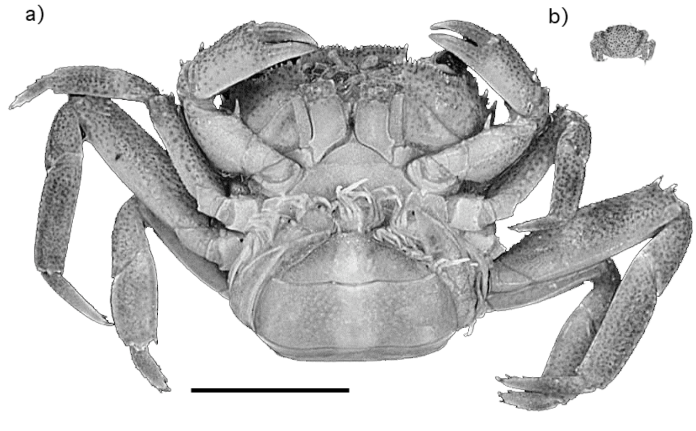

Figure x. (a) *Platythelphusa conculcata* with juveniles in its brood pouch. (b) Juvenile *P. conculcata* at approximately the size of release. Scale bar represents 10 mm. Pictures by Louis van der Laan.

TWO NEW SPECIES OF *PLATYTHELPHUSA* A. MILNE-EDWARDS, 1887 (DECAPODA, POTAMOIDEA, PLATYTHELPHUSIDAE) AND COMMENTS ON THE TAXONOMIC POSITION OF *P. DENTICULATA* CAPART, 1952 FROM LAKE TANGANYIKA, EAST AFRICA

BY

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ABSTRACT

Two new species of *Platythelphusa* (Decapoda, Potamoidea, Platythelphusidae), are described from Lake Tanganyika. *P. immaculata* sp. nov. and *P. praelongata* sp. nov. are distinguished from congeners by a combination of diagnostic characters of the carapace, chelipeds, and pereiopods. *Platythelphusa denticulata* Capart, 1952, is removed from synonymy with *P. conculcata*. This brings the number of platythelphusid species reported from Lake Tanganyika to nine. A key is provided to separate the species of *Platythelphusa*.

RÉSUMÉ

Deux espèces nouvelles de *Platythelphusa* (Decapoda, Potamoidea, Platythelphusidae), sont décrites du lac Tanganyika. *P. immaculata* sp. nov. et *P. praelongata* sp. nov. se distinguent de leurs congénères par une combinaison de caractères diagnostiques concernant la carapace, les chélipèdes et les péréiopodes. *Platythelphusa denticulata* Capart, 1952 est retiré de la synonymie avec *P. conculcata*. Ceci porte le nombre des espèces de Platythelphusidae connues du lac Tanganyika à neuf. Une clé est fournie pour séparer les espèces de *Platythelphusa*.

INTRODUCTION

The present work arises out of a long-term study of Lake Tanganyika, East Africa, aimed at evaluating the ecological and phylogenetic relationships of the

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freshwater crabs in the lake. Systematic surveys of the benthic communities near Kigoma, Tanzania, and sampling elsewhere in the lake, have resulted in the collection of large numbers of freshwater crab specimens from several different localities in Lake Tanganyika. Taxonomic examination of this collection has revealed the existence of two new species, and has also allowed the reappraisal of the taxonomic status of a third species, that is revived in the present work. The freshwater crabs found in Lake Tanganyika are dominated by species belonging to the Platythelphusidae Colosi, 1920, a family that is endemic to Lake Tanganyika. The Platythelphusidae appear to be monophyletic (Cumberlidge & Von Sternberg, 1998; Von Sternberg & Cumberlidge, 1999) and are morphologically highly divergent from other potamonautid and deckeniid freshwater crab taxa found in adjacent rivers and lakes in the African Rift System (Moore, 1903; Cunnington, 1907, 1920; Rathbun, 1933; Balss, 1936; Capart, 1952, 1954; Bott, 1955; Cumberlidge et al., 1999). A revision of the genus *Platythelphusa* by Cumberlidge et al. (1999) recognized six species: *P. armata* A. Milne-Edwards, 1887, *P. maculata* Cunnington, 1899, *P. conculcata* Cunnington, 1907, *P. echinata* Capart, 1952, *P. polita* Capart, 1952, and *P. tuberculata* Capart, 1952. The two new species of *Platythelphusa* described here are distinctly different from known species in this genus with regard to a combination of characters from the carapace, chelipeds, and pereiopods. The taxonomic position of *P. denticulata* Capart, 1952 is reappraised in the light of new material. This taxon was previously considered to be a junior synonym of *P. conculcata* (cf. Cumberlidge et al., 1999), but *P. denticulata* is treated here as a valid taxon, following comparisons of the relevant type specimens. The addition of *P. immaculata*, *P. praelongata*, and *P. denticulata* brings the total number of species of *Platythelphusa* in Lake Tanganyika to nine.

We present a table of characters that distinguish the new species from their congeners and an updated key to the platythelphusid species. The type material of *P. immaculata* and *P. praelongata* has been deposited in the Zoologisch Museum Amsterdam (ZMA).

Terminology is adapted from Cumberlidge (1999) and Cumberlidge et al. (1999). Abbreviations used in the text are: CW = carapace width, CH = carapace height, CL = carapace length, FW = width of the frontal margin, P2-P5 = second to fifth pereiopods, a3-a6 = third to sixth pleonal segments, a7 = telson, s1-s8 = first to eighth thoracic sternites, e4-e7 = fourth to seventh episternites, Go1 = male first gonopod, Go2 = male second gonopod. All measurements are given in mm. IRSN = Institut Royal des Sciences Naturelles, Brussels, Belgium.

TAXONOMY

Family PLATYTHELPHUSIDAE Colosi, 1920

Platythelphusa A. Milne-Edwards, 1887

Platythelphusa immaculata n. sp. (fig. 1A-D)

Material examined. — Holotype, 1 male, CW 18.22 mm (ZMA De.204594), Lake Tanganyika, Cape Mpimbwe near Katondo Point, Tanzania (7°05.59′S 30°30.00′E), 7 m depth, sand and rocks, coll. G. Kazumbe, 9 February 2003. Paratypes, 1 female, adult, CW 25.70 mm (ZMA De.204599), Mzungu Point (4°55.05′S 29°35.73′E), 10 m depth, cobbles and sand, coll. S. Marijnissen, 23 September 2002; 2 females, adult, CW 25.38, 22.31 mm, 1 female, subadult, CW 17.81 (ZMA De.204600), Mzungu Point, 14 m depth, cobbles, 6 March 2001; 1 female, adult, CW 27.06 mm (ZMA De.204596), Mwamahunga (4°54.730′S 29°35.901′E), 12 m depth, trap, coll. P. B. McIntyre, 13 July 2001; 1 female, adult, CW 31.02 mm (ZMA De.204597), Mwamahunga, 3 m depth, cobbles, coll. S. Marijnissen, 29 July 2002; 1 female, subadult, CW 21.15 mm (ZMA De.204598), Mwamahunga, 11 m depth, rocks and sand, 25 March 2002; 1 male, CW 17.01 mm; 1 male, juvenile, CW 12.15 mm; 14 females, adult CW 16.09, 20.27, 20.52, 21.63, 21.73, 21.80, 21.19, 23.04, 24.26, 25.31, 25.34, 25.37, 25.47, 28.67 mm; 1 female, juvenile, CW 13.17 mm (ZMA De.204601), Kigoma, Tanzania (4°54.73′S 29°35.90′E), 2-20 m depth, rocks and cobbles, coll. S. Marijnissen and G. Kazumbe, June-October 2002, 1 female, adult, CW 22.36 mm, 1 male, CW 18.00 mm (ZMA De.204.638), Mbita Island south side, Mpulungu, Zambia (8°45.23′S 31°05.14′E), 7 m depth, rocks and sand, coll. S. Marijnissen, 17 July 2003.

Diagnosis. — Carapace subhexagonal, rounded, wider than long (CW/FW 2.70 ± 0.15; CL/FW 2.19 ± 0.28), very flat (CH/FW 0.86 ± 0.06). Frontal margin granulate, exterior angles produced into sharp, pointed teeth. Exorbital angle produced into broad forward-directed tooth. Anterolateral margin between exorbital and epibranchial teeth granulate. Epibranchial tooth broad, pointed; anterolateral margin behind epibranchial tooth with two large teeth (fig. 1A). Suborbital margin lined with small tooth-like tubercles; medial end of margin with narrow, pointed tooth (fig. 1C). Lateral, superior, and inferior margins of merus of cheliped granulate. Inner margin of carpus of cheliped with two large subequal teeth, articular tooth (at point of articulation with propodus) broad, pointed; outer margin of carpus either granulate or with several small teeth. Cheliped propodal palm concave, fingers of propodus and dactylus with spatula-like tips (fig. 1B). Marked sexual dimorphism in cheliped shape; adult male with enlarged major chela, propodus and dactylus with molar dentition; propodus and dactylus of minor chela with serrated dentition; adult female with almost equally sized, slim chelipeds, fingers of both chelipeds with serrated dentition. Merus of P5 almost as long as FW. Subdistal tooth on superior margin of meri of P2-P4 small and spine-like; distal tooth either spine-like or small and low. Inferior margins of propodi of P2-P4 smooth. Superior margin of dactyli of P3-P4 with row of minute spines and several larger distal spines; inferior margins smooth, with several distal spines.

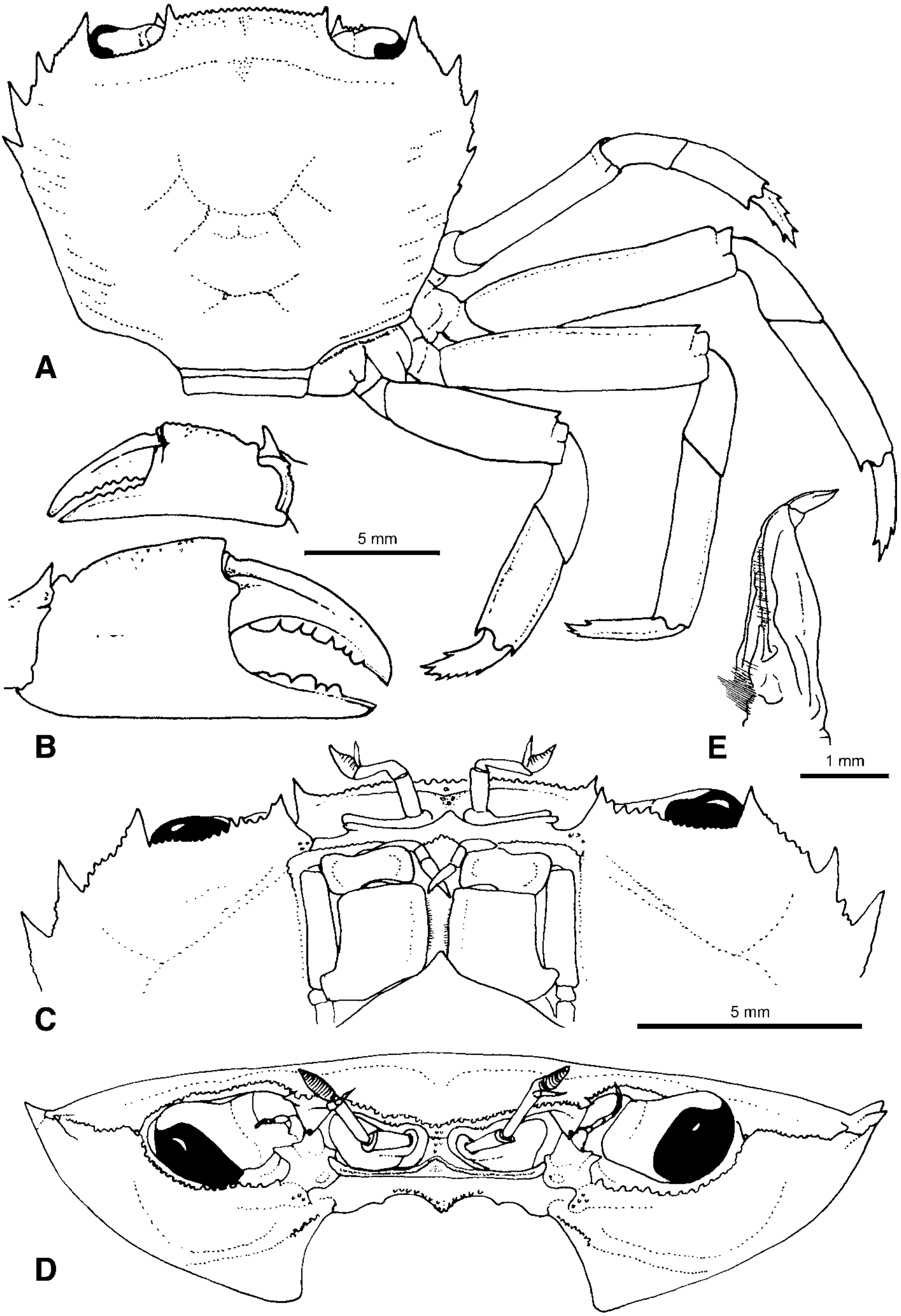

Fig. 1. *Platythelphusa immaculata* n. sp., male, CW 18.22 mm, holotype (ZMA De.204594). A, dorsal view of carapace and pereiopods 2-5; B, frontal view of left (above) and right (below) cheliped; C, ventral view of anterior area of carapace showing suborbital margin and 3^{rd} maxillipeds; D, frontal view of carapace; E, ventral view of right gonopod 1.

Terminal article of Go1 directed outward at a 60° angle to the vertical; slim cone-shaped article tapering strongly to pointed tip (fig. 1E).

Description. — Fields of short carinae in lateral regions of carapace; anterolateral margin of carapace continuous with posterolateral margin. Cardiac region and cervical grooves well defined (fig. 1A). Triangular descending process of front produced into a small tooth. Occlusal (sub-ocular) tooth in orbital hiatus well developed (fig. 1D). Suborbital margin with a prominent shelf, lined with irregularly shaped, tooth-like tubercules (fig. 1C). First antennal segment oval and fused into epistome; second antennal segment large and rectangular, with large transverse process, lying in orbital hiatus between descending frontal tooth and occlusal tooth; distal antennal segment slim and elongated, supporting short antennal flagellum.

Distinct granular endostomial ridges marking medial sides of left and right anterior respiratory channels; epistomial triangle conspicuous, granular, pointing horizontally. Mandibular palp with three segments; proximal two segments of palp incompletely fused so that sulcus between segments is still visible under magnification; terminal segment a single large oval process positioned behind mandible. Third maxillipeds filling entire buccal frame, except for transversely oval anterior respiratory openings at superior lateral ends; merus with flanged edges and conspicuously widened upper lateral margins; ischium same width as merus, suture between ischium and basis marked by distinct line. Inferior lateral corner of ischium of third maxilliped produced into distinct short proximal process overlapping base of exopod of third maxilliped; exopod of third maxilliped long (0.66 × merus length), robust (0.33 × ischium width); distinct distal medial process of exopod, exopod with long flagellum.

Epimeral sulcus present on sidewall of carapace, vertical sulcus between epimeral sulcus and base of epibranchial tooth visible, but not sharply distinct. Anterior margin of front almost horizontal, indented slightly in middle. Postfrontal crest distinct, incomplete, lined by granules and not meeting anterolateral margins; short mid-groove on postfrontal crest.

Male pleon slim, triangular outline formed by pleonal segments a3-a6; telson (a7) triangular; a1-a6 four sided; a3 broadest segment; sides of a4-a7 angled inward. Outline of female pleon broad and shield shaped, telson forming broad triangle.

Thoracic sternal suture s1/s2 short, complete, distinct; sternal suture s2/s3 complete, crossing entire sternum, indistinct; sternal suture s3/s4 incomplete, reduced to two small notches at sides of sternum. Episternal sutures e4/s4, e5/s5, e6/s6, and e7/s7 complete, distinct. Sternal sulci (s4/s5, s5/s6) in sterno-pleonal cavity widely separated medially, sternal sulci s6/s7, s7/s8 almost continuous but not interrupted in the midline by vertical sulcus (medial line); vertical sulcus broad, interrupted in middle by diamond-shaped space. Pair of small rounded sternal condyles ("typical press-buttons", Guinot & Bouchard, 1998) within sterno-pleonal cavity on s5. Female sexual openings in sterno-pleonal cavity on s6.

Subterminal segment of Go1 longer than terminal article of Go1; subterminal segment reaching as far as s5. Subterminal segment of Go1 rectangular, broadest at base and in mid section; ventral side not completely enclosed: medial side exposed, lateral side covered by long lateral flap folded inwards across segment from lateral margin; lateral flap continuous with longitudinal groove of terminal article, reaching from basis of terminal article to gonopod chamber of subterminal segment. Margins of subterminal segment and lateral flap lined with setae. Terminal article of Go1 relatively short, about 1/5 length of subterminal segment. Ventral side of terminal article of Go1 with two lengthways folds (lateral and medial folds) separated by a distinct longitudinal groove. Dorsal side of terminal article of Go1 smooth; distinct dorsal membrane at junction between subterminal segment and terminal article. Go2 slightly longer than Go1. Subterminal segment of Go2 same length as subterminal segment of Go1. Subterminal segment of Go2 widest at base, tapering sharply inward to form long, thin, rod-like process; rounded collar at junction between terminal article and subterminal segment. Terminal article of Go2 flagellum-like, measuring about half as long as subterminal segment of Go2.

Etymology. — The specific name *immaculata* is taken from the Latin adjective 'immaculatus', meaning unstained or spotless. The adjective thus agrees in gender with the (feminine) generic name.

Colour. — In life, carapace uniform grey-pink to orange-brown, lacking stains or spots; tips of chelipeds and pereiopods white.

Distribution. — The species is known currently only from the vicinity of Kigoma, Tanzania and from Mpulungu, Zambia.

Habitat. — Specimens were collected from underneath rocks and cobbles at depths ranging from 2 to 20 meters. *Platythelphusa immaculata* is sympatric with *P. conculcata*, *P. echinata* and juveniles of *P. armata*.

Remarks. — The distal tooth on the superior margin of the merus of P2-P4 varies in size from a small spine in the holotype, to either a low tooth, or being absent altogether on some legs in other specimens (ZMA De.204601). In some specimens (ZMA De.204601), the two teeth on the anterolateral margin behind the epibranchial tooth are interspersed with minute, irregularly shaped teeth.

The general outline of the carapace and the characters of the pereiopods of *P. immaculata* most closely resemble those of *P. conculcata* and *P. echinata*. *Platythelphusa immaculata* is distinguished from *P. conculcata* by differences in the relative height and width of the carapace; in the frontal margin, which is fringed with pronounced tooth-like tubercules in *P. conculcata*, but granular in *P. immaculata;* and in the superior margin of the cheliped merus, which is granular in *P. immaculata* but with a small distal tooth in *P. conculcata* (tables I

TABLE I

Morphological comparison of the nine species of *Platythelphusa* recognized herein

	P. armata A. Milne-Edwards, 1887	*P. denticulata* Capart, 1952	*P. maculata* Cunnington, 1899	*P. praelongata* n. sp.	*P. tuberculata* Capart, 1952
Frontal margin	almost horizontal, indented	almost horizontal, indented	slightly deflexed, slightly indented	slightly deflexed, slightly indented	slightly deflexed, slightly indented
Frontal margin	granular	tuberculated	finely granular	granular	finely granular
Front, external angles	square, with sharp teeth	square, with sharp teeth	square, lacking teeth or with minute teeth	rounded, without teeth	square, with small teeth
Anterolateral margin between exorbital and epibranchial teeth	granular	granular, or lined with small teeth	granular	finely granular	finely granular
Epibranchial tooth	variable size, from medium to large	variable size, from medium to large	variable size, from small to medium	minute	always smaller than anterolateral teeth
Anterolateral margin	variable number of unequal sized teeth	variable number of unequal sized teeth	2 or 3 teeth of variable size, from small to medium	several minute teeth and 1 broad tooth lateral of mesogastric region	2 or 3 teeth, tooth lateral of mesogastric region is always the largest
Suborbital margin	small regular shaped, tooth-like tubercles	irregular tooth-like tubercles	minute regular shaped, tooth-like tubercles	small regular shaped, tooth-like tubercles	minute regular shaped, tooth-like tubercles
Suborb. margin, medial end	large, pointed tooth	narrow, pointed tooth	broad, low tooth	broad, low tooth	broad, pointed tooth
3rd Maxillipeds medial margins	gape absent	gape absent	gape absent	gape absent	slight gape
Epibranchial lobes	slightly raised	slightly raised	slightly raised	not raised	pronouncedly raised

TABLE I
(Continued)

	P. immaculata n. sp.	*P. conculcata* Cunnington, 1907	*P. echinata* Capart, 1952	*P. polita* Capart, 1952
Frontal margin	almost horizontal, indented	almost horizontal, indented	slightly deflexed, slightly indented	deflexed, slightly indented
Frontal margin	granular	tuberculated	finely granular	minutely granular
Front, external angles	square, with sharp tooth	square, with sharp tooth	square, with small low tooth, sometimes lacking tooth	square, without tooth
Anterolateral margin between exorbital and epibranchial teeth	granular	granular	granular	granular
Epibranchial tooth	almost equal size as anterolateral teeth	almost equal size as anterolateral teeth	sometimes lacking, otherwise almost equal size as anterolateral teeth	almost equal size as anterolateral tooth
Anterolateral margin	2 almost equal sized teeth	2 equal sized teeth	1 or 2 teeth	1 tooth
Suborbital margin	irregular shaped tooth-like tubercles	irregular shaped tooth-like tubercles	minute regular shaped, tooth-like tubercles	minute regular shaped, tooth-like tubercles
Suborb. margin, medial end	narrow, pointed tooth	narrow, pointed tooth, sometimes several fused teeth	no tooth	no tooth or small, low tooth
3rd Maxillipeds medial margins	gape absent	gape absent	gape absent	gape absent
Epibranchial lobes	not raised	not raised	not raised	not raised

TABLE I
(Continued)

	P. armata	*P. denticulata*	*P. maculata*	*P. praelongata*	*P. tuberculata*
Intersexual dimorphism between chelipeds	absent	absent	present	no data	present
Cheliped dactylus, dorsal margin	granular	serrated	granular	finely granular	finely granular
Cheliped carpus, articular tooth	broad, pointed	broad, pointed	low and blunt, or small tooth	broad, pointed	low and blunt, or small tooth
Cheliped carpus, dorsal margin	granular	several unequal teeth	granular	granular	granular, or several small teeth
Cheliped merus, medial inferior margin	granular, large distal tooth	granular, large distal tooth	granular, large distal tooth	granular, large distal tooth	granular, large distal tooth
Cheliped merus, superior margin	finely granular	granular, sometimes with small distal tooth	finely granular	finely granular	granular, distal tooth, sometimes several unequal teeth posterior to distal tooth
Ischium P1-P5, inferior margin	smooth	granular	granular	finely granular	distal spine
Merus P2-P4, subdistal tooth	no spine	pointed spine	no spine	no spine	no spine
Merus P2-P4, distal tooth	no spine	no spine, or small spine	no spine	no spine	small spine
Merus P2-P4, inferior margin	minutely serrated	minutely serrated	minutely serrated	granular	minutely serrated
Propodus P2, inferior margin	several minute spines	several minute spines	several minute spines	several minute spines	several minute spines

TABLE I
(Continued)

	P. armata	*P. denticulata*	*P. maculata*	*P. praelongata*	*P. tuberculata*
Propodus P3-P4, inferior margin	smooth	smooth	smooth	smooth	several minute spines
Dactylus P3-P4, superior margin	row of small spines	row of small spines	row of small spines	smooth	row of small spines
Dactylus P3-P4, inferior margin	row of small spines	row of small spines	row of small spines	row of small spines	row of small spines
Gonopod 1, angle of terminal segment	90°	no data	45°	no data	60°

TABLE I
(Continued)

	P. immaculata	*P. conculcata*	*P. echinata*	*P. polita*
Intersexual dimorphism between chelipeds	present	present	present	present
Cheliped dactylus, dorsal margin	serrated	serrated	finely granular	minutely granular
Cheliped carpus, articular tooth	broad, pointed	broad, pointed	low and blunt, or small tooth	low and blunt, or small tooth
Cheliped carpus, dorsal margin	granular, or several small teeth	several unequal teeth	granular, or several minute teeth	granular
Cheliped merus, medial inferior margin	granular, large distal tooth	granular, large distal tooth	granular, large distal tooth, sometimes with several unequal teeth posterior to distal tooth	smooth, small distal tooth
Cheliped merus, superior margin	granular	granular, smaller distal tooth	granular	finely granular

TABLE I
(Continued)

	P. immaculata	*P. conculcata*	*P. echinata*	*P. polita*
Ischium P1-P5, inferior margin	granular	sometimes minute distal spine	granular	finely granular
Merus P2-P4, subdistal tooth	small spine	pointed spine	pointed spine	no spine
Merus P2-P4, distal tooth	small spine, sometimes no spine	pointed spine	small spine, sometimes no spine	no spine
Merus P2-P4, inferior margin	minutely serrated	minutely serrated	row of spines	minutely serrated
Propodus P2, inferior margin	smooth	smooth	row of spines	several minute spines
Propodus P3-P4, inferior margin	smooth	smooth	row of spines	several minute spines
Dactylus P3-P4, superior margin	smooth, with several distal spines	smooth	smooth, with several distal spines	row of small spines
Dactylus P3-P4, inferior margin	smooth, with several distal spines	smooth, with several distal spines	smooth, with several distal spines	row of small spines
Gonopod 1, angle of terminal segment	60°	90°	90°	60°

TABLE II

Carapace proportions of the nine species of *Platythelphusa* recognized herein. The range of the puberty moult denotes the carapace width of the largest subadult female to the carapace width of the smallest adult female

	CH/FW	± SD	CW/FW	± SD	CL/FW	± SD	Merus P5/FW	± SD	Moult of puberty (CW mm)	Largest known specimen (CW mm)
P. polita Capart, 1952 (n = 8)	1.13	0.05	2.38	0.10	1.94	0.08	0.76	0.03	11.4-13.0	18.0*
P. tuberculata Capart, 1952 (n = 92)	1.08	0.12	2.82	0.27	2.29	0.22	1.43	0.09	17.8-18.5	39.9
P. armata A. Milne-Edwards, 1887 (n = 241)	1.07	0.13	2.75	0.20	2.34	0.16	1.07	0.08	35.7-38.3	60.0
P. maculata Cunnington, 1899 (n = 32)	1.02	0.05	2.34	0.10	2.06	0.09	0.92	0.05	11.0-12.9	17.9
P. denticulata Capart, 1952 (n = 19)	0.93	0.04	2.49	0.09	2.12	0.09	1.01	0.04	18.4-21.4	46.0
P. praelongata n. sp. (n = 1)	0.90	–	2.72	–	2.37	–	1.05	–	?	28.9
P. immaculata n. sp. (n = 25)	0.87	0.05	2.70	0.14	2.24	0.22	1.09	0.06	16.9-21.2	31.0
P. echinata Capart, 1952 (n = 45)	0.79	0.09	2.41	0.17	1.92	0.10	0.95	0.14	12.6-17.7	39.0
P. conculcata Cunnington, 1907 (n = 81)	0.78	0.05	2.45	0.11	2.20	0.12	1.11	0.14	11.3-17.8	30.3

* Data from Cumberlidge et al. (1999).

and II). Finally, the angle of the terminal article of gonopod 1 differs between *P. conculcata* and *P. immaculata* (table I). *Platythelphusa immaculata* is most easily distinguished from *P. echinata* by the presence of distinct spines on the inferior margin of the merus of P2-P4 of *P. echinata*, which are lacking in *P. immaculata* (table I).

Platythelphusa praelongata n. sp. (fig. 2A-D)

Material examined. — Holotype, 1 adult female, gravid, CW 28.76 mm (ZMA De.204595), Lake Tanganyika, off Kazi Beach site north of Mbita Island, Zambia (08°45.22′S 31°05.14′E), 40-80 m deep, coll. local fishermen, 19 June 2002.

Diagnosis. — Carapace subhexagonal, rounded, wider than long (CW/FW 2.72; CL/FW 2.37), flat (CH/FW 0.90). Frontal margin granular, corners rounded, lacking teeth. Exorbital angle produced into broad forward-directed tooth. Epibranchial tooth small, anterolateral margin behind epibranchial tooth with several irregularly shaped small teeth and one large broad tooth lateral to mesogastric region (fig. 2A). Suborbital margin lined with large granules; broad low tooth at medial end (fig. 2C). Lateral inferior margin of merus of cheliped granular; superior margin of merus roughly granulated. Inner margin of carpus of cheliped with two large subequal carpal teeth, articular tooth (at point of articulation with propodus) broad, low; outer margin of carpus granular. Chelipeds straight, elongated, slim, with serrated dentition; slight dimorphism between left and right cheliped (fig. 2B). Merus of P5 1.5 times longer than FW. Merus of P3-P4 extremely long (2 times longer than FW); superior margin of merus of P3-P4 with low subdistal meral tooth, and low, rounded distal meral tooth. Propodus of P2-P4 long, smooth, and with thin margins. Dactyli of P3-P4 long, slim, straight, no spines on superior margin, row of small spines on inferior margin.

Description. — Carapace with fields of short carinae in lateral regions; anterolateral margin of carapace continuous with posterolateral margin. Well-defined cardiac region and cervical grooves (fig 2A). Triangular descending process of front not produced into a tooth, but with several small proximal teeth. Well-developed occlusal (sub-ocular) tooth in orbital hiatus (fig. 2D). Suborbital margin with a prominent shelf, lined with small tooth-like tubercules (fig. 2C). First antennal segment oval, fused into epistome; proximalmost antennal segment large and rectangular, with large transverse process, lying in orbital hiatus located between descending frontal tooth and occlusal tooth; distal antennal segment elongate and slim, supporting short antennal flagellum.

Endostomial ridges distinct, marking medial side of left and right anterior respiratory channels, lined with small granules; epistomial triangle conspicuous, pointing horizontally, lined with several very small granules. Mandibular palp with

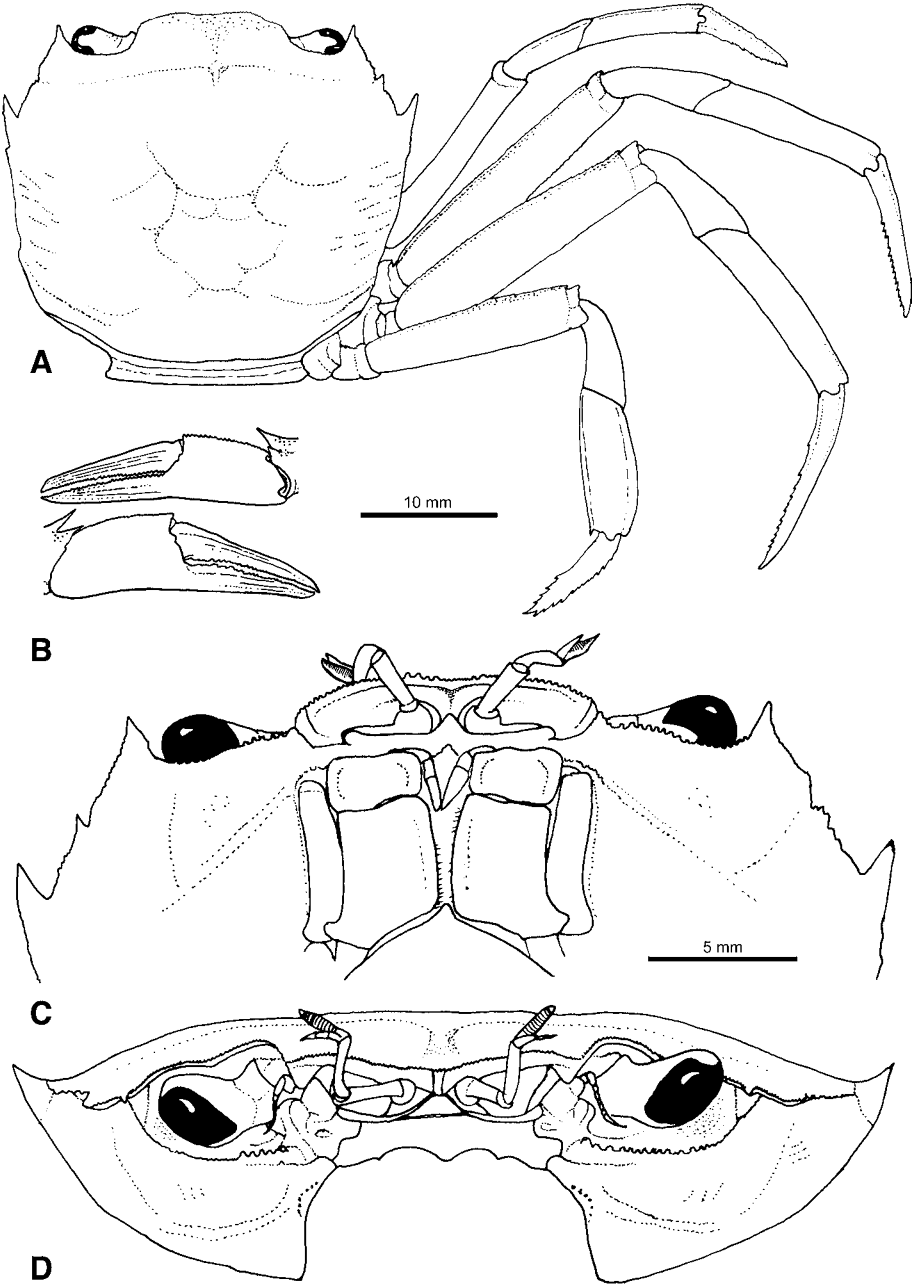

Fig. 2. *Platythelphusa praelongata* n. sp., female (gravid), CW 28.76 mm, holotype (ZMA De.204595). A, dorsal view of carapace and pereiopods 2-5; B, frontal view of left (above) and right (below) cheliped; C, ventral view of anterior area of carapace showing suborbital margin and 3rd maxillipeds; D, frontal view of carapace.

three segments; proximal two segments of palp incompletely fused and sulcus between segments is still visible; terminal segment as a single large oval process positioned behind mandible. Third maxillipeds filling entire buccal frame, with transversely oval anterior respiratory openings exposed at superior lateral ends; merus with flanged edges and conspicuously widened at lateral margins; ischium of same width as merus, suture between ischium and basis marked; inferior lateral corner produced into distinct short proximal process overlapping base of exopod. Exopod of third maxilliped long (0.66 × merus length), robust (0.33 × ischium width); with distinct distal medial process and long flagellum.

Carapace with epimeral sulcus on its sidewall, vertical sulcus between epimeral sulcus and base of epibranchial tooth visible, but rather indistinct. Anterior margin of front slightly deflexed, indented slightly in the middle. Postfrontal crest distinct, granular, incomplete, not meeting anterolateral margins; short midgroove on postfrontal crest.

Outline of female pleon broad and shield shaped, telson forming broad triangle. Thoracic sternal suture s1/s2 short, complete, distinct; sternal suture s2/s3 complete, crossing entire sternum, indistinct; sternal suture s3/s4 incomplete, reduced to two small notches at sides of sternum. Episternal sutures e4/s4, e5/s5, e6/s6, and e7/s7 complete, distinct. Two of four posterior sternal sulci (s4/s5, s5/s6) widely separated medially within sterno-pleonal cavity, whereas s6/s7, s7/s8 almost continuous but not interrupted in the midline by vertical sulcus (medial line); vertical sulcus broad and interrupted in middle by diamond-shaped space. Pair of small rounded sternal condyles (“boutons pressions”) within sterno-pleonal cavity on s5. Female sexual openings in sterno-pleonal cavity on s6.

Juveniles. — The pleonal brood pouch contained 32 juveniles. Carapaces almost square (CW = 3.02 ± 0.08 mm, CL = 2.83 ± 0.12 mm). Anterior margin of front granular, corners rounded, lacking teeth. Exorbital angles produced into broad forward-directed tooth. One broad tooth on anterolateral margin. Pereiopods long and slim; merus of P5 approximately 1.5 times longer than FW.

Etymology. — The specific name *praelongata* is taken from the Latin adjective ‘praelongus’, meaning very long, referring to the elongated pereiopods of the species. It is an adjective that agrees in gender with the feminine generic name.

Colour. — Carapace pink to grey-pink; tips of chelipeds and pereiopods white; propodus and dactylus of chelipeds red.

Distribution. — The species is known only by the holotype and associated juveniles from the vicinity of Mbita Island, Zambia, where they were collected using a gill net set at 40-80 meters depth by fishermen.

Habitat. — We have no direct observations on the habitat of *P. praelongata*. However, it was collected together with *Hemibates stenosoma* Boulenger, 1901 (Cichlidae, Bathybatini) a benthic fish species that is known to have a preference for deep sandy or muddy substrates (Coulter, 1991). *Platythelphusa praelongata* is probably sympatric with *P. tuberculata*, since the latter species shows a strong affinity for deep, muddy habitats (Coulter, 1991; Cumberlidge et al., 1999) and is caught regularly in the nets of fishermen seeking deep-dwelling fish species in the vicinity of Mpulungu (L. Makassa, pers. comm.).

Remarks. — *Platythelphusa praelongata* bears a superficial resemblance to *P. tuberculata* because both species have elongated pereiopods and a similar carapace outline. The two species can be distinguished by differences in the height of the carapace, the shape of the epibranchial lobes, the gape between the third maxillipeds, the size of the external angles of the frontal margin, and by other characters of the pereiopods (tables I and II).

DISCUSSION

The platythelphusid crabs from Lake Tanganyika form a small species flock that is morphologically highly divergent from other African freshwater crab taxa. The number of valid species within the genus *Platythelphusa* and the higher taxonomy of Lake Tanganyika's endemic freshwater crabs have been a subject of debate for almost a century. For example, Cunnington (1899) recognized only two species of crabs from Lake Tanganyika, which he assigned to two different genera: *Platythelphusa armata* A. Milne-Edwards, 1887 and *Limnothelphusa maculata* Cunnington, 1899. However, his proposal to place the latter in a genus separate from *Platythelphusa* was based on the morphological description presented by A. Milne-Edwards (1887), which Cunnington (1899) acknowledged lacked sufficient information to determine the exact relationships between the two genera. In a later paper, Cunnington (1907) suppressed the genus *Limnothelphusa* and recognized three species of crabs from Lake Tanganyika in the genus *Platythelphusa* (*P. armata*, *P. maculata*, and *P. conculcata*). The genus has subsequently been assigned to various families and subfamilies, including the Potamonidae (cf. Rathbun, 1904, 1905; Alcock, 1910; Bouvier, 1917a, b, 1921; Cunnington, 1920; Capart, 1952; Bott, 1955; Balss, 1957), the Plathythelphusinae (cf. Colosi, 1920), and the Potamonautidae (cf. Coulter, 1991).

The taxonomic instability of the group is most likely the result of a limited focus by each worker on a small number of morphological characters. Moreover, informative taxonomic characters such as those of the gonopods were neglected in the early accounts of African freshwater crab taxa. Cumberlidge (1999) and Cumberlidge et al. (1999) revised the genus *Platythelphusa* by focusing on characters of the gonopods, mouthparts, pereiopods, and sternum, and by including morphometric data. The validity of the genus *Platythelphusa* and the establishment of the family Platythelphusidae were supported by cladistic analyses based on morphological characters, and indicate a monophyletic origin of the platythelphusid species flock (Cumberlidge & Von Sternberg, 1998; Cumberlidge, 1999; Von Sternberg & Cumberlidge, 1999).

Distinguishing morphological characters that set *Platythelphusa* apart from all other taxa of African freshwater crabs include (1) a terminal article of Go1 that is directed at a 45° to 90° angle to the vertical and that is smooth, short and strongly tapering to a pointed tip; (2) a three-segmented mandibular palp with a simple terminal segment; (3) a robust exopod on the third maxilliped that is 0.33 × as wide as the ischium; (4) the lack of a vertical sulcus on the ischium of the third maxilliped; (5) the presence of a prominent, shelf-like suborbital margin that is lined with tooth-like tubercles; (6) the presence of tuberculated lateral carinae on the branchial regions of the carapace; and (7) a frontal margin that is either granular or toothed (Cumberlidge, 1999; Von Sternberg & Cumberlidge, 1999).

Previous authors have expressed incongruent views about the validity of *P. maculata*, *P. conculcata*, and *P. denticulata*. Capart (1952) recognized six species of *Platythelphusa*: *P. armata*, *P. maculata*, *P. tuberculata*, *P. polita*, *P. echinata*, and *P. denticulata*, but expressed uncertainty about the validity of *P. conculcata* and considered Cunnington's (1907) type to be a junior synonym of either *P. armata* or *P. maculata*. Cumberlidge et al. (1999) recognized the validity of *P. conculcata* following comparisons of the type (NHML 1908.1.31.15) with type material of *P. armata*. Capart (1952) suggested on the basis of the relative length of P5 with respect to the front width, that the specimen of *P. conculcata* depicted by Balss (1936) is in fact *P. tuberculata*. We agree with Capart's (1952) opinion, on the basis of Balss' (1936) remarks, that the carapace of his specimen is somewhat arched, and that the pereiopods have a distal meral spine, whereas the carapace of the type of *P. conculcata* is flat and the pereiopods lack a distal meral spine. Bott (1955) recognized only one species of platythelphusid (*P. armata*), which he considered to be a subgenus of *Potamonautes*, treating *P. maculata* as a junior synonym of *P. armata*, and *P. conculcata* as a subspecies of *P. armata*. Cumberlidge et al. (1999) recognized six species of *Platythelphusa*: *P. armata*, *P. maculata*, *P. tuberculata*, *P. polita*, *P. echinata*, and *P. conculcata*.

Cumberlidge et al. (1999) tentatively treated *P. denticulata* as a junior synonym of *P. conculcata* on the basis of the figure of *P. denticulata* provided by Capart (1952, fig. 2), which clearly shows characters that are characteristic of *P. conculcata*, such as a distinctive carpus of the chelipeds with a sharp and pointed articular tooth and an outer margin that is lined by a row of sharp, pointed teeth; an anterolateral margin between the exorbital and epibranchial teeth that is lined with fine teeth; and a frontal margin that is lined with fine teeth. Capart (1952) provided a brief description and illustrations of this species, based on a single adult female specimen (CW 46.0 mm) from Edith Bay, Tanzania (6°30.00′S 29°55.00′E). In his description, Capart (1952) expressed uncertainty as to the identity of this specimen, because it bears close similarity to *P. armata*. In the present study, we examined the holotype of *P. denticulata* (IRSN I.G. 30021) and compared it with the other species of *Platythelphusa*, particularly *P. conculcata* and *P. armata*. Our comparisons revealed that *P. denticulata* differs notably from *P. conculcata* in carapace proportions, the degree of elevation of the epibranchial lobes, and the absence of sexual dimorphism in the shape and size of the chelipeds (tables I and II). Based on these characters, we here remove *P. denticulata* from synonymy with *P. conculcata*. It should be noted, however, that *P. denticulata* does bear remarkable resemblance to *P. armata*. Nevertheless, these species can be distinguished by a number of diagnostic characters, including differences in carapace proportions, the lining of the suborbital margin, the margins of the cheliped dactylus and carpus, and the distal tooth on the meri of P2-P4 (tables I and II).

KEY TO THE KNOWN SPECIES OF *PLATYTHELPHUSA*

The following key can be used to separate the currently recognized species of *Platythelphusa*:

1. Anterior margin of front deflexed or slightly deflexed, slightly indented in the middle, lacking well-defined teeth on external corners 2
– Anterior margin of front almost horizontal, indented in the middle, with well-defined, sharp teeth on external corners 3
2. External angles of frontal margin rounded, frontal margin granular. Epibranchial tooth small, one larger tooth on anterolateral margin in mesogastric region . . . . *P. praelongata* n. sp.
– External angles of frontal margin square shaped 4
3. Frontal margin with fine teeth 7
– Frontal margin granular 8
4. Merus of P5 shorter than front width. One anterolateral tooth behind the epibranchial tooth, equal in size to the epibranchial tooth . . . . *P. polita* Capart, 1952
– Merus of P5 longer than, or almost equal to, front width 5
5. Epibranchial lobes pronouncedly raised. Inferior margin of ischium of P1-P5 with distal spine . . . . *P. tuberculata* Capart, 1952
– Epibranchial lobes low. Inferior margin of ischium of P1-P5 lacking distal spine 6
6. Inferior margins of merus and propodus of P2-P4 with row of distinct spines . . . . *P. echinata* Capart, 1952
– Inferior margins of merus of P2-P4 granulate, inferior margin of propodus of P2 with several minute spines, P3-P4 smooth . . . . *P. maculata* Cunnington, 1899
7. Subdistal and distal tooth of merus of P2-P4 with pointed spine. Two teeth on anterolateral margin, almost equal size as epibranchial tooth . . . . *P. conculcata* Cunnington, 1907
– Subdistal tooth of merus of P2-P4 with pointed spine, distal tooth of merus of P2-P4 without spine, or with small spine. Variable number of unequal teeth on anterolateral margin . . . . *P. denticulata* Capart, 1952
8. Subdistal and distal teeth of merus P2-P4 low, blunt, not spiny. Outer margin of cheliped carpus granular. Variable number of unequal-sized teeth on anterolateral margin . . . . *P. armata* A. Milne-Edwards, 1887
– Subdistal tooth of merus of P2-P4 sharp spine, distal tooth of merus of P2-P4 either lacking or small. Outer margin of cheliped carpus granular or with several small teeth. Two sub-equal teeth on anterolateral margin of carapace . . . . *P. immaculata* n. sp.

ACKNOWLEDGEMENTS

The authors would like to express their gratitude to Pierre-Denis Plisnier, who collected the holotype of *P. praelongata*. We are greatly indebted to George Kazumbe, who helped to collect specimens of *P. immaculata*. We also like to thank Karel Wouters (Institut Royal des Sciences Naturelles, Brussels), for loan of the holotype of *P. denticulata*; Paul Clark and Miranda Lowe (Natural History Museum, London), Roland Melzer (Zoologische Staatssammlung, Munich), and Charles Oliver Coleman (Humboldt Museum für Naturkunde, Berlin) for loaning the type specimens of *Platythelphusa* used for the comparisons in this work; Jonathan Todd (The Natural History Museum, London) for taxonomic discussions; Lawrence Makassa (Department of Fisheries, Mpulungu, Zambia) for his assistance in Zambia; the Tanzanian Commission for Science and Technology (COSTECH) for permission to conduct research at Lake Tanganyika; the Tanzanian Fisheries Research Institute, Kigoma and acting director D. Chitamwebwa, University of Dar es Salaam, the Nyanza Project (NSF Paleoclimates ATM-9619458) and Andy Cohen for logistical assistance; Sven Lange for his support and Jan van Arkel (University of Amsterdam) for his help with the illustrations. The first author is funded by grants from the Netherlands Foundation for the Advancement of Tropical Research (WOTRO W84-489) and the Schure-Beijerinck-Popping Fund of the Royal Netherlands Academy of Arts and Sciences (SBP/JK/2003-27).

REFERENCES

ALCOCK, A., 1910. On the classification of the Potamonidae. Records of the Indian Museum, **5**: 253-261.

BALSS, H., 1936. Beiträge zur Kenntnis der Potamonidae (Süsswasserkrabben) des Kongogebietes. Revue Zoologique et Botanique d'Afrique, **28**: 65-204.

— —, 1957. Decapoda VIII: Systematik. In: Bronn's Klassen und Ordnungen des Tierreichs, **5** (1) (7) (12): 1505-1672. (Akademische Verlagsgesellschaft, Leipzig).

BOTT, R., 1955. Die Süsswasserkrabben von Afrika (Crust., Decap.) und ihre Stammesgeschichte. Annales du Musée Royal du Congo Belge, (C, Zoologie) **1** (3) (3): 209-352.

— —, 1970. Betrachtungen über die Entwicklungsgeschichte und Verbreitung der Süßwasser-Krabben nach der Sammlung des Naturhistorischen Museums in Genf/Schweiz. Revue Suisse de Zoologie, **77** (2): 327-344.

BOUVIER, E. L., 1917a. Sur la classification des Eupotamonea, crabes d'eau douce de la famille des Potamonidés. Comptes-rendus de l'Académie des Sciences, Paris, **165**: 613-621.

— —, 1917b. Sur la classification des Parapotamonea, crabes d'eau douce de la famille des Potamonidés. Comptes-rendus de l'Académie des Sciences, Paris, **165**: 657-659.

— —, 1921. Voyage de Ch. Alluaud et R. Jeannel en Afrique orientale (1911-1912). Résultats scientifiques, Crustacés, Decapoda. Librairie des Sciences Naturelles, **3**: 23-62. (L. Lhomme, Paris).

CAPART, A., 1952. Exploration hydrobiologique du Lac Tanganyika (1946-1947), Resultats scientifiques — Crustacés Décapodes Brachyures. Institut Royal des Sciences Naturelles de Belgique, **3** (3): 41-67.

— —, 1954. Révision des types des espèces de Potamonidae de l'Afrique tropicale conservés au Muséum d'Histoire naturelle de Paris. Volume jubilaire de Victor van Straelen, Directeur de l'Institut Royal des Sciences Naturelles de Belgique, 1925-1934, **2**: 819-847.

COLOSI, G., 1920. I Potamonidi conservati del R. Museo Zoologico di Torino. Bolletino dei Musei di Zoologia ed Anatomia comparata della R. Università di Torino, **35** (734): 1-39.

COULTER, G. W., 1991. Lake Tanganyika and its life: 1-354. (Oxford University Press, Oxford).

CUMBERLIDGE, N., 1998. The African and Madagascan freshwater crabs in the Zoologische Staatssammlung, Munich. Spixiana, **21** (3): 193-214.

— —, 1999. The freshwater crabs of West Africa, family Potamonautidae. Faune et Flora Tropicale, **35**: 1-382. (Institut de Recherche pour le Développement Collection Faune et Flore Tropicales, Paris).

CUMBERLIDGE, N. & R. VON STERNBERG, 1998. Phylogenetic relationships of the freshwater crabs of Lake Tanganyika (Decapoda, Brachyura). In: F. R. SCHRAM & J. C. VON VAUPEL KLEIN (eds.), Crustaceans and the biodiversity crisis. Proceedings of the 4th International Crustacean Congress, **1**: 405-422.

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, London, **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.

— —, 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.

— —, 1920. The fauna of the African Lakes: a study in comparative limnology with special reference to Lake Tanganyika. Proceedings of the Zoological Society, London, **3**: 507-622.

GUINOT, D. & J. M. BOUCHARD, 1998. Evolution of the abdominal holding systems of brachyuran crabs (Crustacea, Decapoda, Brachyura). Zoosystema, **20** (4): 613-694.

MILNE-EDWARDS, A., 1887. Observations sur les crabes des eaux douces de l'Afrique. Annales des Sciences Naturelles, Paris, **7** (4): 161-191.

RATHBUN, M. J., 1904. Les crabes d'eau douce (Potamonidae). Nouvelles Archives du Muséum d'Histoire naturelle, Paris, **6** (4): 255-312.

— —, 1905. Les crabes d'eau douce (Potamonidae). Nouvelles Archives du Muséum d'Histoire naturelle, Paris, **7** (4): 159-322.

— —, 1933. Reports on the scientific results of an expedition to the southwestern highlands of Tanganyika territory. No. 5, Crabs. Bulletin of the Museum of Comparative Zoology at Harvard College, **75**: 251-260.

STERNBERG, R. VON & N. CUMBERLIDGE, 1999. A cladistic analysis of *Platythelphusa* A. Milne-Edwards, 1887, from Lake Tanganyika, East Africa (Decapoda: Potamoidea: Platythelphusidae) with comments on the phylogenetic position of the group. Journal of Natural History, London, **33**: 493-511.

First received 14 October 2003.
Final version accepted 24 February 2004.

Available online at www.sciencedirect.com

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Molecular Phylogenetics and Evolution 40 (2006) 628–634

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Short communication

Molecular evidence for recent divergence of Lake Tanganyika endemic crabs (Decapoda: Platythelphusidae)

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Received 13 September 2005; revised 9 March 2006; accepted 10 March 2006

1. Introduction

The East African Rift lakes are renowned as hotspots of endemism and as exemplary settings for studies on processes that generate biodiversity (Lowe-McConnell, 2003 and references therein). The cichlids in the East African lakes have received considerable scientific attention, leading to an increase of our understanding of the phylogenetic relationships of these fish, as well as of the mechanisms underlying the rapid radiations of their species flocks (Kocher, 2004; Kornfield and Smith, 2000). Species relationships and evolutionary processes in other endemic species-rich groups in Africa's Rift lakes, however, are less well studied and remain poorly understood (but see Martens, 1994; Michel, 2000; West and Michel, 2000; Wilson et al., 2004).

Lake Tanganyika is the only lake in the world that harbors a decapod crustacean radiation (Martens and Schön, 1999). The lake and its catchment are a hotspot of freshwater crab biodiversity, representing 44% of the species known from East Africa (N. Cumberlidge, personal communication). Of the 10 species of freshwater crabs endemic to Lake Tanganyika, nine are in the family Platythelphusidae (Cumberlidge et al., 1999; Marijnissen et al., 2004) and one, *Potamonautes platynotus* (Cunnington, 1907), is a member of the widespread African family Potamonautidae. The genus *Platythelphusa* shows extensive morphological disparity, which is especially striking compared to other African crab genera (*Potamonautes*, *Sudanonautes*) that occupy much broader geographical ranges but show limited morphological differentiation (e.g., Bott, 1955; Cumberlidge, 1999). Several species of *Platythelphusa* exhibit morphological characters that are considered atypical for freshwater crabs, but are instead reminiscent of marine ancestry (von Sternberg and Cumberlidge, 1999). These unusual morphological features prompted the suggestion that platythelphusids are among the most primitive of the extant species of African freshwater crabs. It was posited that they were able to retain a suite of plesiomorphic characters due to favorable marine-like environmental conditions in Lake Tanganyika (Bott, 1955; Cunnington, 1899; Moore, 1903). Alternatively, it was suggested that convergent evolution caused the unusual appearance of platythelphusids (Cunnington, 1920; von Sternberg and Cumberlidge, 1999). These two hypotheses lead to fundamentally different predictions regarding (a) the phylogenetic placement of platythelphusids with respect to other freshwater crabs and (b) the position of the most derived platythelphusid within its own clade.

So far, only morphological characters have been used to infer evolutionary relationships of the platythelphusid crabs (von Sternberg and Cumberlidge, 1999). Recent genetic analyses, however, indicate that the external morphological characters previously used in studies of African freshwater crabs are of limited power in resolving phylogenetic relationships (Daniels et al., 2002, unpublished data). Here, we use two mitochondrial markers (12S rRNA and 16S rRNA) to establish a genetic framework to test hypotheses on the origin of the morphological disparity and species diversity of Lake Tanganyika's endemic crabs.

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doi:10.1016/j.ympev.2006.03.025

2. Materials and methods

Platythelphusid crabs were collected from 11 localities along the Tanzanian and Zambian shoreline of Lake Tanganyika between 2001 and 2003 (Table 1). We included representatives for eight of the nine species of the endemic Tanganyikan genus *Platythelphusa*. For seven of these we included multiple representatives, however a single individual of *Platythelphusa praelongata* was available (see Marijnissen et al., 2004). Extensive efforts to collect *Platythelphusa polita* were unsuccessful at the sites surveyed. Crabs were collected either by hand through SCUBA diving, or obtained from local fishermen (*Platythelphusa tuberculata*, *P. praelongata*, and outgroup taxa), and preserved in 95% ethanol. Vouchers were deposited at the Zoological Museum Amsterdam (ZMA De. 204594–96, De. 204686–95). Sequences from six mitochondrial and nuclear genes indicated that *Platythelphusa* nests robustly within East African potamonautid crabs (Daniels et al., unpublished data), so we included a range of potamonautids for outgroup sampling: the Tanganyikan endemic *P. platynotus*, the East African representatives *P. emini*, *P. lirrangensis*, and *P. niloticus* and three species from southern Africa, *P. brincki*, *P. clarus*, and *P. depressus* (Table 1).

Total genomic DNA was extracted from muscle tissue of each crab, following standard procedures outlined by Daniels et al. (2002). Two primer sets, 12S rRNA (Kocher et al., 1989) and 16S rRNA (Palumbi et al., 1991), were used to amplify each of the two mitochondrial gene regions using standard polymerase chain reaction (PCR) methods. Individual 25 µl PCR contained 14.9 µl millipore water, 3 µl of 25 mM $MgCl_2$, 2.5 µl of 10× Mg^{2+} free buffer, 0.5 µl of a 10 mM dNTP solution, and 0.5 µl of each primer set (at 10 µM each), 0.1 µl of Taq polymerase, and 1 µl template DNA. PCR conditions were as follows: 3 min at 95 °C, then 32 cycles of 95 °C for 35 s, 48 °C for 45 s, 72 °C for 40 s, followed by 48 °C for 5 min, 72 °C for 10 min, and 20 °C for 10 min. PCR products were purified using a QIAquick PCR purification kit (Qiagen), then cycle sequenced following standard protocols (3 µl purified PCR product, 4 µl ABI PRISM fluorescent dye terminators, 3 µl of a 1 µM of primer solution), followed by analysis on an ABI 3100 automated DNA sequencer.

Table 1
Specimens of *Platythelphusa* and *Potamonautes* included in the phylogenetic analyses, localities where crabs were collected, and GenBank Accession numbers

Species	Code	Locality		Latitude, longitude	12S	16S
Platythelphusa armata (A. Milne-Edwards, 1887)	JKB	Jakobsen	LT, TZ	4°54.87′S, 29°35.85′E	DQ203187	DQ203213
Platythelphusa armata	MBT	Mbita	LT, ZM	8°45.23′S, 31°05.14′E	DQ203188	DQ203214
Platythelphusa armata	UJJ	Ujiji	LT, TZ	4°58.00′S, 29°41.82′E	DQ203189	DQ203215
Platythelphusa conculcata (Cunnington, 1907)	HTP	Hilltop	LT, TZ	4°53.20′S, 29°36.90′E	DQ203190	DQ203216
Platythelphusa conculcata	JKB	Jakobsen	LT, TZ	4°54.73′S, 29°35.90′E	DQ203191	DQ203217
Platythelphusa conculcata	KIG	Kigoma	LT, TZ	4°53′21′S, 29°37.21′E	DQ203192	DQ203218
Platythelphusa denticulata (Capart, 1952)	KAB	Kabwe	LT, TZ	7°01.60′S, 30°33.00′E[a]	DQ203194	DQ203220
Platythelphusa denticulata	MZG	Mzungu	LT, TZ	4°55.05′S, 29°35.73′E	DQ203193	DQ203219
Platythelphusa echinata (Capart, 1952)	HTP	Hilltop	LT, TZ	4°53.45′S, 29°35.80′E	DQ203196	DQ203222
Platythelphusa echinata	MPL	Mpulungu	LT, ZM	N.A.	DQ203197	DQ203223
Platythelphusa echinata	UJJ	Ujiji	LT, TZ	4°58.75′S, 29°43.27′E	DQ203195	DQ203221
Platythelphusa immaculata (Marijnissen et al., 2004)	JKB	Jakobsen	LT, TZ	4°54.73′S, 29°35.90′E	DQ203199	DQ203225
Platythelphusa immaculata	KTB	Katabe	LT, ZM	4°54.21′S, 29°35.67′E	DQ203200	DQ203226
Platythelphusa immaculata	MBT	Mbita	LT, TZ	8°45.23′S, 31°05.14′E	DQ203198	DQ203224
Platythelphusa maculata (Cunnington, 1899)	KAS	Kasanga	LT, TZ	8°28.00′S, 31°08.60′E[a]	DQ203201	DQ203227
Platythelphusa maculata	KMJ	Kangamoja	LT, TZ	4°57.92′S, 29°41.20′E	DQ203202	DQ203228
Platythelphusa maculata	MPL	Mpulungu	LT, ZM	8°45.99′S, 31°06.40′E	DQ203203	DQ203229
Platythelphusa praelongata (Marijnissen et al., 2004)	MPL	Mpulungu	LT, ZM	8°45.22′S, 31°05.14′E	DQ203204	DQ203230
Platythelphusa tuberculata (Capart, 1952)	UJJ	Ujiji	LT, TZ	4°54.20′S, 29°30.00′E[a]	DQ203206	DQ203232
Platythelphusa tuberculata	MBT	Mbita	LT, ZM	8°44.91′S, 31°05.34′E	DQ203205	DQ203231
Potamonautes emini (Hilgendorf, 1892)	GMB	Gombe	LT, TZ	4°38.15′S, 29°37.81′E	DQ203207	DQ203233
Potamonautes emini	KIV	Ruzizi	LK, DC	N.A.	DQ203208	DQ203234
Potamonautes niloticus (H. Milne-Edwards, 1837)	SRD	N.A.	N.A.	N.A.	AY803496	AY803536
Potamonautes lirrangensis (Rathbun, 1904)	KIV	Ruzizi	LK, DC	N.A.	DQ203210	DQ203236
Potamonautes lirrangensis	MAL	Thumbi West	LM, MW	N.A.	DQ203209	DQ203235
Potamonautes lirrangensis	ZAM	Uazua	LT, ZM	N.A.	DQ203211	DQ203237
Potamonautes platynotus (Cunnington, 1907)	KAL	Kalemie	LT, DC	5°55.60′S, 29°11.60′E[a]	DQ203212	DQ203238
Potamonautes clarus (Gouws et al., 2000)	OLI	Oliviershoekpas	KZ, SA	N.A.[b]	AY042320	AY042241
Potamonautes brincki (Bott, 1960)	FER	Fernkloof	WC, SA	N.A.[b]	AY042322	AY042244
Potamonautes depressus (Krauss, 1843)	COL	Coleford	KZ, SA	N.A.[b]	AY042325	AY042247

DC, Democratic Republic Congo; KZ, Kwa Zulu Natal; LK, Lake Kivu; LM, Lake Malawi; LT, Lake Tanganyika; MW; Malawi; SA, South Africa; TZ, Tanzania; WC, Western Cape; ZM, Zambia; SRD, sequences provided by Savel Daniels; N.A., not available.

[a] Indicates location not verified with GPS.

[b] Samples from Daniels et al. (2002).

Sequences were aligned in CLUSTALX 1.81 (Thompson et al., 1997) under default settings and optimized manually (Page and Holmes, 1998). Although this methodology is widely used, it should be noted that it has received criticism due to its sensitivity to arbitrary selection of alignment parameters (e.g., Giribet, 2003, and references therein). Regions that could not be unambiguously aligned were identified, and the effect of omitting those from the analyses was tested. A partition homogeneity test was carried out in PAUP* 4b10 (Swofford, 2002) to test for congruence among the genes (Farris et al., 1994). MODELTEST 3.06 (Possada and Crandall, 1998) was used to determine the best-fit model of sequence evolution under the Akaike information criterion (AIC). Phylogenetic analyses were reconstructed using maximum likelihood and parsimony procedures in PAUP* 4b10 under default settings. Maximum likelihood and parsimony analyses were performed using heuristic searches and TBR branch swapping with 10 random additions. Bootstrap support was calculated over 100 and 1000 permutations for maximum likelihood and parsimony, respectively. Bayesian trees were inferred using MrBayes 3.0b4 (Ronquist and Huelsenbeck, 2003). Bayesian inference of phylogeny (BI) was performed using eight Markov chains, 10 million generations with a burn-in of 10%. The posterior distributions were approximated three times under the Bayesian approach, to determine successful convergence of the Markov chains. All the analyses above were performed on the separate data sets of 12S and 16S rRNA, as well as on the combined data set. To obtain an approximation of the relative timeframe of platythelphusid diversification a molecular clock was applied to the 16S rRNA sequence data set. A likelihood ratio test was carried out to the 16S rRNA data in PAUP* 4b10 prior to performing molecular clock inferences. Divergence time estimates were obtained by applying a rate of 0.0032–0.0045 substitutions per site per lineage per million years to corrected divergence values. This rate corresponds to estimates obtained for taxa in the marine crab genera *Sesarma* and *Uca*, which range from ≈0.65% to ≈0.9% pairwise sequence divergence per million years (Ma) for 16S rRNA (Schubart et al., 1998a,b; Sturmbauer et al., 1996).

3. Results

Both 12S rRNA and 16S rRNA exhibited heterogeneity in sequence variation. Exclusion of regions of ambiguous alignments, which were primarily between ingroup and outgroup taxa, resulted in no loss of ingroup phylogenetic signal. The combined 12S and 16S rRNA sequence data included 754 base pairs, with 127 variables and 66 parsimony informative sites. The results from the partition-homogeneity test were not significant, and thus the 12S and 16S rRNA genes were combined in the analyses. The best-fit maximum likelihood model was chosen using the AIC. The TVM+I maximum likelihood model was selected for 12S rRNA, and GTR + I for 16S rRNA, whereas the GTR + I + G model was selected for the combined data set. Similarity of log likelihood values after burn-in, indicated that the Markov chains successfully reached convergence during all three Bayesian runs.

The platythelphusids from Lake Tanganyika form a well supported clade in all analyses (Fig. 1). *Potamonautes emini* and a clade consisting of *P. niloticus*, the Tanganyikan endemic *P. platynotus* and *P. lirrangensis* were placed sister to the Platythelphusidae. Average 12S rRNA and 16S rRNA sequence divergence (uncorrected *p*-distances) between *Platythelphusa* individuals was 1.21% (range 0.4–2.7%), 8.94% (range 0.1–11.5%) within the potamonautid outgroup, and the minimum divergence between the ingroup and outgroup was 7.56%. The hypothesis of a molecular clock was not rejected ($\chi^2 = 33.7$ $df = 29$ $P > 0.05$). Applying a molecular clock of 0.65–0.9% sequence divergence per Myr to the 16S rRNA sequence data suggests that the platythelphusid lineage separated from Potamonautidae approximately 9.0–6.5 Myr ago, while divergence of the platythelphusid clade is estimated to have taken place approximately 3.3–2.5 Myr ago (node C1 and C2, respectively in Fig. 1).

The combined 12S and 16S rRNA data set resolved some, but not all species relationships within Platythelphusidae (Fig. 1). The different phylogenetic reconstruction methods resulted in congruent topologies for the combined data set, however, separate analysis of the 12S and 16S rRNA sequences differ in the position of several individuals: (i) *P. armata* JKB (respectively unresolved, and sister to *P. armata* UJJ), (ii) *P. denticulata* MZG (in a clade with *P. maculata* KAB and *P. maculata* MPL, and sister to *P. maculata* KMJ), (iii) *P. maculata* KAS (in an unresolved clade with *P. armata* MBT, *P. armata* UJJ and *P. maculata* KMJ, and sister to *denticulata* KAB, and (iv) *P. immaculata* KTB (sister to *P. echinata* UJJ, and in a polytomy with *P. immaculata* and *P. conculcata*) (data not shown).

4. Discussion

The platythelphusids from Lake Tanganyika are the first example of a recent diversification among African freshwater crabs. The phylogenetic patterns recovered by our analyses of 12S and 16S rRNA mtDNA sequences reveal that Platythelphusidae is an unequivocal genetic clade, with surprisingly short internal branches. The endemic Tanganyikan potamonautid *P. platynotus* does not cluster with the platythelphusids, and instead it is sister to the widespread East African *P. lirrangensis.* The 12S and 16S rRNA mtDNA genes did not resolve phylogenetic patterns within Platythelphusidae well enough to confidently detect species level relationships. This was an unexpected result, because these mitochondrial markers have been successfully employed for resolving brachyuran crab species-level phylogenies (Bossuyt et al., 2004; Daniels et al., 2003; Schubart et al., 1998a). The limited sequence divergence (0.4–2.7%) between the platythelphusid taxa indicates that their lineages might have diverged too recently for the 12S rRNA and 16S rRNA

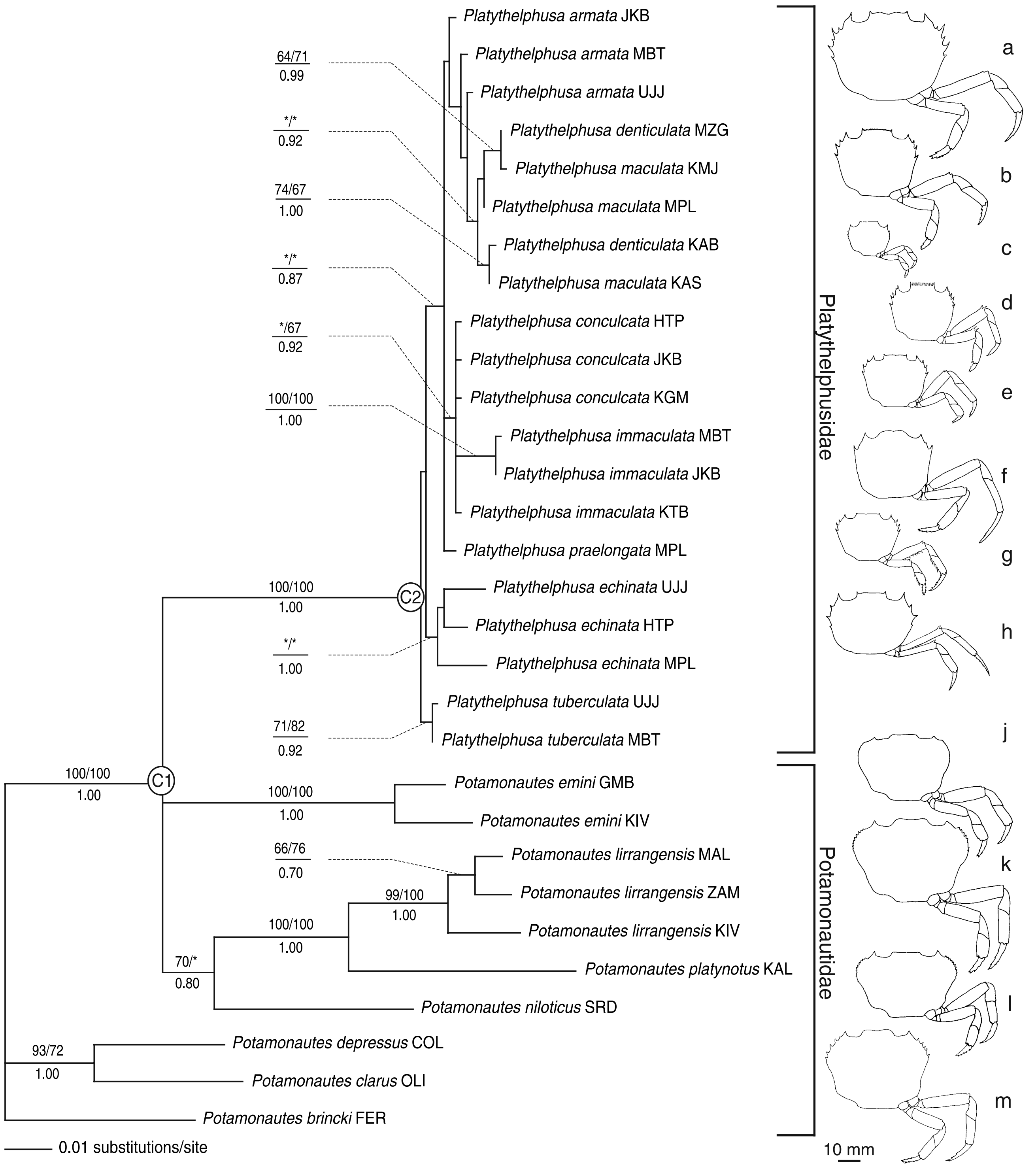

Fig. 1. Maximum likelihood tree of combined 12S and 16S rRNA mtDNA sequences, with branch lengths proportional to number of changes. Taxon labels indicate morphological species diagnosis and locality acronym (see Table 1). Numbers above nodes denote maximum likelihood and parsimony bootstrap support values, followed by Bayesian posterior probabilities. *Indicates support less than 60% in otherwise supported branches. Node C1 represents the origin of the platythelphusid lineage, estimated 9–6.5 Myr ago; C2 was estimated at 3.3–2.5 Myr (see Materials and methods). (a) *Platythelphusa armata*, (b) *P. denticulata*, (c) *P. maculata*, (d) *P. conculcata*, (e) *P. immaculata*, (f) *P. praelongata*, (g) *P. echinata*, (h) *P. tuberculata*, (j) *Potamonautes emini*, (k) *P. lirrangensis*, (l) *P. platynotus*, and (m) *P. niloticus*. a–h and l, endemic to Lake Tanganyika; j, k, and m, riverine species from eastern Africa.

to become fixed and provide sufficient phylogenetic signal, resulting in incongruence between the gene trees and the species tree (Neigel and Avise, 1986). Incomplete lineage sorting of ancestral polymorphisms is common in newly evolved species, and has been reported recurrently in studies of the cichlid fish species flocks in the African rift lakes (Albertson et al., 1999; Moran and Kornfield, 1993; Takahashi et al., 2001).

A study of morphologically almost indistinguishable allopatric populations of *P. clarus* and *P. depressus* yielded several distinct clades, with 16S rRNA sequences divergences of 2.9–17.0% between lineages (Daniels et al., 2003). By applying a molecular clock of 0.65–0.9% pairwise divergence per Myr (Schubart et al., 1998b; Sturmbauer et al., 1996), the major cladogenetic events between *P. clarus* and *P. depressus* are estimated to have taken place between ≈8–17 Myr ago, in the Miocene (recalculated from Daniels et al., 2003). Applying the same molecular clock to our data suggests that the divergence of the platythelphusid clade was initiated during the Pliocene. We present these dates for relative comparison only, and caution that substantial errors may be associated with vicariance dated molecular clocks. The molecular clocks that we used here were based on dating of the closure of the Panama land bridge of 3.1 Myr (Schubart et al., 1998b) and 3.0 Myr (Sturmbauer et al., 1996). Phylogenetic responses to closure of the Central American seaway have been shown to be unpredictable and often older than the commonly used 3–3.5 Myr geologic date for complete uplift of the Isthmus of Panama (e.g., Knowlton and Weight, 1998; Marko, 2002). Thus, the molecular clock for freshwater crabs is conservative, and other potential dates would provide an even younger time of divergence for the platythelphusid radiation. Evidently, the diversification of the endemic Tanganyikan clade occurred recently, and explanations for the morphological disparity of these crabs should be sought in situ.

The recent diversification (≈3.3–2.5 Myr ago) of the platythelphusids underlines that the unusual morphologies of these crabs are not a reflection of retained plesiomorphies. This is corroborated by (a) cladistic analyses (von Sternberg and Cumberlidge, 1999), and recent analyses of six mitochondrial and nuclear genes (Daniels et al., unpublished), which place Platythelphusidae well within the African freshwater crabs, and (b) the placement of *Platythelphusa conculcata*, the species with the most 'marine-like' morphological characters (see von Sternberg and Cumberlidge, 1999), on short, internal branches instead of basal in the platythelphusid clade. There are several factors that can be causal to the morphological disparity of platythelphusids. Their diversification occurred in the context of the dynamic geological history of Lake Tanganyika (central basin initiation 9–12 Myr ago, three tectonic basins fused into single deep lake 5–6 Myr ago, followed by intermittent re-separation during episodes of dramatic water level fluctuations (Cohen et al., 1997; Scholz and Rosendahl, 1988; Tiercelin and Mondeguer, 1991)). This led to possibilities for speciation in allopatric populations on a range of geographic scales, ecological divergence in vacant niches and periods of potential secondary contact. The phylogenies of several cichlid lineages have been correlated with climatic events and fluctuations in lake level during the Pleistocene (Sturmbauer et al., 2001; Verheyen et al., 1996). Platythelphusids have markedly flattened carapaces, characteristic for freshwater crab taxa that have adapted to a fully aquatic life (Cumberlidge, 1999, p. 279), and this could have resulted in limited dispersal between sub-basins during periods of lowest water levels. Future work with broader geographic sampling of crabs will allow testing the influence of physical barriers on Tanganyikan crab species boundaries.

Examples of ecological niche diversification among species of *Platythelphusa* provide clues to sympatric mechanisms that could be causal to their rapid radiation. For instance, several species exhibit clear habitat specificity. *P. maculata* has a small, rounded body and shows a preference for living in empty gastropod shells (Capart, 1952; Cunnington, 1899), whereas *P. tuberculata* shows affinity for deep lake floor habitats (Coulter, 1991; Marijnissen et al., 2004). *P. armata* is equipped with enlarged claws that were suggested to have coevolved with Lake Tanganyika's heavily armoured gastropods (West et al., 1991). On the other hand, there is evidence of ecological niche overlap between morphologically distinctly different species (*P. conculcata*, *P. echinata*, and *P. immaculata*) that coexist in the same habitat (Marijnissen et al., unpublished data). Although the degree to which allopatric factors and sympatric speciation mechanisms have contributed to the diversification of platythelphusids remains speculative at present, these observations demonstrate that the Tanganyikan crabs show an unequivocal potential to serve as an invertebrate model system for studies of speciation in ancient lakes.

Acknowledgments

We are grateful to George Kazumbe, Willibrord Kazumbe, Mbalassa Mulongaibalu, Lawrence Makassa, Pierre-Denis Plisnier, Bert Hidding, Martin Genner, and Christian Sturmbauer for field collections. We thank the Tanzanian Fisheries Research Institute and the University of Stellenbosch, South Africa for support; the Tanzanian Commission for Science and Technology for granting S. Marijnissen and E. Michel permission to conduct research at Lake Tanganyika; Jon Todd, Miguel Vences, Lukas Rüber, Patrick Meirmans, Neil Cumberlidge and two anonymous reviewers for insightful comments; and Jan van Arkel for his help with the figure. The first author received funding from The Netherlands Foundation for the Advancement of Tropical Research (WOTRO W84-489), and the Royal Netherlands Academy of Arts and Sciences' Schure-Beijerinck-Popping Fund (SBP/JK/2003-27). S. Marijnissen and E. Michel received logistical support from the Nyanza Project (NSF Paleoclimates ATM-9619458).

References

Albertson, R.C., Markert, J.A., Danley, P.D., Kocher, T.D., 1999. Phylogeny of a rapidly evolving clade: the cichlid fishes of Lake Malawi, East Africa. Proc. Natl. Acad. Sci. USA 96, 5107–5110.

Bossuyt, F., Meegaskumbura, M., Beenaerts, N., Gower, D.J., Pethiyagoda, R., Roelants, K., Mannaert, A., Wilkinson, M., Bahir, M., Manamendra-Arachchi, K., Ng, P.K., Schneider, C.J., Oommen, O.V., Milinkovitch, M.C., 2004. Local endemism within the Western Ghats–Sri Lanka biodiversity hotspot. Science 306, 479–481.

Bott, R., 1955. Die Süsswasserkrabben von Afrika (Crust., Decap.) und ihre Stammesgeschichte. Ann. Mus. Royal Congo Belge C. (Zool.) 3 (série, 3, 1), 209–352.

Capart, A., 1952. Exploration hydrobiologique du Lac Tanganyika (1946–1947), Resultats scientifiques - Crustacés, Décapods, Brachyures. Inst. Roy. Sci. Nat. 3, 41–67.

Cohen, A.S., Lezzar, K.E., Tiercelin, J.J., Soregan, M., 1997. New paleogeographic and lake-level reconstructions of Lake Tanganyika: implications for tectonic, climatic and biological evolution in a rift lake. Basin Res. 9, 107–132.

Coulter, G.W., 1991. Composition of the flora and fauna. In: Coulter, G.W. (Ed.), Lake Tanganyika and its Life. Oxford University Press, London, pp. 253–257.

Cumberlidge, N., 1999. The Freshwater Crabs of West Africa, Family Potamonautidae. Faune et Flore Tropicales. No. 35. IRD, Paris. pp. 63–123.

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

Cunnington, W.A., 1899. On a new brachyurous crustacean from Lake Tanganyika. Proc. Roy. Soc. Lond. 1899, 697–704.

Cunnington, W.A., 1907. Zoological results of the third Tanganyikan expedition, conducted by Dr. W.A. Cunnington, 1904–1905, Report on the Brachyurous Crustacea. Proc. Zool. Soc. Lond. 2, 258–276.

Cunnington, W.A., 1920. The fauna of the African Lakes: a study in comparative limnology with special reference to Lake Tanganyika. Proc. Zool. Soc. Lond. 3, 507–622.

Daniels, S.R., Stewart, B.A., Gouws, G., Cunningham, M., Matthee, C.A., 2002. Phylogenetic relationships of the southern African freshwater crab fauna (Decapoda: Potamonautidae: *Potamonautes*) derived from multiple data sets reveal biogeographic partitioning. Mol. Phylogenet. Evol. 15, 511–523.

Daniels, S.R., Gouws, G., Stewart, B.A., Coke, M., 2003. Molecular and morphometric data demonstrate the presence of cryptic lineages among freshwater crabs (Decapoda: Potamonautidae: *Potamonautes*) from the Drakensberg Mountains, South Africa. Biol. J. Linn. Soc. 78, 129–147.

Farris, JS., Källersjö, M., Kluge, A.G., Bult, C., 1994. Testing significance of incongruence. Cladistics 10, 315–320.

Giribet, G., 2003. Stability in phylogenetic formulations and its relationship to nodal support. Syst. Biol. 52, 554–564.

Knowlton, N., Weight, L.A., 1998. New dates and new rates for divergence across the Isthmus of Panama. Proc. Roy. Soc. Lond. B. 265, 2257–2263.

Kocher, T.D., 2004. Adaptive evolution and explosive speciation: the cichlid fish model. Nature Rev. Gen. 5, 288–298.

Kocher, T.D., Thomas, W.K., Meyer, A., Edwards, S.V., Pääbo, S., Villablanca, F.X., Wilson, A.C., 1989. Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. Proc. Natl. Acad. Sci. USA 68, 6196–6200.

Kornfield, I., Smith, P.F., 2000. African cichlid fishes: model systems for evolutionary biology. Annu. Rev. Ecol. Syst. 31, 163–196.

Lowe-McConnell, R.H., 2003. Recent research in the African Great Lakes: fisheries, biodiversity and cichlid evolution. Freshwater Forum 20, 1–64.

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

Marko, P.B., 2002. Fossil calibration of molecular clocks and the divergence times of germinate species pairs separated by the Isthmus of Panama. Mol. Biol. Evol. 19, 2005–2021.

Martens, K., 1994. Ostracod speciation in ancient lakes: A review. In: Martens, K., Goddeeris, B., Coulter, G. (Eds.), Speciation in Ancient Lakes, Arch. Hydrobiol. Beih. Ergebn. Limnol. 44, pp. 203–222.

Martens, K., Schön, I., 1999. Crustacean biodiversity in ancient lakes: a review. Crustaceana 72, 899–910.

Michel, E., 2000. Phylogeny of a gastropod species flock: exploring speciation in Lake Tanganyika in a molecular framework. In: Rossiter, A., Kawanabe, H. (Eds.), Ancient Lakes: Biodiversity, Ecology and Evolution. Advances in Ecological Research, vol. 31. Academic Press, UK, pp. 276–302.

Moore, J.E.S., 1903. The Tanganyika problem. Hurst and Blackett, London. pp. 279-286.

Moran, P., Kornfield, I., 1993. Retention of ancestral polymorphism in the *Mbuna* species flock (Teleostei: Cichlidae) of Lake Malawi. Mol. Biol. Evol. 10, 1015–1029.

Neigel, J.E., Avise, J.C., 1986. Phylogenetic relationships of mitochondrial DNA under various demographic models of speciation. In: Karlin, S., Nevo, E. (Eds.), Evolutionary Processes and Theory. Academic Press, Orlando, Florida, pp. 515–534.

Page, R.D.M., Holmes, E.C., 1998. Molecular evolution: a phylogenetic approach. Blackwell Science Ltd., NY. pp. 138-144.

Palumbi, S.R., Martin, A., Romano, S., Mcmillan, W.O., Stice, L., Grabowski, G., 1991. The simple fools guide to PCR. A collection of PCR protocols, version 2. Honolulu, University of Hawaii.

Possada, D., Crandall, K.A., 1998. Modeltest: testing the model of DNA substitution. Bioinformatics 14, 817–819.

Ronquist, F., Huelsenbeck, J.P., 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19, 1572–1574.

Scholz, C.A., Rosendahl, B., 1988. Low lake stands in Lakes Malawi and Tanganyika, delineated with multifold seismic data. Science 240, 1645–1648.

Schubart, C.D., Neigel, J.E., Felder, D.L., 1998a. Use of the mitochondrial 16S rRNA gene for phylogenetic and population studies of Crustacea. In: von Vaupel Klein, J.C., Schram, F.R. (Eds.), The Biodiversity Crisis and Crustacea. Balkema Pub., Rotterdam, pp. 817–830.

Schubart, C.D., Diesel, R., Blair Hedges, S., 1998b. Rapid evolution to terrestrial life in Jamaican crabs. Nature 393, 363–365.

Sturmbauer, C., Baric, S., Salzburger, W., Rüber, L., Verheyen, E., 2001. Lake level fluctuations synchronize genetic divergences of cichlid fishes in African lakes. Mol. Biol. Evol. 18, 144–154.

Sturmbauer, C., Levinton, J.S., Christy, J., 1996. Molecular phylogeny analysis of fiddler crabs: test of the hypothesis of increasing behavioral complexity in evolution. Proc. Natl. Acad. Sci. USA 93, 10855–10857.

Swofford, D. 2002. PAUP* Phylogenetic analyses using Parsimony (*and other methods). Sinnauer Associates, Sunderland, MA.

Takahashi, K., Terai, Y., Nishida, M., Okada, N., 2001. Phylogenetic relationships and ancient incomplete lineage sorting among cichlid fishes in Lake Tanganyika as revealed by analyses of the insertion of retroposons. Mol. Biol. Evol. 18, 2057–2066.

Thompson, J.D., Gibson, T.J., Plewniak, F., Jeanmougin, F., Higgins, D.G., 1997. The ClustalX Windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic Acid Res. 24, 4876–4882.

Tiercelin, J.-J., Mondeguer, A., 1991. The geology of the Tanganyika trough. In: Coulter, G.W. (Ed.), Lake Tanganyika and its Life. Oxford University Press, London, pp. 7–48.

Verheyen, E., Rüber, L., Snoeks, J., Meyer, A., 1996. Mitochondrial phylogeny of rock-dwelling cichlid fishes reveals evolutionary influence of historical lake level fluctuations of Lake Tanganyika, Africa. Phil. Trans. R. Soc. Lond. B. 351, 797–805.

von Sternberg, R., Cumberlidge, N., 1999. A cladistic analysis of *Platythelphusa* A. Milne-Edwards, 1887, from Lake Tanganyika, East Africa (Decapoda: Potamoidea: Platythelphusidae) with comments on the phylogenetic position of the group. J. Nat. Hist. 33, 493–511.

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

West, K., Michel, E., 2000. The dynamics of endemic diversification: molecular phylogeny suggests an explosive radiation of the thiarid gastropods in Lake Tanganyika. In: Rossiter, A., Kawanabe, H. (Eds.), Ancient Lakes: Biodiversity, Ecology and Evolution. Advances in Ecological Research, vol. 31. Academic Press, UK, pp. 331–334.

Wilson, A.B., Glaubrecht, M., Meyer, A., 2004. Ancient lakes as evolutionary reservoirs: evidence from the thalassoid gastropods of Lake Tanganyika. Proc. Roy. Soc. Lond. B. 271, 529–536.

Influence of ecological and sexual selection on divergence of decapod claw morphologies: a model from Lake Tanganyika endemic crabs

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Abstract

Decapod claws are multifunctional appendages that provide ideal character sets to track the interplay between selective processes. We characterize the evolution of divergence of claw functional morphologies using the Lake Tanganyika crab radiation as a model. Species in the endemic genus *Platythelphusa* exhibit marked disparity in claw phenotypes. The enlarged claws of *Platythelphusa armata* have prompted past consideration of a coevolutionary arms race. We expand this argument to include related and potentially convergent taxa, as well as alternate selection pressures. We contrasted biting performance and claw occlusion properties of *P. armata* with the endemic *Potamonautes platynotus*, which has evolved molluscivorous specializations independently, and *Platythelphusa tuberculata*, which exhibits marked sexual dimorphism. We compared claw functional traits among males and females of other *Platythelphusa* species, and we examined principal habitat correlates. Our data demonstrate that both ecological partitioning as well as sexual selection are involved in the Lake Tanganyika endemic crab diversification.

INTRODUCTION

Identifying the role of different selection pressures is central to understanding the evolution of phenotypic diversity in closely related species. Contemporary species radiations are championed as model systems for studying speciation processes in a natural setting. Because speciation in these systems can be recent and ongoing, phenotypic differences between young lineages can often be linked to causal processes in diversification (Danley & Kocher, 2001). The African lake Tanganyika harbours multiple species of freshwater crabs, including an endemic genus, *Platythelphusa* (Cumberlidge et al., 1999; Reed & Cumberlidge, 2006; Cumberlidge et al., 2007). In contrast to their marine relatives that have planktonic larvae, freshwater crabs brood their young and thus have a higher speciation potential. The platythelphusid crabs from Lake Tanganyika diverged recently (Marijnissen et al., 2006) and exhibit striking disparity in claw phenotypes, offering an excellent opportunity to use them as indicators for studying alternate selection pressures among phylogenetically closely related species.

Claws are conspicuous appendages whose ecological performance is crucial to the survival of an individual decapod. As a consequence, an intimate relationship exists between claw phenotype and resource utilization. Comparative functional morphology is an established tool to study the nature of such relationships and the processes of selection underlying performance differences (e.g. Wainwright & Reilly, 1994). Assessments of crab claw functional traits can provide insight in patterns of ecological diversification (Brown et al., 1979; Lawton & Elner, 1985; Freire et al., 1996; Behrens Yamada & Boulding, 1998; Smith, 2004). While decapod claws serve a principal purpose as feeding structures, their morphology cannot be understood as adaptations to trophic factors alone (reviewed in Lee, 1995). Claws also serve an important role in social interactions as signalling tools and armaments. Male claw shape in particular can be strongly influenced by processes of sexual selection (Crane, 1975). Ecological performance of male claws might be compromised or enhanced by sexual selection (e.g. Caravello & Cameron, 1987; Lee & Seed, 1992). Characterizing the interplay between ecological and sexual selection within a phylogenetic framework is thus imperative to understand claw evolution. However, empirical phylogenetic treatments of claw functional morphology that explicitly address the effects of these two selection pressures are rare (Lee, 1995). Furthermore, studies of claw functional morphologies have thus far focused predominantly on marine taxa, and comparable work on freshwater taxa is lacking.

The aim of the present paper is twofold: i) to characterize diversification of claw phenotypes in Lake Tanganyika endemic crabs, and ii) to assess the relative contribution of ecological- and sexual selection in the evolution of the different claw phenotypes. We first focus on the largest-bodied platythelphusid, *Platythelphusa armata*, in which both sexes exhibit massive molariform dentition and marked dimorphism in claw height. It has been suggested that these claw traits are highly derived specializations resulting from an intralacustrine coevolutionary arms race between *P. armata* and its gastropod prey (West et al., 1991; West & Cohen, 1994, 1996). Although it was shown that enlarged claws offer an advantage in crushing the heavily calcified and ornamented shells of endemic Lake Tanganyika gastropods, the comparative phylogenetic context that is essential for understanding the evolutionary underpinning of *P. armata*'s specialized claw traits has thus far been lacking. To determine the functional traits underlying the evolution of molluscivory in Lake Tanganyika endemic crabs we compare external claw traits and performance properties of *P. armata* with those of *Potamonautes platynotus*. This latter species is the only endemic Lake Tanganyika representative of this otherwise widespread African genus (Reed & Cumberlidge, 2006), and it also exhibits claw traits that are indicative of predation on hard-shelled prey. Assessing claw performance properties of *P. armata* and *Po. platynotus* allows us to identify possible constraints or advantages in claw functional morphology across genera.

We then compare claw performance properties of a third species, *Platythelphusa tuberculata*. While male *P. tuberculata* exhibit extreme dimorphism in claw size and shape, females exhibit isomorphic claws. This indicates that sexual selection has acted upon the evolution of enlarged claws in this species (Lee, 1995). By contrasting functional morphology and performance traits of male and female *P. tuberculata* with those of *P. armata*, we can distinguish elements of claw design related to sexual selection. We subsequently focus on divergence of claw functional traits within the platythelphusid clade as a whole. We identify and evaluate intersexual differences in claw size dimorphism and occlusion, and use a molecular phylogeny to examine how patterns of divergence in claw functional morphologies correspond to evolutionary patterns. This is the first study to examine divergence of claw functional traits in a molecular framework.

Our results indicate that both ecological partitioning as well as sexual selection interact in generating diversity in Lake Tanganyika endemic crabs.

MATERIALS AND METHODS

Specimens were collected by hand from nine localities in Lake Tanganyika between 2001 and 2004 using SCUBA diving, or obtained from local fishermen (*P. tuberculata* and *P. praelongata*). Ecological data including habitat type (mud, sand, rocks, shells), depth, and co-existing species was recorded during systematic habitat surveys using 50*50 cm quadrates (434 in total). Additional information about species depth ranges was obtained using baited traps, and extracted from the literature (Coulter, 1991 and references therein). Outgroup taxa were collected by hand from localities in the Democratic Republic of Congo, Malawi, Tanzania, Uganda and Zambia (electronic Appendix A). Samples for genetic analyses were preserved in 95-98% ethanol. We aimed to collect multiple specimens of each species, however only a single individual of *P. praelongata* was available, and *P. polita* was not found in any of our sampled localities. Taxonomic assignments were based on diagnostic characters described in the systematic literature (Bott, 1955; Cumberlidge et al., 1999; Marijnissen et al., 2004; Reed & Cumberlidge, 2006).

Genetic analyses

A list of specimens included in this study, collection localities, and Genbank Accession numbers is provided in supplementary table S1. Selection of outgroup taxa was based on Daniels et al. (2006) and analysis of 16S rRNA sequences from 48 freshwater crab species from Africa, Asia and Europe (Marijnissen, unpublished data). Genomic DNA was extracted from muscle tissue of each crab, and isolated using Qiagen DNeasy^{TM}. Two primer sets, 16S rRNA (Palumbi et al., 1991), and COII mtDNA (Morrison et al. 2002) were used to amplify a 437, and 503 bp segment respectively of the two mitochondrial gene regions using polymerase chain reaction methods. Details of our molecular protocols are provided as supplementary material.

Sequences of the 16S rRNA gene were aligned using ProAlign v.0.5a0 (Löytynoja & Milinkovitch, 2003). An alignment with gap opening of 10, and extension penalty of 5 was used for phylogenetic analyses, treating gaps as missing data. Sequences of COII mtDNA contained no gaps and were aligned in CLUSTALX 1.81 (Thompson et al., 1997). Maximum likelihood (ML) and parsimony (MP) analyses were performed in PAUP*4b10 using 100 heuristic searches with TBR branch swapping and 10 random sequence-addition replicates. MrModeltest v.2.2 (Nylander, 2004) selected the GTR+I+G model for the combined 16S rRNA and COII mtDNA sequences. Bootstrapped analyses were obtained over 1000 (MP) and 100 (ML) pseudoreplicates. Bayesian analyses were implemented in MrBayes 3.0b4 (Ronquist & Huelsenbeck, 2003) by running four chains for ten million generations with a burn-in of 10%, and repeating this search three times.

Mechanical advantage, occlusion and dimorphism

Using digital callipers, we measured claw height (CH), distance from the dactyl fulcrum to the insertion of the dactyl closer muscle apodeme (L_0), distance from the fulcrum to the dactyl tip (L_1) (Fig. 1a), and carapace width (CW). Because the force produced by the claw lever system and the speed of any resultant movement are inversely related, interspecific comparisons of the ideal mechanical advantage (MA) can provide insight in functional differences (Warner & Jones, 1976; Milke & Kennedy, 2001; Behrens Yamada & Boulding, 1998). We estimated MA as the ratio between L_0 and L_1 (Alexander, 1968; Warner & Jones, 1976). Because the relationship between resource use and force generation ability cannot be fully understood without considering force distribution, we characterized the geometry of the opposing occlusive surfaces at the propodus and dactylus of the claws (Fig. 1b; Brown et al. 1979). We used digitized images with an overlaying grid to estimate the relative percentage of each occlusion type. An index of asymmetry for males (AIM) and females (AIF) was obtained for each individual specimen by determining the ratio between CH of the major and minor claw. The extent of sexual size dimorphism (SDI) within species was assessed by contrasting CH of the major claws of similar sized (CW) males and females. *Platythelphusa praelongata* (n=1) was excluded from statistical analyses. To reduce allometric variability related to ontogenetic patterns, we used only adult specimens of approximately the same size for each species. Intra- and interspecific dependency of CH on CW was tested using ordinary least squares regression on log-transformed data. Differences in CH and MA among species and between sexes were tested using single-factor analysis of variance (ANOVA), and Tukey's HSD post-hoc pairwise comparisons.

Claw performance

Adult, intermolt male and female specimens of *P. armata* (n = 39 & 38 respectively), *P. tuberculata* (male n = 37, female n = 36) and *Po. platynotus* (male n = 40, female n = 42) were collected from localities near Kigoma, Tanzania. We used an established protocol to measure crab claw biting forces (Behrens Yamada & Boulding, 1998; Taylor 2001). Biting force trials were performed with major claws only. Crabs were stimulated to forcefully grasp two bite plates at the midpoint of the dactylus and the propodus for approximately one minute. One plate was fixed while the second, movable plate was connected to a Vernier Dual-Range Force Sensor. The sensor output was displayed in real time and saved on a computer via an interface (Vernier LabPro). A maximum of two measurements was carried out per claw per day, with intervals between observations of at least four hours. Tests were repeated within a period of six days and a total of 4-6 trials were performed per crab. To reduce variation due to differences in motivational states, we included only the maximum biting force produced per individual crab in the analysis.

By assuming that the dactylus pivot point is frictionless, the maximum force exerted by the closer muscle to the dactylus at the point of apodeme insertion (F_0) can be determined as: $F_0 = (F_s)(L_f)/ L_{0,}$ where F_s is the force measured with the force transducer, L_f is the distance between the area of force application and the dactylus pivot, and L_0 is the distance between the dactylus pivot and the point at which the closer apodeme inserts on the dactylus (Govind & Blundon, 1985). Female *P. tuberculata* were non-cooperative, and excluded from statistic analyses. Inter- and intraspecific differences in bite force were tested using ANOVA and Tukey's HSD post-hoc pairwise comparisons. Statistical analyses were performed with α=0.05 in SPSS 11.0.4 (SPSS Inc. 2005).

RESULTS

Genetics

The combined 16S rRNA and COII mtDNA sequence data included 939 base pairs, with 299 variables and 284 parsimony informative sites. The platythelphusids from Lake Tanganyika form a well-supported clade in all analyses (Fig. 2.), with *Potamonautes* *niloticus* and *P. emini* as sister. The Tanganyikan endemic *Po. platynotus* is in a separate clade with *P. lirrangensis* and *P. raybouldi*. Average 16S rRNA and COII mtDNA sequence divergence (uncorrected *p*-distances) was 1.59% (range 0.11-3.46%) between *Platythelphusa* individuals, 4.71% (range 3.25-4.75) between individuals of *Po. platynotus*, and 11.35% (range 0.11-15.79%) within the potamonautid outgroup.

Mechanical advantage, occlusion and dimorphism

Significant differences were found in maximum CH and CW among species (ANOVA, df=402, F=461.705, $P<0.001$, and F=785.887, $P<0.001$). Regression analyses indicated a significant dependence of CH on CW among species ($r^2=0.76$, $P<0.01$) but not within species ($r^2 < 0.25$, $P > 0.05$ for all species). Mean MA of major claws ranged from 0.22 to 0.30 (table 1). MA did not scale with CW ($P > 0.05$, $r^2 < 0.05$ within species, $r^2 < 0.25$ among species). Species and sex showed significant differences in major claw MA (ANOVA, df=402, F=185.880, $P<0.001$). Post-hoc comparisons indicated that MA of males and females is significantly different in all species except *P. armata* (Tukey's HSD, $P<0.05$). MA of male *P. conculcata*, *P. immaculata*, *P. maculata*, *P. polita*, and *Po. platynotus* does not differ significantly from that of *P. armata* (Tukey's HSD, $P>0.05$).

We found marked differences in geometry and extent of differentiation of claw occlusive surfaces, ranging from predominantly compressive occlusion in *P. armata*, to asymmetrical in *P. conculcata*, *P. immaculata*, and *P. maculata*, to predominantly serrated in *P. praelongata* and *P. tuberculata* (Table 1). Clear differences also existed in the level of asymmetry in size between major and minor claw among species and sexes. Asymmetry indices were highest for male and female *P. armata* (AIM 1.9; AIF 1.8). Claws of female *P. immaculata, P. conculcata*, *P. praelongata* and *P. tuberculata* were near symmetrical (AIF ≤ 1.1). *Platythelphusa denticulata* exhibits extensive variability in AIF as well as occlusive geometry of its claws.

Significant differences were found in the extent of sexual dimorphism among species (ANOVA df=191, F=51.198, $P<0.001$). Sexual dimorphism index (SDI) decreases in the following order: *P. tuberculata* > *P. maculata* > *P. conculcata*, *P. immaculata* > *P. echinata*, *P. polita* > *P. armata* (Table 1). Low SDI in *P. armata* and *P. polita* is related to enlargement of the female claw (AIF 1.8 and 1.6 respectively), whereas in *P. echinata* it is related to limited expression of male dimorphism (AIM 1.4).

Claw performance

Maximum bite force ranged from 47.0-145.5 N in *P. armata*, 56.5-149.6 N in *Po. platynotus* and 30.6-85.1 in male *P. tuberculata*. A significant difference in mean bite force was indicated by ANOVA (df=176, F=26.653, $P<0.001$) (Fig. 3). Male *P. tuberculata* exerted the lowest mean bite forces of all pairwise comparisons, and female *Po. platynotus* exerted significantly lower bite forces than male *Po. platynotus* and both sexes of *P. armata* (Tukey's HSD $P>0.05$).

DISCUSSION

Phylogenetic framework

Our analyses of 16S rRNA and COII mtDNA confirm that the platythelphusids from Lake Tanganyika form a single, well-supported clade, whereas the endemic *Potamonautes platynotus* is derived from a lineage that invaded the lake separately (Fig. 2). In contrast with the level of sequence divergence and resolution exhibited by the outgroup taxa and by *Po. platynotus*, the level of resolution between platythelphusid species is low. The limited phylogenetic signal within the platythelphusid clade is a likely consequence of recent divergence (Marijnissen et al., 2006) and might be attributable to incomplete lineage sorting and/or mitochondrial introgression (Avise, 2000, 2004; Funk & Omland, 2003; Chan & Levin 2005). The status of *P. denticulata* is uncertain, as it is phenotypically variable and it shares morphological traits with both *P. armata* and *P. conculcata*, but it shares mitochondrial haplotypes with *P. armata* and *P. maculata* (Fig. 2; Cumberlidge et al., 1999; Marijnissen et al., 2004; 2006). It is tempting to interpret potentially transgressive character states such as novel, irregular and inconsistent colour patterns in *P. denticulata* as evidence for hybridization (Bert et al., 1996; Riesenberg et al., 1999; Imai & Takeda, 2005). Although hybridization is a common feature of rapid radiations (Seehausen, 2004), and can readily occur between recently diverged African freshwater crab species (Daniels et al., 2002), our current mitochondrial data prevents us from testing this hypothesis. While we recognize there may be some discussion about whether morphologically distinct forms of platythelphusid crabs have actually attained biological species status (Cumberlidge et al., 1999; Marijnissen et al., 2004), the present paper is not intended to address taxonomic issues. Instead, we emphasize that our evidence strongly indicates that the platythelphusid clade is currently undergoing speciation, and the patterns observed here are consistent with those that characterize recent radiations (Freeland & Boag, 1999; Seehausen, 2004; Parchman et al., 2006; Seehausen, 2006). Diversification within *Platythelphusa* is occurring at the interface of ecologically relevant population-level processes and long-term patterns of cladogenesis, underscoring the utility of this clade for studying evolutionary processes.

Evolution of molluscivory in Lake Tanganyika

Lake Tanganyika is unique in harbouring two endemic species of freshwater crabs in different genera (*Platythelphusa* and *Potamonautes*) that have independently acquired functional morphological traits that are indicative of molluscivorous adaptations. Both *P. armata* and *Po. platynotus* exhibit dimorphism of claw height in both sexes, as well as molariform dentition (Table 1). The combination of these traits is lacking in non-lacustrine African freshwater crabs (West et al., 1991; this study), whose diet typically consists predominantly of vegetable matter and soft-bodied prey (Williams, 1961, 1962; Dominey & Snyder, 1988; Hill & O'Keeffe, 1992; Harrison, 1995). Furthermore, the average ideal mechanical advantage of the major claw lever system (MA) of female *P. armata* (0.30) and *Po. platynotus* (0.27) is high compared to that of other African freshwater crabs, in which female major claw MA typically ranges between 0.20-0.26 (S.A.E. Marijnissen, unpublished data).

Previous studies assigned a critical role to *P. armata* as key predator in a coevolutionary arms race with Lake Tanganyika endemic gastropods (West et al., 1991; West & Cohen, 1994, 1996). It was suggested that because *P. armata*'s claws are larger relative to body size, they are stronger than those of most African freshwater crabs (West et al., 1991). Although the individuals of *P. armata* and *Po. platynotus* used in this study on average had similar body sizes (CW=46.35±3.9 and CW=46.81±3.7), major claws of *P. armata* were on average 60% larger than those of *Po. platynotus* (CH=24.58±4.0 and CH=15.72±2.6). Interestingly, MA and maximum bite force did not differ significantly between these two species (Fig. 3). This implies that, in theory, both species should be able to crush Lake Tanganyika gastropods with similar shell load strengths.

Maximum bite forces of *P. armata* and *Po. platynotus* are in the same range as those reported for some marine molluscivore crab species (Taylor,, 2000; Mitchel et al., 2003). These forces are low compared with the load strength of Lake Tanganyika gastropod shells reported in literature, which can be as high as 278-933 N (West et al., 1991; West & Cohen, 1996). It is known that effective molluscivory does not depend on strength alone. Crabs can partially compensate lack of shell crushing strength using a series of behavioural tactics, such as aperture peeling and repeated fracture loading (reviewed in Seed & Hughes 1995), which we have observed in both *P. armata* as well as *Po. platynotus* (West et al., 1991; Rosales et al., 2002; this study). Nonetheless, outright crushing is the most preferred strategy for attacking hard-shelled prey because it fulfils criteria of both profitability (time-investment versus energy gain) and minimization of claw damage (Elner & Hughes, 1978; Juanes, 1992; Juanes & Hartwick, 1990; Smallegange & van der Meer, 2003; see also review by Seed & Hughes, 1995).

Occlusive mechanisms critically influence the range of prey that can be exploited. By altering the position of a shell along the occlusive surface of the claw, the effective MA can be adjusted and a variety of forces can be exerted (Brown et al., 1979; Mitchel et al., 2003). Laterally displaced occlusion produces forces that are useful for cutting and chipping, while forces exerted via horizontally aligned molariform dentition are most effective for crushing (Brown et al., 1979). The major claw of *P. armata* and *Po. platynotus* exhibit a region of purely compressive occlusion pairs on the dactyl and propodus extending to ~80% and ~20% respectively (Table 1). *Platythelphusa armata* therefore has a clear competitive advantage as a molluscivore. This is corroborated by preliminary predation experiments indicating that *P. armata* is more efficient in crushing a wider range of shell sizes than *Po. platynotus* (Rosales et al., 2003; Michel et al., unpublished data).

Differences in claw functional morphological traits between *P. armata* and *Po. platynotus* should be interpreted in the context of their habitat preferences. Adult *P. armata* occur at depths between ~5-60 m. In contrast, *Po. platynotus* has a narrower depth range, and is restricted to shallower areas (Fig. 2). Depth is an important indirect determinant of herbivorous gastropod distribution and community composition (West et al. 2003; Michel et al. 2004; McIntyre et al. 2004). The observed differences between *P. armata* and *Po. platynotus* could thus be linked to vertical distribution patterns of their prey. Testing this hypothesis will require a combination of predator preference experiments and detailed analyses of gastropod distribution patterns.

The short branches on which *P. armata* occurs in our molecular phylogeny suggest strikingly narrow time constraints for the formation of its highly derived claw traits (Fig. 2; Marijnissen et al., 2006). The evidence that molluscivorous derivations can be acquired within a narrow evolutionary timescale (also see Smith & Palmer, 1994; Smith, 2004) has crucial ramifications for the interpretation of coevolutionary dynamics in Lake Tanganyika. Our results underscore the importance of examining coevolutionary processes in Lake Tanganyika not only by focusing on long-term patterns of cladogenesis (West & Michel, 2000; Wilson et al., 2004), but also by exploring ongoing evolutionary interactions in a recent temporal framework (e.g. Thompson 1999). To understand rapid phenotypic specialization in *P. armata*, we must take into account the template of functional diversity that exists among its congeners (Table 1, Fig. 2, see below).

Support for ecological divergence

Species in the endemic Lake Tanganyika clade exhibit remarkable divergence in claw functional morphologies. This contrasts with most potamonautid species that occupy broad geographical ranges but generally exhibit little differentiation in claw functional morphologies (West & Cohen, 1991; Daniels et al., 2006; Marijnissen et al., 2006; this study). To examine the possible factors underlying platythelphusid divergence, we treat male and female claws separately. In male crabs, sexual selection can confound inferences of the relationship between claw functional traits and the use of trophic resources. Female claw functional traits are considered to be morphologically more conservative, and they can be valuable indicators of trophic differentiation (Lee, 1995).

It has been shown that even small differences in the functional morphology of a claw can influence the efficiency with which a crab can exploit its resources (Takeda et al., 2004). As such, the differentiation in claw phenotypes, occlusion patterns and mechanical advantages exhibited by female platythelphusids (Table 1) is suggestive of a considerable level of interspecific trophic partitioning (e.g. Brown et al., 1979). Moreover, a correlation is apparent between principal adult habitat type and female claw morphology. The claws of soft substrate inhabitants exhibit predominantly serrated dentition patterns. Claws of species that principally inhabit rocky areas are characterized by the presence of an extended area of rounded or molariform dentition, and/or a sharp ridge (Table 1, Fig. 2).

The presence of trophic differentiation as well as habitat-phenotype correlations could be interpreted as evidence that adaptive ecological partitioning facilitated divergence of the platythelphusid crabs (Schluter, 2000). Other habitat-phenotype associations exhibited by platythelphusid species could provide additional evidence for ecological divergence. The deep lake dwelling species *P. praelongata* and *P. tuberculata* are both characterized by slender, elongated legs that presumably facilitate movement on soft mud (Coulter, 1991; Marijnissen et al., 2004). *Platythelphusa maculata* has a small, rounded body and shows a preference for living in empty *Neothauma* gastropod shells (Capart, 1952; Cunnington, 1899). *Platythelphusa conculcata* and *P. immaculata* inhabit narrow spaces under rocks and boulders and both have extremely flattened carapaces (Cumberlidge, 1999; Marijnissen, et al. 2004; Marijnissen, pers. obs.). Although there thus appears to be evidence of ecological divergence, demonstrating that the abovementioned traits are indeed the result of adaptive speciation will require tests of differential selection and utility (Schluter, 2000).

Interestingly, *P. denticulata* exhibits extensive variability in AIF as well as occlusive geometry of its claws (data not shown). Such variability could either result from hybridization and transgressive segregation (e.g. Rieseberg, 1999), or it could be a plastic response to local differences in prey characteristics (e.g. Smith & Palmer, 1994; Smith, 2004). We consider plasticity to be the least likely explanation for two reasons: (i) both symmetric (AIF ≤ 1.2) and markedly asymmetric (AIF ≥ 1.5) forms have been found in sympatry without evidence of intermediates; and (ii) variation in claw traits is accompanied by apparently random variability in other morphological traits. Furthermore, in spite of extensive surveys for the present study and examination of all known museum collections containing specimens of platythelphusid species, our sample sizes of *P. denticulata* remain small. This would be expected if *P. denticulata* is a hybrid taxon, but not if it is a highly plastic species. The presence of hybridization would have important consequences for processes generating phenotypic diversity in the Lake Tanganyika endemic crabs, because it potentially facilitates adaptive diversification by elevating rates of response to selection (Seehausen, 2004; Grant et al., 2005).

While ecological partitioning is evident among most platythelphusid species, some coexist without showing apparent evidence of ecological differentiation. *Platythelphusa conculcata* and *P. immaculata*, as well as *P praelongata* and *P. tuberculata* exhibit similar claw functional traits and overlapping habitat distributions (Table 1, Fig. 2). If these species are truly ecologically equivalent their initial divergence was driven either by non-sympatric processes such as major lake level fluctuations (e.g. Verheyen et al., 1996; Sturmbauer et al., 2001), or by sexual selection (see below).

Sexual selection

The presence of marked intraspecific differences in relative claw size between males and females (Table 1) suggests that sexual selection pays an important contribution to the divergence of Lake Tanganyika endemic crabs. However, the extent of sexual dimorphism (SDI) varies among species. The most extreme sexual dimorphism is exhibited by *P. tuberculata*. Whereas females exhibit isomorphic claws, males are equipped with one exceptionally enlarged claw relative to their body size (Table 1). In spite of enlargement and the presence of molariform dentition, the major claw of male *P. tuberculata* has a low mechanical advantage (Fig. 3 *a*). According to biomechanical principles this reflects a trade-off between selection for increased velocity and strength (Warner & Jones 1976). The low maximum biting forces exerted by male *P. tuberculata* corroborate that disengagement exists between major claw size and strength in this species (Fig. 3b). Capacity of rapid claw closing movements confers an advantage during male-male combat (Levinton et al., 1995; Levinton & Allen, 2005). Male-male antagonistic interactions appear to be the most common cause for intersexual claw size dimorphism in decapods (reviewed in Lee 1995), although female preference might also affect directional selection on male claw size and/or shape (Oliveira & Custodia, 1998; Gherardi et al., 2006).

Explanations for the discontinuous distribution of the extent of sexual dimorphism among platythelphusid crabs might be found in interspecific competition for resources. For instance, the principal habitats of *P. tuberculata* and *P. maculata* are largely segregated from those of their congeners (Fig. 2). The strong sexual dimorphism exhibited by these species could reflect character release in allopatry from competitors (Simberloff et al., 2000). Directional selection on sexually selected armament structures might also be indirectly influenced by costs and benefits that are directly related to the specific habitat in which the species occurs (Christy, 1987; Emlen et al., 2005).

Speciation in Lake Tanganyika endemic crabs

The manifestation of divergence in ecologically important traits combined with evidence of sexual selection, illustrates the potential of Lake Tanganyika endemic crabs to serve as an invertebrate model system for studying processes that can drive speciation. Our findings add to previous studies on patterns of rapid speciation in natural systems that have thus far been focused mainly on vertebrates (Streelman & Danley, 2003). Theoretical models indicate that ecological differentiation and sexual selection can be mutually reinforcing processes (van Doorn & Weissing, 2001; van Doorn et al., 2004). Comparisons of cichlid species complexes have generated support for a model in which the initial stage of a radiation is characterized by adaptation to distinct macrohabitats, followed by a second stage driven by competition for trophic resources resulting in divergence of functional morphologies, and a third stage in which divergence of sexually selected characters takes place (Danley & Kocher, 2001; Barluenga & Meyer, 2004; Kid et al., 2006). In our invertebrate model, the components of the radiation are similar but the sequence in which they occur is different (Fig. 2). An important distinction between cichlid fish and crabs is the level of linkage between ecological and sexual traits. In crabs, the phenotypic markers of natural and sexual selection are associated tightly. Other taxa in which macrohabitat- or trophic morphological differentiation is tied to sexual communication characters such as Anolis lizards, Darwin's finches (*Geospiza*), and snapping shrimp (*Alpheus*) exhibit similar divergence patterns as the Lake Tanganyika endemic crab radiation (Streelman & Danley, 2003; Anker et al., 2006).

The strong interdependence of fitness traits and sexual signalling traits that exists in crabs might pose an important constraint on further divergence of the platythelphusid clade (e.g. Streelman & Danley, 2003). Because directional natural selection and sexual selection are acting on the same phenotypic traits, it is likely that a fitness trade-off exists between environments (Svensson et al. 2006). Furthermore, the presence of sexual dimorphisms could restrict the likelihood of ecological speciation, particularly if sexual selection is based on female preference rather than male-male interactions (Bolnick & Doebeli, 2003). Future work aimed at understanding the behavioural aspects of mate choice and at identifying the ecological correlates of population differentiation in the endemic crabs of Lake Tanganyika will help to enhance our conception of the origin of phenotypic diversity and evolutionary diversification.

Acknowledgements

We are grateful to George Kazumbe for his invaluable assistance with the fieldwork in Lake Tanganyika; Willibrord Kazumbe, and Moniek Kars for providing additional field collections; Keith Ursel, Sven Lange and Jon Todd for providing support; Jan van Arkel for his help with the illustrations. We thank the Tanzanian Commission for Science and Technology (COSTECH) for permission to conduct research at Lake Tanganyika; the Tanzanian Fisheries Research Institute, Kigoma, the Department of Fisheries in Mpulungu Zambia, and the Nyanza Project (NSF Paleoclimates ATM 0223920) for logistical assistance. This research was supported by grants from the Netherlands Foundation for the Advancement of Tropical Research (WOTRO W84-489) and the Schure-Beijerinck-Popping Fund of the Royal Netherlands Academy of Arts and Sciences (SBP/JK/2003-27, and SBP/JK/2002-25).

REFERENCES

Alexander, R.M. 1968 *Animal mechanics*. London: Sedgewick and Jacksons.

Anker, A., Ahyong, S.T., Noël, P.Y. & Palmer, A.R. 2006 Morphological phylogeny of alpheid shrimps: parallel preadaptation and the origin of a key morphological innovation, the snapping claw. *Evolution* **60**, 2507-2528.

Avise J.C. 2000 *Phylogeography: The history and formation of species*. Cambridge, MA: Harvard University Press.

Avise, J.C. 2004 *Molecular markers, natural history and evolution*. Sunderland, MA: Sinauer Associates.

Barluenga, M. & Meyer, A. 2004 The Midas cichlid species complex: incipient sympatric speciation in Nicaraguan cichlid fishes? *Mol. Ecol.* **13**, 2061-2076.

Behrens Yamada, S. & Boulding, E. G. 1998 Claw morphology, prey size selection and foraging efficiency in generalist and specialist shell-breaking crabs. *J. Exp. Mar. Biol. Ecol.* **220**, 191-211.

Bert, T. M., McCarthy, K. J., Cruz-Lopez, H. & Bogdanowicz, S. 1996 Character discriminatory power, character-set congruence, and the classification of individuals from hybrid zones: an example using stone crabs (*Menippe*). *Evolution* **50**, 655-671.

Bolnick, D. I. & Doebeli, M. 2003 Sexual dimorphism and adaptive speciation: two sides of the same ecological coin. *Evolution* **57**, 2433-2449.

Bott, R. 1955 Die Süsswasserkrabben von Afrika (Crust., Decap.) und ihre Stammesgeschichte. *Ann. Mus. Royal Congo Belge C. (Zool.)* **3 (série, 3, 1),** 209-352.

Brown, S. C., Cassuto S. R. & Loos, R. W. 1979 Biomechanics of chelipeds in some decapod crustaceans. *J. Zool. Lond.* **188**, 143-159.

Capart, A. 1952 Exploration hydrobiologique du Lac Tanganyika (9146-1947), resultats scientifiques – Crustacés, Décapods, Brachyures. *Inst. Roy. Sci. Nat.* **3**, 41-67.

Caravello, H. E. & Cameron, G. N. 1987 The effects of sexual selection on the foraging behaviour
of the Gulf Coast fiddler crab, *Uca panacea*. *Anim. Behav.* **35**, 1864-1874.

Chan, K. M. & Levin, S. A. 2005 Leaky prezygotic isolation and porous genomes: rapid introgression of maternally inherited DNA. *Evolution* **59**, 720-729.

Christy, J. H. 1987. Competitive mating, mate choice and mating associations of brachyuran crabs. *Bull. Mar. Sci.* **41**, 177-191.

Coulter, G. W. 1991. Composition of the flora and fauna. In *Lake Tanganyika and its life* (ed. G.W. Coulter), pp. 253–257. London: Oxford University Press.

Crane, J. 1975 *Fiddler Crabs of the World: Ocypodidae: Genus Uca.* Princeton University Press.

Cumberlidge, N. 1999. The Freshwater Crabs of West Africa, Family Potamonautidae. *Faune et Flore Tropicales No. 35*. IRD, Paris.

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

Cumberlidge, N., von Sternberg, R. & Daniels, S.R. 2007 A revision of the higher taxonomy of the Afrotopical freshwater crabs (Decapoda: Brachyura) with a discussion of their biogeography. *J. Linn. Soc.*, in press.

Cunnington, W. A. 1899 On a new brachyurous crustacean from Lake Tanganyika. *Proc. Roy. Soc. Lond.* **1899**, 697-704.

Daniels, S. R., Stewart, B. A., Gouws, G., Cunningham, M. & Matthee, C. A. 2002 Phylogenetic relationships of the southern African freshwater crab fauna (Decapoda: Potamonautidae: Potamonautes) derived from multiple data sets reveal biogeographic patterning. *Mol. Phyl. Evol.* **25**, 511-523.

Daniels, S. R., Cumberlidge, N., Pérez-Losada, M., Marijnissen, S. A. E. & Crandall, K. A. 2006 Evolution of Afrotropical freshwater crab lineages obscured by morphological convergence. *Mol. Phylogenet. Evol.* **40**, 227–23 (DOI 10.1016/j.ympev.2006.02.022.)

Danley, P. D. & Kocher, T. D. 2001 Speciation in rapidly diverging systems: lessons from Lake Malawi. *Mol. Ecol.* **10**, 1075-1086.

Dominey, W. J. & Snyder, A. M. 1988 Kleptoparasitism of freshwater crabs by cichlid fishes endemic to Lake Barombi Mbo, Cameroon, West Africa. *Env. Biol. Fish.* **22**, 155-160.

Elner, R. W. & Hughes, R. N. 1978 Energy maximization in the diet of the shore crab, *Carcinus maenas*. *J. Anim. Ecol.* **47**, 103-116.

Emlen, D. J. Marangelo, J. Ball, B. & Cunningham, C. W. 2005 Diversity in the weapons of sexual selection: Horn evolution in the beetle genus *Onthophagus* (Coleoptera: Scarabaeidae). *Evolution* **59**, 1060-1084.

Freeland, J. R. & Boag, P. T. 1999 The mitochondrial and nuclear genetic homogeneity of the phenotypically diverse Darwin's ground finches. *Evolution* **53**, 1553-1563.

Freire, J., Paz Sampedro, M. & Gonzáles-Gurriarán, E. 1996 Influence of morphometry and biomechanics on diet selection in three portunid crabs. *Mar. Ecol. Prog. Ser.* **137**, 111-121.

Fryer, G. 2000 Unanticipated diversity: The discovery and biological exploration of Africa's ancient lakes. *Adv. Ecol. Res.* **31**, 1-16.

Funk, D. J. & Omland, K. E. 2003 Species-level paraphyly and polyphyly: Frequency, cause and consequences with insights from animal mitochondrial DNA. *Annu. Rev. Ecol. Syst.* **34**, 397-423.

Gherardi F., Renai, B., Galeotti, P. & Rubolini, D. 2006 Nonrandom mating, mate choice, and male-male competition in the crayfish *Austropotamobius italicus*, a threatened species. *Arch. Hydrobiol.* **165**, 557-576. (DOI 10.1127/0003-9136/2006/0165-0557.)

Govind, C. K. & Blundon, J. A. 1985 Form and function of the asymmetric chelae in blue crabs with normal and reversed handedness. *Bioll. Bull.* **168**, 321-331.

Grant, P. R., Grant, B. R. & Petren, K. 2005 Hybridization in the recent past. *Am. Nat.* **166**, 56-67.

Harrison, E-M. 1995 The zonation of freshwater crabs with altitude in a mountain stream in the East Usambara Mountains, Tanzania. *Frontier Tanzania Expedition Report TZ943*. pp. 1-56.

Hill, M. P., & O'Keeffe, J. H. 1992. Some aspects of the ecology of the freshwater crab (*Potamonautes perlatus* Milne Edwards) in the upper reaches of the Buffalo River, Eastern Cape Province, South Africa. *Sth. Afr. J. Aquat. Sci.* **18**,42-50.

Imai, H. & Takeda M. 2005 A natural hybrid mud crab (Decapoda: Portunidae) from Japan. *J. Crust. Biol.* **25**, 620-624.

Juanes, F. 1992 Why do decapod crustaceans prefer small sized molluscan prey? *Mar. Ecol. Prog. Ser.*, **87**, 239–249.

Juanes, F. & Hartwick, E. B. 1990 Prey size selection in Dungeness crabs: the effects of claw damage. *Ecology* **71**, 744–758.

Lawton, P. & Elner, R. W. 1985 Feeding in relation to morphometrics within the genus *Cancer*. Evolutionary and ecological considerations. In *Proceedings of the symposium on Dungeness crab biology and management* (ed. Metleff, B. R.), pp. 357-379. Fairbanks, Alaska: University of Alaska.

Lee, S. Y. 1995 Cheliped size and structure: the evolution of a multi-functional decapod organ. *J. Exp. Mar. Biol. Ecol.* **193**, 161-176.

Lee, S. Y. & Seed, R. 1992 Ecological implications of cheliped size in crabs: some data from *Carcinus maenas* and *Liocarcinus holsatus*. *Mar. Ecol. Prog. Ser.* **84**, 151-160.

Levinton, J. S. & Allen, B. J. 2005 The paradox of the weakening combatant: trade-off between closing force and gripping speed in a sexually selected combat structure. *Funct. Ecol.* **19**, 159-165.

Levinton, J. S., Judge, M. L. & Kurdziel, J. P. 1995 Functional differences between the major and minor claws of fiddler crabs (Uca, family Ocypodidae, Order Decapoda, Subphylum Crustacea): A result of selection or developmental constraint? *J. Exp. Mar. Biol. Ecol.* **193**, 147-160.

Löytynöja, A. & Milinkovitch, M. C. 2003 A hidden Markov model for progressive multiple alignment. *Bioinformatics* **19**, 1505-1513. (DOI 10.1093/bioinformatics/btg193.)

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

Marijnissen, S. A. E., Michel, E., Daniels, S. R., Erpenbeck, D., Menken, S. B. J. & Schram, F. R. 2006 Molecular evidence for recent divergence of Lake Tanganyika endemic crabs (Decapoda: Platythelphusidae). *Mol. Phylogenet. Evol.* **40**, 628-634. (DOI 10.1016/j.ymper.2006.03.025.)

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

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

Milke, L. M. & Kennedy, V. S. 2001 Mud crabs (Xanthidae) in Chesapeake Bay: claw characteristics and predation on epifaunal bivalves. *Inv. Biol.* **120**, 67-77.

Mitchell, S. C., Kennedy, S. M., Williams, P. J. & DeMont, M. E. 2003 Morphometrics and estimates of force generation by the chelae of a North American population of the invasive green crab, *Carcinus maenas* (L.). *Can. J. Zool.* **81**, 203-215. (DOI 10.1139/Z02-236.)

Morrison, C. L., Harvey, A. W., Lavery, S., Tieu, K., Huang, Y. & Cunningham, W. 2002 Mitochondrial gene rearrangements confirm the parallel evolution of the crab-like form. *Proc. R. Soc. Lond. B.* **269**, 345-350. (DOI 10.1098/rspb.2001.1886.)

Nylander, J. A. A. 2004 *MrModeltest v2*. Uppsala, Sweden: Department of Systematic Zoology, Uppsala University.

Oliveira, R. F. & Custodio, M. R. 1998 Claw size, waving display and female choice in the European fiddler crab, *Uca tangeri*. *Ethol. Ecol. Evol.* **10**, 241-251.

Palumbi, S. R., Martin, A., Romano, S., Mcmillan, W. O., Stice, L., & Grabowski, G. 1991. The simple fools guide to PCR. A collection of PCR protocols, version 2. Honolulu: University of Hawaii.

Parchman, T. L., Benkman, C. W. & Britch, S. C. 2006 Patterns of genetic variation in the adaptive radiation of New World crossbills (Aves: *Loxia*). *Mol. Evol.* **15**, 1873-1887.

Reed, S. K. & Cumberlidge, N. 2006 Taxonomy and biogeography of the freshwater crabs of Tanzania, East Africa. *Zootaxa* **1262**, 1-139.

Riesenberg, L. H., Archer, M. A. & Wayne, R. K. 1999 Transgressive segregation, adaptation and speciation. *Heredity* **83**, 363-372.

Ronquist, F. & Huelsenbeck, J.P. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* **19**, 1572–1574.

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

Schluter D. 2000 *The ecology of adaptive radiation*. New York: Oxford University Press.

Schenk, S. C. & Wainwright, P. C. 2001 Dimorphism and the functional basis of claw strength in six brachyuran crabs. *J. Zool. Lond.* **255**, 105-119.

Seehausen, O. 2004. Hybridization and adaptive radiation. *Trends Ecol. Evol.* **19,** 198-207. (DOI 10.1016/j.tree.2004.01.003)

Seehausen, O. 2006 African cichlid fish: a model system in adaptive radiation research. *Proc. R. Soc. B.* **273**, 1987-1998 (DOI 10.1098/rspb.2006.3539.)

Seed, R. & Hughes, R. N. 1995 Criteria for prey size selection in molluscivorous crabs with contrasting claw morphologies. *J. Exp. Mar. Biol. Ecol.* 193, 177-195.

Simberloff, D., Dayan, T. Jones, C. & Ogura, G. 2000 Character displacement and release in the small Indian mongoose, *Herpestes javanicus*. *Ecology* **81**, 2086-2099.

Smallegange, I. M. & van der Meer, J. 2003 Why do shore crabs not prefer the most profitable mussels? *J. Anim. Ecol.* **72**, 599-607.

Smith, L.D. 2004 Biogeographic differences in claw size and performance in an introduced crab predator *Carcinus maenas*. *Mar. Ecol. Prog. Ser.* **276**, 209-222.

Smith, L. D. & Palmer, A. R. 1994 Effects of manipulated diet on size and performance of brachyuran crab claws. *Science* **264**, 710-712.

Smith, T. B. & Skúlason, S. 1996 Evolutionary significance of resource polymorphisms in fishes, amphibians, and birds. *Ann. Rev. Ecol. Syst.* **27**, 111-138.

Strauss, S. Y., Sahli, H. & Conner, J. K. 2004 Towards a more trait-centered approach to diffuse (co)evolution. *New Phytologist*, **165**, 81-90. (DOI 10.1111/j.1469-8137.2004.01228.x.)

Streelman, J.T. & Danley, P.D. 2003 The stages of vertebrate evolutionary radiation. *Trends Ecol. Evol.* **18**, 126-131.

Sturmbauer, C., Baric, S., Salzburger, W., Rüber, L. & Verheyen, E., 2001 Lake level fluctuations synchronize genetic divergences of cichlid fishes in African lakes. *Mol. Biol. Evol.* **18**, 144-154.

Svensson, E.I., Eroukhmanoff, F. & Fieberg, M. 2006 Effects of natural and sexual selection on adaptive population divergence and premating isolation in a damselfly. *Evolution* **60**, 1242-1253.

Takeda, S. & Murai, M. 2003 Morphological and behavioral adaptations to the rocky substrate by the fiddler crab *Uca panamensis* (Stimpson, 1859): preference for feeding substratum and feeding mechanism. *J. Exp. Mar. Biol. Ecol.* **287**, 179-191.

Taylor, G. M. 2000 Maximum force production: Why are crabs so strong? *Proc. Roy. Soc. Lond. B*. **267**, 1475-1480 (DOI 10.1098/rspb.2000.1167

Taylor, G. M. 2001 The evolution of armament strength: evidence for a constraint on the biting performance of claws of durophagous decapods. *Evolution* **55**, 550-560.

Thompson, J. N. 1999 Coevolution and escalation: Are ongoing evolutionary meanderings important? *Am. Nat.* **153**, S92-S93.

Thompson, J. D., Gibson, T. J., Plewniak, F., Jeanmougin, F. & Higgins, D. G. 1997 The ClustalX Windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acid Res.* **24**, 4876–4882.

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

Van Doorn, G. S., Dieckman, U. & Weissing, F. J. 2004 Sympatric speciation by sexual selection: a critical reevaluation. *Am. Nat.* **163**, 709-725.

Verheyen, E., Rüber, L., Snoeks, J. & Meyer, A. 1996 Mitochondrial phylogeny of rock-dwelling cichlid fishes reveals evolutionary influence of historical lake level fluctuations of Lake Tanganyika, Africa. *Phil. Trans. R. Soc. Lond. B*. **351**, 797-805.

Von Sternberg, R. & Cumberlidge, N. 1999 A cladistic analysis of *Platythelphusa* A. Milne-Edwards, 1887, from Lake Tanganyika, East Africa (Decapoda: Potamoidea: Platythelphusidae) with comments on the phylogenetic position of the group. *J. Nat. Hist.* **33**, 493-511.

Wainwright, P. C. & Reilly S. M. 1994 Ecological morphology: integrative organismal biology. The University of Chicago Press.

Warner, G. F. & Jones, A. R. 1976 Leverage and muscle type in crab chelae (Crustacea: Brachyura). *J. Zool. Lond.* **180**, 57-68.

West, K. & Cohen, A. 1994 Predator-prey coevolution as a model for the unusual morphologies of the crabs and gastropods of Lake Tanganyika. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* **4**, 267-283.

West, K. & Cohen, A. 1996 Shell microstructure of gastropods from Lake Tanganyika, Africa: Adaptation, convergent evolution, and escalation. *Evolution* **50**, 672-681.

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

West, K. & Michel, E. 2000 The dynamic of endemic diversification: molecular phylogeny suggests an explosive origin of the thiarid gastropods of Lake Tanganyika. *Adv. Ecol. Res.* **31**, 331-354.

West, K., Michel, E., Todd, J., Brown, D. & Clabaugh, J. 2003 The gastropods of Lake Tanganyika: Diagnostic key, classification and notes on the fauna. *International*

Association of Theoretical and Applied Limnology SIL. Occasional Publication **2**, 1-132.

Williams, T. R. 1961 The diet of freshwater crabs associated with *Simulum neavei* in East Africa. I. Crabs from west and east Uganda, collected by the Cambridge East Africa expedition, 1959. *Ann. Trop. Med. Parasit.* **55**, 128-131.

Williams, T. R. 1962 The diet of freshwater crabs associated with *Simulum neavei* in East Africa. II. The diet of Potamon berardi from Mount Elgon, Uganda. *Ann. Trop. Med. Parasit.* **56**, 362-367.

Wilson, A. B., Glaubrecht, M. & Meyer, A. 2004 Ancient lakes as evolutionary reservoirs: evidence from the thalassoid gastropods of Lake Tanganyika. *Proc. R. Soc. Lond. B* **271**, 529-536. (DOI 10.1098/rspb.2003.2624.)

FIGURES

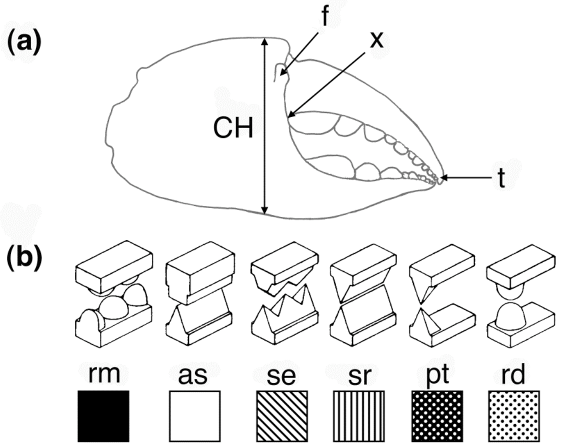


Figure 1. (*a*) Claw illustrating morphometric measurements and dimensions for force calculations. CH, claw height; L_0, distance from the fulcrum (f) to the site of force generation at the insertion of the dactyl closer muscle apodeme (x); L_1, distance from the fulcrum to the site of force application at the dactyl tip (t). L_0 and L_1 were measured for major claws only. (*b*) Mechanical analogues of claw occlusive regions. Based on newly moulted specimens we distinguished two basic crown shapes: rounded or molariform (rm), and serrated (se). If a difference existed in the shape of teeth on the dactyl and propodus, this was distinguished as an asymmetrical occlusive area (as). Further distinction was based on the occlusion of the claw tip region, which could have a sharp ridge (sr), with a blunt, rounded tip (rd), or with an acutely pointed, sharp tip (pt). Figure adapted from Brown et al. (1979).

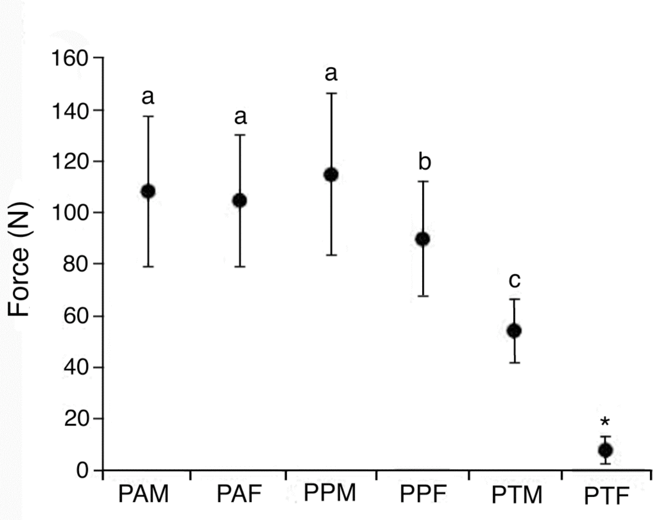


Figure 3. Comparison of major claw biting force (in Newton). Means with different letters are significantly different (Tukey's test: $P < 0.05$). PAM, *Platythelphusa armata* male (n = 39); PAF, *Platythelphusa armata* female (n = 38); PPM, *Potamonautes platynotus* male (n = 40); PPF, *Potamonautes platynotus* female (n = 42); PTM, *Platythelphusa tuberculata* male (n = 37); PTF, *Platythelphusa tuberculata* female (n = 36).

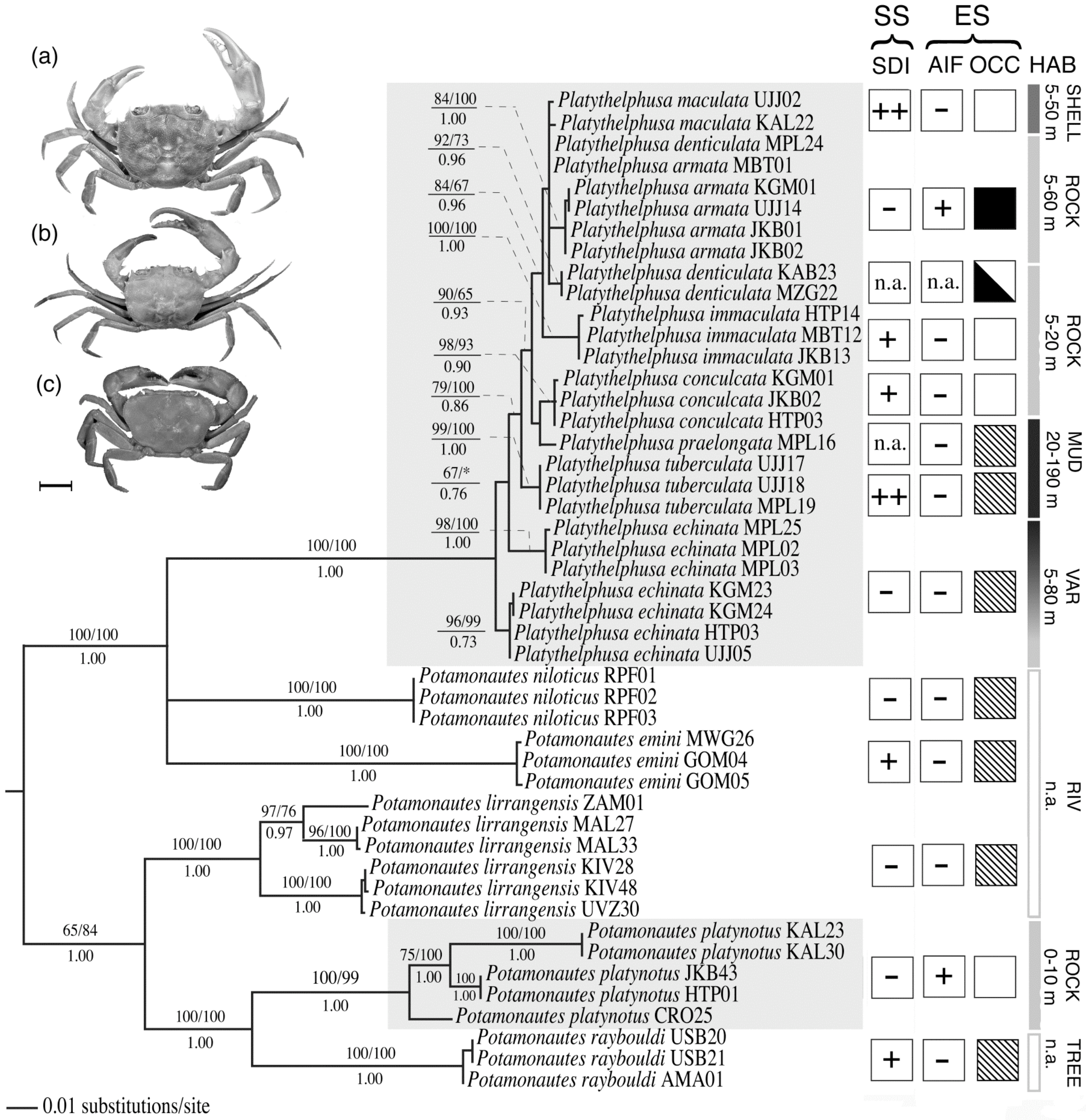


Figure 2. Maximum likelihood tree of Lake Tanganyika endemic crabs and outgroup taxa based on combined 16S rRNA and COII mtDNA sequences, with branch lengths proportional to the number of changes. Numbers above nodes denote maximum likelihood and parsimony bootstrap values, followed by Bayesian posterior probabilities. *Indicates support less than 60% in otherwise supported branches. Taxon labels indicate morphological species diagnosis and locality acronym (see supplementary material S1). Lake Tanganyika endemics are indicated with grey shading. (a) *Platythelphusa armata*; (b) *P. tuberculata*; (c) *Potamonautes platynotus* (all males). Scale bar = 20 mm; SS = proxies for sexual selection; ES = proxies for ecological selection; SDI = index of sexual dimorphism; AIF = index of asymmetry females; OCC = dominant occlusive geometry of female claw; white = asymmetric; black = rounded/molariform; hatched = serrated; n.a. = not available; - indicates values ≤ 1.4; + indicates values ≥ 1.4; ++ indicates values ≥ 1.8 (also see Fig. 1, Table 1); HAB = principal habitat information of adults; SHELL, empty *Neothauma tanganycense* shells; ROCK, rocky habitats; MUD, fine silt and mud; VAR, rocky- as well has mud habitats; RIV, rivers, streams and lakes; TREE, tree holes. Level of sympatry among Lake Tanganyika endemic species is indicated by similarity in colouration of vertical bars.

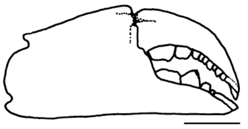
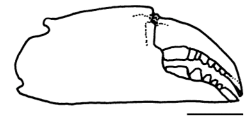
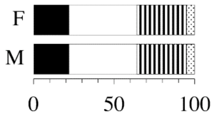
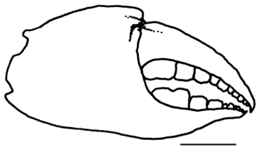
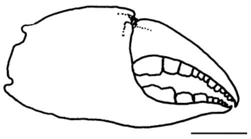
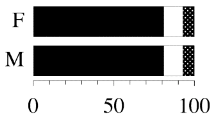
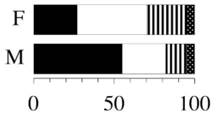
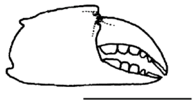
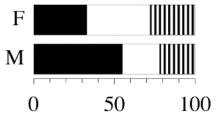
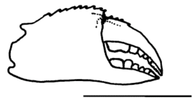
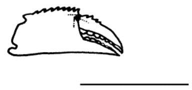
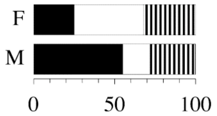
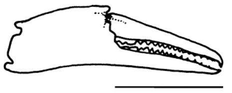
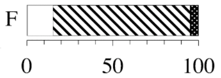
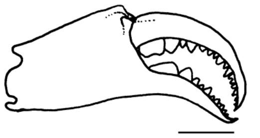
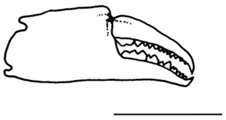
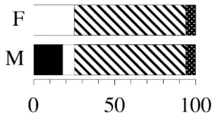
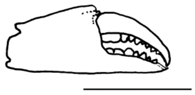
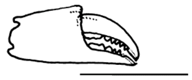
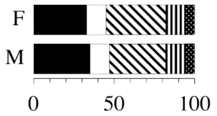
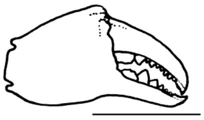
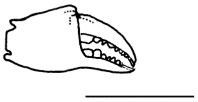
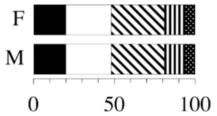
	Male	Female	Occlusion (%)	Dimensions	N	MA
Potamonautes platynotus				AIF 1.4 AIM 1.5 SDI 1.3	37 36 36	F 0.27 M 0.28
Platythelphusa armata				AIF 1.8 AIM 1.9 SDI 1.1	39 38 37	F 0.30 M 0.30
maculata				AIF 1.2 AIM 1.8 SDI **1.8**	19 18 18	F 0.22 M 0.29
immaculata				AIF 1.0 AIM 1.8 SDI **1.6**	15 12 12	F 0.26 M 0.29
conculcata				AIF 1.0 AIM 1.8 SDI **1.6**	23 19 15	F 0.26 M 0.29
praelongata	n.a.			AIF 1.1	1	F 0.18
tuberculata				AIF 1.1 AIM 1.6 SDI **1.9**	36 37 25	F 0.22 M 0.26
echinata				AIF 1.2 AIM 1.4 SDI 1.4	28 23 20	F 0.25 M 0.28
polita				AIF 1.6 AIM 1.8 SDI 1.4	22 16 14	F 0.27 M 0.29

Table 1. Characteristics of endemic Lake Tanganyika crab major claws, with diagrammatic characterization of occlusive geometry from claw base to tip (for description of occlusive analogues see Fig. 2). Taxa are ordered approximately conforming to phylogenetic affinity*. Note that different scales are used; scale bar = 10 mm; F = female and M = male; AIM = index of asymmetry males; AIF = index of asymmetry females; SDI = index of sexual dimorphism; N = number of specimens examined. MA = mechanical advantage.

*See Fig. 2. *Platythelphusa polita* was not included in the phylogenetic analyses; however, cladistic analyses suggest a basal position (Sternberg & Cumberlidge, 1999). *Platythelphusa denticulata* exhibits an extensive level of variability and is not included here (see text).

EXPLORING ECOLOGICAL CORRELATES OF SPECIES DIFFERENCES IN THE LAKE TANGANYIKA CRAB RADIATION

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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 (*Platythelphusa*) (Cumberlidge et al., 1999; Marijnissen et al., 2004; Reed and Cumberlidge, 2006). In spite of marked levels of phenotypic diversity within the Lake Tanganyika endemic crab clade, phylogenetic resolution based on mitochondrial markers is remarkably low (Marijnissen et al., 2006; Marijnissen et al., unpublished data). There is evidence that divergence of the platythelphusid clade is recent (Marijnissen et al., 2006), which could explain the apparent incongruence between phenotypic diversity and limited genetic divergence (e.g. Moran & Kornfield, 1993; Albertson et al., 1999). The approximate period of platythelphusid divergence 3.3-2.5 Myr ago (Marijnissen et al., 2006) corresponds to inferred periods of major cladogenesis in several Lake Tanganyika cichlid lineages (Duftner et al., 2005; Koblmüller et al., 2004, 2005, 2007), as well as the endemic *Synodontis* catfish species flock (Day & Wilkinson, 2006). It is likely that the contemporary divergence of these clades was induced by substantial environmental changes, when the lake level dropped considerably during a period of aridification in eastern Africa (Cane & Molnar, 2001). Subsequent phenotypic diversification and sympatric speciation may have taken place in novel ecological niches generated by lake level change-associated habitat changes. The theory of adaptive ecological speciation (Schluter, 2000) has been tested extensively in the African cichlid species flocks. There is increasing evidence that the outstanding phenotypic diversity and rapid speciation of these flocks is to a large extent facilitated by ecological niche diversification (Albertson & Kocher, 2006, and references therein). The platythelphusid radiation provides an excellent opportunity to test if the shared environmental history that significantly influenced vertebrate speciation patterns can have similar effects on other taxonomic groups.

There are some indications that ecological niche partitioning possibly played an important role in facilitating platythelphusid divergence. The majority of the nine platythelphusid species occur sympatrically, and up to five species can be found to coexist in rocky littoral areas (S.A.E. Marijnissen, personal observations). 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 (Evert, 1970; Marijnissen et al., 2004). Marked differences also exist in the shape and maximum size of the carapace (Marijnissen et al., 2004: table II). The small, rounded body of *P. maculata* Cunnington, 1899 and *P. polita* Capart, 1952 may be advantageous 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), and they appear to exhibit a preference for narrow crevices in rocky substrates (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 & Baron, 1991). Furthermore, comparative analyses revealed marked differences in claw functional morphologies between all platythelphusid species, indicating a considerable level of trophic partitioning (Marijnissen et al., unpublished data). Although there are thus several phenotypic clues to differentiation in resource use, it is still unknown to which extent platythelphusid species occupy distinct ecological niches.

The aim of this paper is to examine if the morphological species of *Platythelphusa* (Marijnissen et al., 2004) differ in ecological niche realisation, by combining data from habitat surveys, gut contents and stable isotope analyses. We include *P. denticulata*, although its taxonomic status is uncertain, and it has been proposed that this might be 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 different from that of the platythelphusid species with which it coexists. Determining ecological correlates of species differences in Lake Tanganyika endemic crabs is relevant not only from an evolutionary point of view, but it is also essential for conservation purposes. There is growing concern about the status of biodiversity in Lake Tanganyika (Cohen et al., 2005; McIntyre et al., 2005; Darwal et al., 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, 1990; Hori et al., 1993) and consumers of benthic organisms (e.g. West, Cohen & Baron, 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 implies high sensitivity to habitat disturbances. Alternatively, species might be functionally equal and diversity could be maintained through versatility (Bellwood et al., 2006).

Because this is the first study to empirically examine the ecology of the Lake Tanganyika crabs, our approach is exploratory rather than diagnostic. Our data show substantial overlap of niche parameters among individuals of sympatric species in the rocky littoral zone. Concomitantly, there is evidence of interspecific ecological differentiation based on depth and substrate type. Furthermore, we found significant differences in mean stable isotope signatures between sympatric species. We consider these 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 my) and deepest (max. 1470 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 10-1000 m, but even on smaller scales substrates can be highly 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 (figure 1). The substrate at 12 sites (MWG to ZGU) was composed of boulders, cobbles, pebbles, and/or aggregations of empty *Pleiodon spekii* (Woodward, 1859) freshwater mussel shells, interspersed with sand. Four sites were situated west of a river delta (Luichi river, see figure 1), where the substrate consisted of mud alternating with extensive shell beds of the endemic gastropod *Neothauma tanganyicense* Smith, 1880, and *Coelatura burtoni* (Woodward, 1859) shell hash.

Habitat specificity

To provide relatively exhaustive 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 was 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, Cumberlidge 1999: 324; Marijnissen et al., 2004: table II) 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), and aggregations of *Pleiodon spekii* or *Neothauma tanganyicense*. Information about the habitat of *P. tuberculata*, which can occur to depths of 190 m (Coulter, 1991), was obtained by combining catch data 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 figure 1) in rocky littoral areas. At each site, divers established 20 replicate 50*50 cm quadrats at 5 m depth. The slope of the substrate was recorded for each quadrat. We also collected 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, as well as the relative amount of organic and inorganic matter, following the method used by McIntyre et al. (2005). By firmly emplacing 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, and homogenized. Subsamples were collected on precombusted glass-fibre filters (Whatman GF/C, Maidstone, UK). One subsample was extracted in 90% ethanol for 24 hours, and analysed for chlorophyll *a* after acidification (Moed & Hallegraeff, 1978). Another subsample was dried to a constant mass at 60ºC, weighted, combusted at 500ºC for three hours, 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 depth). After log (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 (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 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 50 bins were used on both axes (2500 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 tests of normality indicated that the data deviated significantly from normality and would not follow a normal distribution following appropriate transformations ($P<0.001$). Because of our large sample size ($N=1734$) parametric methods are nevertheless 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 $\alpha=0.05$ 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 figure 1) 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 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% 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 $(N_1/N_2)*100$, where N_1 is the number of individual crabs that consumed food item x, and N_2 represents the total number of individuals.

Stable isotope analyses

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. 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 $\delta^{13}C$ and $\delta^{15}N$. To examine patterns of trophic segregation between species, a dual-isotope plot $\delta^{13}C$ and $\delta^{15}N$ 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 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 1401 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 *Neothauma tanganyicense* shells near the outlet of the Luichi River (figure 1), where the substrate is comprised of silt and mud. Out of a total of 1805 crabs that were collected during our surveys, the numbers of individuals per species decreased in the following order: *Platythelphusa 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 0-30 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 (figure 1), at depths ranging from 50 to ≥ 100 m. Most of the sediments on this platform are comprised 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 the Principal Coordinates Analysis (PCO) based on the surveys of substrate type across depths (0-30 m) are shown in figure 2. 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 ($\text{Pseudo-F}_{5,321} = 10.029$, $P < 0.001$). 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 ($P > 0.05$).

Additional information on species habitat specificity was obtained from the quadrat surverys at 5 m depth within the rocky littoral zone. The first two axes of the PCO explained 64.2 % and 24.6 % respectively of the total variance in the species dataset (figure 3, 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 relative snail abundance and inorganic matter, while *P. immaculata* was only associated with slope, total organic matter and chlorophyl *a*. Significant differences were found among species ($\text{Pseudo-F}_{7,1463} = 108.680$, $P < 0.001$). 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* ($P = 0.490$), *P. denticulata* and *Po. platynotus* ($P = 0.554$).

Both the mean body size (carapace width) as well as the life stages of crabs had a significant effect on 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 (figure 4).

Diet composition

We collected a total of 574 adult crabs for dietary analyses, of which 386 had ≥ 50% full foreguts. Figure 5 shows the diet composition of the six species that were included in the gut content analyses. 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., *Surirella* sp.), and green algae (*Oocystis* sp. *Ulothrix* sp.) as well as cyanobacteria (*Anabaena* sp. *Chroococcus* sp. *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 Tangayikan genera *Lavigeria*, *Stormsia/Reymondia* and *Vinundu*. Gut contents revealed no apparent differences in the types of dietary constituents that were ingested between 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.

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 ($\text{Pseudo-F}_{6,94} = 23.622$, $P < 0.001$). There was no difference between sexes ($\text{Pseudo-F}_{1,94} = 0.008$, $P = 0.920$), nor was there a significant interaction ($\text{Pseudo-F}_{6,94} = 1.453$, $P = 0.165$). 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 figure 6. 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 $\delta^{13}C$ as well as $\delta^{15}N$ values (table 3).

Discussion

The combined evidence from our habitat surveys and dietary analyses indicates that species diversity of the Lake Tanganyika crabs is to some extent supported by partitioning of ecological niche variables. Our results corroborate previous indications that *P. tuberculata* exhibits a distinct preference for deeper parts of the lake (Coulter, 1991; Marijnissen et al., 2004), and this species was not found in rocky littoral habitats. In spite of extensive survey efforts, we did not find *P. praelongata* at our study sites. This species is thought to be sympatric with *P. tuberculata* in deep lake habitats, and has thus far only been found in the southernmost part of the Lake Tanganyika basin (Marijnissen et al., 2004). Our surveys show that *P. maculata* exhibits a marked preference for empty *N. tanganyicense* shells. Although we did not find *P. polita* at any of our present study sites, this species is known from several localities along the northern, southern and western shorelines of the lake, and its habitat preferences appear to be similar to those of *P. maculata* (Cumberlidge et al., 1999, and references therein). The following seven species occur sympatrically in rocky littoral areas: *P. armata*, *P. conculcata*, *P. denticulata, P. echinata*, *P. immaculata*, and *Potamonautes platynotus.* The latter species is unique among the lake's endemics 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.

The results of the Principal Coordinates Analyses (PCO) demonstrate that a substantial amount of overlap exists in habitat specificity among individuals of the different species (figure 2 and 3). Pairwise tests based on the Ochiai similarity index nevertheless revealed significant differences among the majority of species. It should be noted that our comparisons could be biased by the limited 5 m depth quadrat data from *P. denticulata* (n=8). If differences based on pairwise comparisons with *P. denticulata* are not taken into account, this implies that all platythelphusid species as well as *Po. platynotus* show overlapping patterns with respect to the habitat variables that were measured at 5 m depth (slope of the substrate, amount of inorganic matter, organic matter, chlorophyll *a*, and snail abundance). The results of the substrate type surveys across depths indicate that although individual crabs can be associated with a wide variety of habitat variables, the majority of individuals within species exhibit overall similarity in habitat specificity. Differentiation in habitat specificity within the rocky littoral appears to be mainly a function of substrate size (figure 4). Adults of small-bodied species such as *P. conculcata*, *P. immaculata*, and *P. echinata* are partially mitigated 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 substrate type selection. 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). 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 revealed marked differences among the endemic Lake Tanganyika crab species, indicating a considerable level of trophic divergence (Marijnissen et al., unpublished data). In contrast, our gut content analyses showed no clear evidence of specialization (figure 5). 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 values 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 indicating that *P. armata* is a highly derived molluscivore (West et al., 1991; West & Cohen, 1994; Rosales et al., 2002; Marijnissen et al., unpublished data; 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 that they reflect a spatio-temporal integration of the composition of assimilated food, and are thus useful in providing additional insight in questions of dietary partitioning. Comparison of mean $\delta^{13}C$ and/or $\delta^{15}N$ values between our focal taxa revealed that signatures of individual specimens show considerable overlap. However, there were significant differences in mean $\delta^{13}C$ and/or $\delta^{15}N$ 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).

The platythelphusid clade adheres to at least three out of four criteria that characterize adaptive radiations (Schluter, 2000): (i) common ancestry, (ii) rapid divergence, and (iii) differentiation in functional traits (Coulter, 1991; Marijnissen et al., 2006; Marijnissen et al., unpublished data). 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 possibly signifies some resilience to habitat disturbance. It is possible that niche partitioning occurs along variables that we haven't yet measured. However, we have addressed the most common ecological niche segregation variables in this study and our data should thus 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- 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, Kidd & Kocher, 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 et al. unpublished data), but this remains to be tested. 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, Baric & Sturmbauer, 2002; Smith, Konings & Kornfield, 2003; Schliewen & Klee, 2004; Schelly et al., 2006; Koblmüller et al., 2007). It is readily conceivable that the 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 pressing 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

This work would not have been possible without the invaluable help of George Kazumbe with the fieldwork in Lake Tanganyika. Martin Genner and Pete McIntyre provided comments on the stable isotope analyses; Christine Cocuyt, Hilde Eggermont, Jon Todd, and Koen Martens helped with identification of algae and invertebrates for gut content analyses; Jan van Arkel (Institute for Biodiversity and Ecosystem Dynamics) helped with the figures; Keith Ursel, Sven Lange, and Fred Schram provided support. We thank the Gombe Stream Research Centre for facilitating surveys along the coastline of Gombe National Park. We are grateful to the Tanzanian Commission for Science and Technology for permission to conduct research at Lake Tanganyika. The Tanzanian Fisheries Research Institute, Kigoma, D. Chitamwebwa and Mr. Muhosa, as well as the Nyanza Project (NSF Paleoclimates ATM 0223920) are thanked for logistical assistance. This research was supported by grants from the Netherlands Foundation for the Advancement of Tropical Research (WOTRO W84-489), the Schure-Beijerinck-Popping Fund of the Royal Netherlands Academy of Arts and Sciences (SBP/JK/2003-27, and SBP/JK/2002-25), Iso-analytical Limited, VSB Fund, Stichting Vrijvrouwe van Renswoude te 's Gravenhage, STUNT Fund, Genootschap ter Bevordering van de Natuur- Genees- en Heelkunde, Stichting AUV Fonds, and Stichting Fonds Dr. Christine Buisman. Finally, we would like to thank the organizers of the SIAL IV symposium in Berlin for the opportunity to present our results in a stimulating forum, with particular thanks to Frank Riedel, Annette Kossler and Thomas Wilke.

Literature cited

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.

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 (9146-1947), 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. Oxford University Press, London, UK.

Cumberlidge, N., 1999. The freshwater crabs of West Africa, family Potamonautidae. Faune et Flore Tropicales 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.

Darwal, W., Smith, K. Lowe, T. & Vié, J.-C. 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.

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 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., 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., 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.

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.

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

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

Marijnissen, S. A. E., F. R., Schram, N. Cumberlidge & E. Michel, 2004. Two new species of *Platythelphusa* A. Milne-Edwards, 1887 (Decapoda, Potamoidea, Platythelphusidae) and 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, 2005. Individual- and assemblage-level effects of anthropogenic sedimentation on snails in Lake Tanganyika. Conservation Biology 19: 171-181.

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.

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.

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). Freshwater Biolology *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.

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 of 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.

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.

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 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 coevolution. Evolution 45: 589-607.

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). Jounral of Experimental Marine Biology and Ecology 52: 103-113.

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

FIGURES AND TABLES

Table 3. Pairwise distances (Tukey's test) of mean δ^{13}C and δ^{14}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	*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 difference of means at α=0.05; ns is non-significant difference at α=0.05.

Table 1**.** Percentage of variation explained by individual axes of Principal Coordinates Analysis of the parameters relating to figure 2.

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

Table 2. Percentage of variation explained by individual axes of Principal Coordinates Analysis of the parameters relating to figure 3.

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

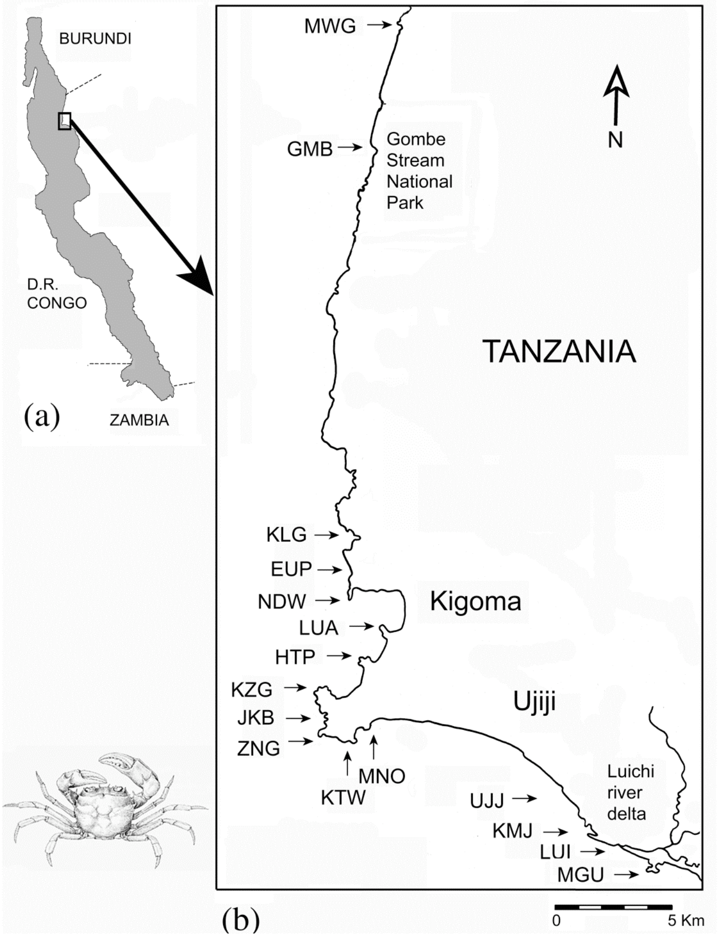

Figure 1. (a) Map of Lake Tanganyika, and (b) study sites that were surveyed for crab habitat specificity. Acronyms (local names in brackets): MWG = Mwamgongo village; GMB = Gombe Stream National Park; KLG = Kalalangabo (Lemba village); EUP = Euphorbia (Kasazi Hill); NDW = Nondwa Point; LUA = Luansa 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.

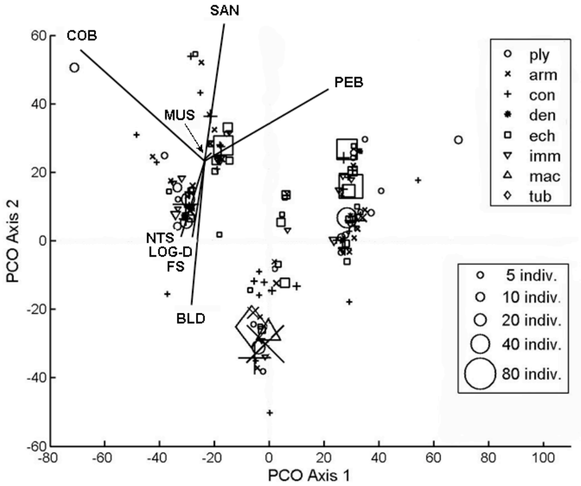

Figure 2. Principal coordinate (PCO) ordination plot of the two first axes of crab species habitat specificity based on random surveys of different substrate types across depths (0-30 m) at 16 sampling sites along the Tanzanian coastline of Lake Tanganyika. Species abbreviations: arm = *Platythelphusa armata*; con = *P. conculcata*; den = *P. denticulata*; ech = *P. echinata*; imm = *P. immaculata*; mac = *P. maculata*; tub = *P. tuberculata*; ply = *Potamonautes platynotus*. 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.

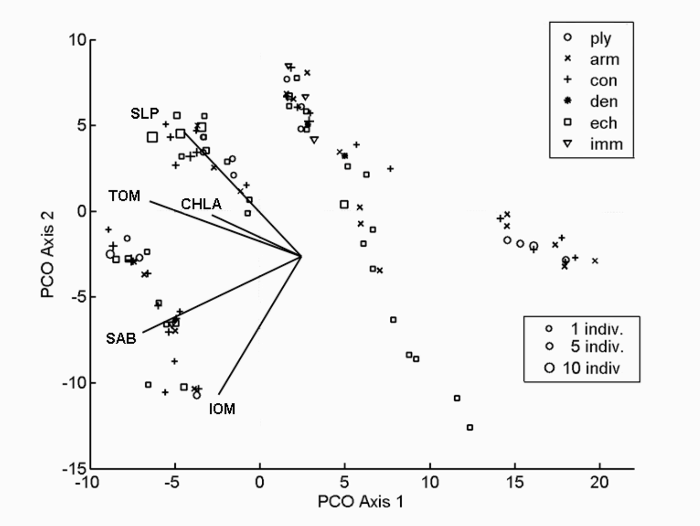

Figure 3. Principal coordinate (PCO) ordination plot of the two first axes of crab species habitat specificity within the rocky littoral zone at 5 m depth in Lake Tanganyika. Species abbreviations as in figure 2. The relative size of the symbols is proportional for the number of individual observations 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.

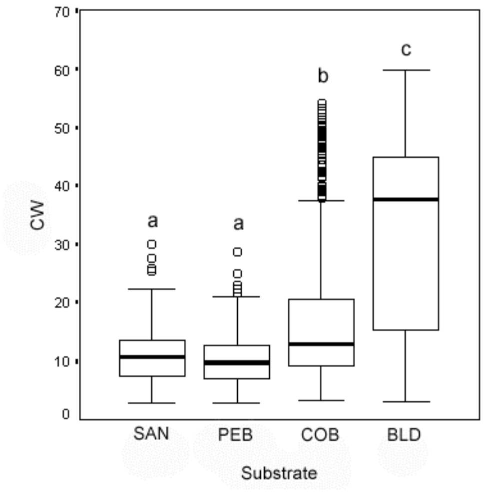

Figure 4. Distribution of crab carapace widths (CW) among different substrate types in the rocky littoral zone. Box plots represent CW median, and interquartile range with whisker ends corresponding to the first and the last decile. Individual observations beyond these limits are plotted as circles. Abbreviations as in figure 2. Different letters above box plots indicate significant differences at α = 0.05 (Tukey's test: P < 0.001).

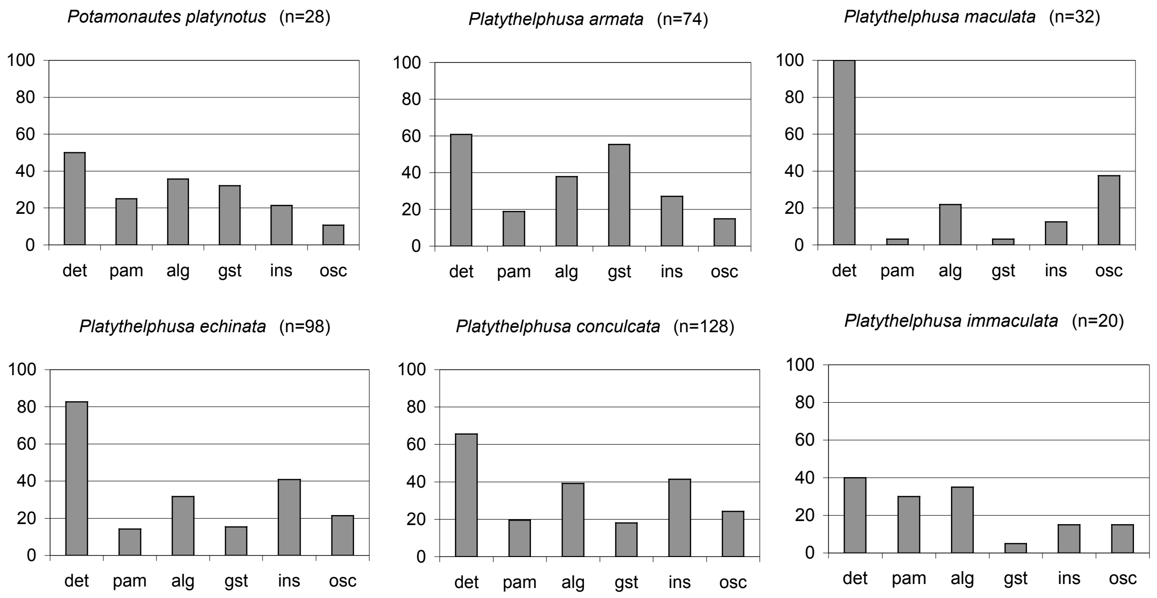

Figure 5. Percentage occurrence of the various food categories in the six species analysed. Numbers of specimens analysed per species are shown in brackets. *Potamonautes platynotus* n = 28; *Platythelphusa armata* n = 74; *P. maculata* n = 32; *P. echinata* n = 98; *P. conculcata* n = 128; *P. immaculata* n = 20. Det = detritus; pam = vascular plant matter; alg = algae; gst = gastropods; ins = aquatic insects; osc = ostracods.

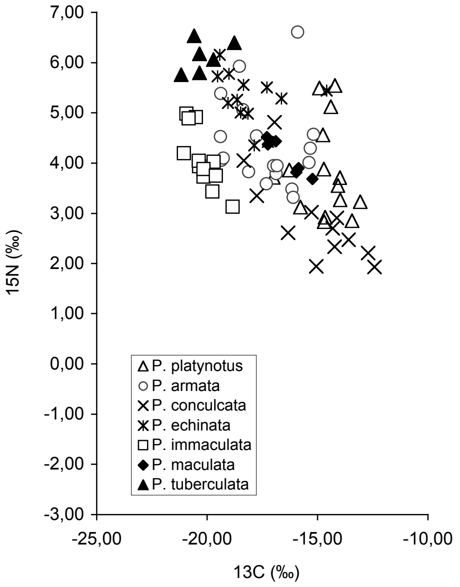

Figure 6. Stable carbon and nitrogen isotope signatures of Lake Tanganyika endemic crab species. Each data point represents an individual organism.

CONSERVATION OF FRESHWATER SPECIES DIVERSITY IN LAKE TANGANYIKA: FOCUS ON THE ENDEMIC CRAB FAUNA

5

INTRODUCTION

Freshwater habitats and the species they support are among the most threatened ecosystems worldwide (Dudgeon 2000; Abell 2001; Beeton 2002; Jenkins 2003; Dudgeon et al. 2005; Revenga et al. 2005; Thieme et al. 2005; Abell et al. 2007). This problem is particularly pressing in the African Rift Valley region, where the need for reliable freshwater resources is increasing due to rampant population growth while degradation of freshwater habitats continues unabated (Ogutu-Ohwayo et al. 1997; Odada et al. 2003, 2004; Darwall et al. 2005; UNEP 2005; Olago & Odada 2007). The African Great Rift Valley Lake Tanganyika provides a classic example of the problems associated with the need to provide essential resources for expanding human populations and simultaneously conserving biodiversity.

Conservation of biodiversity in Lake Tanganyika is important for several reasons. The lake is a globally significant hotspot of freshwater biodiversity and endemicity (Groombridge & Jenkins 1998). Although species numbers vary according to taxonomic authority, estimates suggest that the lake contains almost 1500 species in total (Coulter 1991). Approximately 500 species are endemic to Lake Tanganyika, including 162 fish species (Genner et al. 2004), 65 gastropod species (West et al. 2003), 80 ostracod species (Park & Downing 2000), 13 shrimp species (Fryer 2006) and 10 crab species (Marijnissen et al. 2004; Reed & Cumberlidge 2006). The lake basin includes two Ramsar Sites, namely the Rusizi River Delta in Burundi and the Malagarasi-Muyovozi Floodplains in Tanzania (Ramsar 2007). Moreover, Lake Tanganyika contains approximately 17% of the world's surface freshwater supplies. The lake provides an important source of drinking- and domestic water, means of transportation and direct or indirect economic venues for an estimated total of 10 million people in its four riparian countries (Mölsä et al. 2005). Lake Tanganyika sustains the second largest inland fishery on the African continent (Mölsä et al. 1999). An estimated 45.000 people are directly involved in its fisheries, which supply between 25-40% of the protein needs of local communities (Jorgensen et al. 2005). Maintaining the integrity of Lake Tanganyika's aquatic ecosystem is thus of crucial importance not only to the survival of its endemic fauna, but also to the millions of people that depend on the lake and its natural resources for their subsistence.

In general, the conservation of tropical freshwater biodiversity is hampered by a dearth of essential ecological data (Dudgeon 2000, 2003; Abell 2001). Available data relevant to the conservation of aquatic species is heavily skewed towards fish (Abell 2001; Strayer 2006). Furthermore, there is increasing concern that the emphasis of applied research on economically important taxa reduces the capacity to understand the functioning of aquatic ecosystems as a whole (Denny 2000, 2001; Moss 2000; Meester & Declerck 2005; Lévêque et al. 2005; Moustakas & Karakassis 2005). To better understand patterns of freshwater biodiversity and the functioning of aquatic ecosystems, data on key functional groups is critical. We here use benthic faunal communities in Lake Tanganyika as a case study for examining ramifications for conservation decisions. Our main focus will be on endemic crabs. Assessments conducted in the framework of an evaluation of the status and distribution of freshwater biodiversity in Eastern Africa (Darwall et al. 2005) indicate that Lake Tanganyika and its catchment basin are regionally important areas of freshwater crab species diversity (e.g. Cumberlidge et al. 2006). Furthermore, a preliminary evaluation based on museum collection data and pilot surveys (Cumberlidge & Marijnissen 2004c, e, h) tentatively listed two of the ten endemic crab species (*Platythelphusa denticulata* and *P. praelongata*) from Lake Tanganyika as vulnerable (VU D2), and one (*P. immaculata*) as near threatened (NT B1ab(i); D1) under version 3.1 (2001) of the IUCN Red List of Threatened Species.

In marine ecosystems, decapod crabs are known to be important predators that can limit the distribution and abundance of their food resources (Smith et al. 1991; Lee and Kneib 1994; Bertness et al. 2003; Silliman et al. 2004). It has also been shown that crabs can act as keystone predators in marine trophic cascades by suppressing densities of grazers and indirectly enhancing plant biomass (Silliman & Bertness 2002; Trussell et al. 2002). In terrestrial systems, land crabs can be important in the control and maintenance of tropical forests, through differential herbivory and manipulation of significant quantities of leaf litter (O'Dowd & Lake 1990; Green et al. 1997; Sherman 2003). In freshwater ecosystems, crabs are expected to play key roles because of their relative abundance and dominance in terms of biomass (Turnbull-Kemp 1960; Hill & O'Keeffe 1992; Somers & Nel 1998; Dobson et al. 2007a, b), their potential to link terrestrial and aquatic energy flows (Gherardi & Vannini 1989; Gherardi et al. 1989; Dobson et al. 2002; Moss 2005) and their central position in aquatic foodwebs as primary and secondary consumers (Williams 1961, 1962; Gherardi et al. 1987; Harrison 1995). Furthermore, crabs are effective indicators of pollution and general aquatic ecosystem health (Schuwerack et al. 2001; Bowen & Depledge and references therein). Although these qualities make it relevant to include crabs in monitoring schemes, efforts to obtain data for conservation purposes in Lake Tanganyika have thus far neglected the endemic crabs (e.g. Allison et al. 2000; but see Darwall et al. 2005). The current lack of knowledge on the functional role of crabs in Lake Tanganyika's foodwebs limits our ability to predict the impact of human-induced environmental disturbances on benthic communities and ultimately on lake fisheries that depend on benthic food resources.

The objective of this paper is to provide baseline empirical data on the endemic crabs that can serve as a framework for initiatives aiming to preserve benthic species diversity in Lake Tanganyika. Specifically, we aim to (i) examine patterns of crab species distributions and abundance across sites and depths; (ii) determine the functional role of the endemic crabs in Lake Tanganyika's aquatic ecosystem, and (iii) infer the level of vulnerability of the endemic crab fauna to habitat perturbations. Furthermore, we discuss general implications for the conservation of species diversity in Lake Tanganyika.

METHODS

Study system and sites

Lake Tanganyika is situated in the western branch of the African Great Rift Valley, and is bordered by Burundi, Tanzania, Zambia and the Democratic Republic of Congo. It is the oldest (approximately 9-12 my) and deepest (max. depth 1470 m) lake in Africa (Cohen et al. 1997; Scholtz & Rosendahl 1988; Tiercelin & Mondeguer 1991). The deepest parts of the lake are anoxic, and only oxygenated water is only found in the upper 100-250 m (Coulter 1991). Different substrate types are interspersed along the shoreline on scales of 10-1000 m, but even on smaller scales substrates can be highly patchy (Michel et al. 2004). Most of the lake's shoreline is rocky and steeply sloped, and consists of a narrow fringe that rapidly drops to > 50 meters depth over distances of less than a kilometer. Predominantly sandy or muddy areas with more gentle slopes are present near the outlet of large rivers such as the Malagarasi in Tanzania, and the Rusizi in Burundi. Within an area of approximately 50 km along the Tanzanian shoreline of the lake, we selected 12 study sites that were surveyed between 2001 and 2004 (Figure 1). Nine sites (MWG to ZGU) were situated in rocky littoral areas where the substrate is composed of boulders, cobbles, pebbles, and/or aggregations of empty *Pleiodon spekii* (Woodward, 1859) freshwater mussel shells, interspersed with sand. Among our nine rocky littoral study sites, five were adjacent to deforested areas (MWG, KLG, NDW, LUA, HTP) and four were adjacent to areas with relatively natural vegetation (MTB, EUP, JKB, KTW). Three additional study sites (KMJ, LUI, MGU) were situated west of a river delta (Luichi river, see Figure 1), where the substrate consists of mud alternated with extensive shell beds of the endemic gastropod *Neothauma tanganyicense* Smith, 1880, and *Coelatura burtoni* (Woodward, 1859) shell hash.

Abundance and species distributions

To determine a sampling strategy, a preliminary study was conducted in 2002 at two sites in Lake Tanganyika (HTP and JKB). SCUBA divers randomly established 20 replicate 50*50 cm quadrats at four depths (5, 10, 20, 30), and collected all crabs within each quadrat. The results indicated that crabs are absent from entirely sandy substrates (i.e. not interspersed with cobbles, boulders, or rocks). Furthermore, mean densities of crabs below 20 m depth at these two sites were ≤ 0.7 ($\pm$ 1.5) individuals per m^2 with > 80% of quadrats yielding 0 individuals. Based on these results, it was decided to use a stratified random sampling strategy focusing on 5, 10, and 20 m depth. The three sites west of the Luichi River delta were only sampled at a depth of approximately 10 m. SCUBA divers established 20 replicate 50*50 cm quadrats at each depth. Within each quadrat, all cobbles and boulders were turned over to check for the presence of crabs. At the three sites near the Luichi River delta (KMJ, LUI, MGU) all *Neothauma tanganyicense* shells within each quadrat were collected, transported to the surface and checked for the presence of crabs. Each individual crab was determined, sexed and measured. Only crabs with a carapace width of ≥ 10 mm were used for our analyses. The algorithms provided by Krebs (1999) were used to calculate statistical parameters and confidence intervals of density estimates. To obtain a tentative estimate of crab biomass, we used a power function that was derived from potamonautid crabs in Kenyan rivers (Dobson et al 2007a):

$$\log(\text{dry mass}) = -3.75+2.89\log(CW)$$

where mass is measured in grams and CW (carapace width) in millimeters.

Variation in crab species composition among different study sites was analyzed with multidimensional scaling (MDS) and principal component analysis (PCA). In all analyses, quadrats were pooled for each site and depth combination. We performed MDS on a matrix of species abundance to generate a measure of the community similarity between samples based on the Bray Curtis index. This index is frequently used for ecological ordinations and it has excellent properties for ordination of species data (Legendre & Gallagher 2001; Cleary 2003; Cleary & Genner, 2004; Cleary & Mooers, 2004). MDS analyses were conducted using the CRAN package MASS in R (http://www.r-project.org). Prior to performing PCA, we transformed the species abundance data because of inherent problems of Euclidean-based distance metrics (in standard PCA) for community data (Legendre & Gallagher 2001). The species abundance matrix was transformed using the Vegan CRAN package (http://cc.oulu.fi/~jarioksa/softhelp/vegan.html) in R, so that subsequent analyses preserved a specific distance among objects (sample sites). In this case, we used the Hellinger distance (Rao 1995; Legendre & Gallagher 2001). PCA was performed using the ADE4 CRAN package (http://pbil.univ-lyon1.fr/ADE-4/) in R.

Variation in species richness and evenness was tested for significance among depths and sites using a two-way Permanova in PRIMER v6 (Primer-E Ltd, Plymouth, UK) with depth as a fixed factor and site as a random factor. Variation in the incidence of species (number of plots occupied per site) among sites, species and depth was tested for significance with a three way Permanova with depth and species as fixed factors and site as a random factor.

Stable isotope analyses

To determine the trophic position of crabs in benthic foodwebs, stable isotope analyses were conducted. Values of $\delta^{15}N$ are typically used to characterize relative trophic positions of focal organisms, while $\delta^{13}C$ values can be useful to determine the source and flow of carbon in a food web (Peterson & Fry 1987). Crabs as well as samples of potential food resources were collected between August and November 2002. Samples for stable isotope analyses were collected from three sites (HTP, JKB and KMJ) along the Tanzanian shoreline of Lake Tanganyika (Figure 1). Samples of the deep-lake dwelling species *Platythelphusa tuberculata* 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) of the following endemic crab species: *Platythelphusa armata*, *P. conculcata*, *P. echinata*, *P. immaculata*, *P. maculata*, *P. tuberculata*, and *Potamonautes platynotus*. Each individual specimen was measured and sexed, after which a piece of leg muscle tissue was dissected.

Potential food resources included algae, terrestrial-derived plant litter, detritus, aquatic insect larvae, and gastropods. Samples were collected from the following endemic gastropod species: *Lavigeria coronata*, *L. grandis*, *L.* new sp. J., *L.* new sp. M., *L. nassa, L. paucicostata*, *Paramelania damoni*, *Reymondia horei*, *Spekia zonata*, and *Vinundu guillemei* (see West et al. 2003 for species descriptions), as well as the bivalve *Coelatura typica* (Leloup 1950). At least four individuals were collected per gastropod species. After each shell was measured a piece of muscle tissue was dissected from the gastropod foot. Aquatic insect larvae were homogenised entirely, and pooled according to taxonomic group (caddisflies, mayflies, and midges). Detritus samples were acidified with 1 M HCl to remove inorganic carbonates, and rinsed with distilled water. Terrestrial plant matter was obtained from woody debris and leaves that were found on the lake floor. Periphyton was scrubbed from the top of cobbles, and processed using a colloidal silica separation technique (Hamilton & Lewis 1992). Each sample was homogenised and approximately 5 ml of slurry was transferred to a tube containing a 70% Ludox colloidal silica solution, which was centrifuged at 1000 rpm for 15 minutes. The uppermost layer containing the algal fraction was removed, and the separation procedure was repeated. The clean algal fraction was then vacuum-filtrated onto a precombusted filter, and rinsed with distilled water to remove excess silica.

All samples for isotope analyses were transferred onto ethanol-cleaned aluminium foil, and dried until constant weight at 60°C for ≥ 48 hours. 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 $\delta^{13}C$ and $\delta^{15}N$. To examine patterns of trophic segregation between species, a dual-isotope plot $\delta^{13}C$ and $\delta^{15}N$ values was constructed.

RESULTS

Abundance and species distributions

A total of 892 individual crabs with a carapace width ≥ 10 mm (range 10.0-56.8 mm, average 17.8 ± 8.9 mm) were collected in a total of 600 quadrats. *Platythelphusa polita* and *P. praelongata* were not found during our quadrat surveys. We could not obtain density data on *P. tuberculata* using quadrats, since this species occurs predominantly in habitats that are below safe SCUBA diving depths (e.g. this thesis, Chapter 4). Distribution patterns were patchy, and median values of individuals per quadrat were generally low, often zero. Densities at the nine rocky littoral sites ranged from 0-28 crabs m^{-2}. Densities at the three soft substrate sites near the outlet of the Luichi River ranged from 0-8 crabs m^{-2}. Mean densities of quadrats pooled for each depth ranged from 2.0 ± 1.2 to 12.2 ± 5.9 crabs m^{-2} (Figure 4).

Estimates of crab dry mass were highly variable, and ranged from 0.0-117.7 g m^{-2}. Mean biomass estimates of quadrats pooled for each depth ranged from 0.9 ± 0.7 to 21.0 ± 21.7 g m^{-2} (Figure 2). Biomass was not equally distributed across size classes (Figure 3). *Platythelphusa armata* and *Po. Platynotus* contributed disproportionately with carapace widths exceeding 40 mm (5.3% of the total amount of individuals collected), which accounted for 42.5% of the total dry mass.

Rarefied species richness varied from 1.8 species ($n = 19$) at EUP to 5.0 species at JKB (Figure 4). There was considerable variation among sites with respect to depth trend in species richness. For example, species richness at JKB and KLG decreased and increased respectively with increasing depth. Evenness ranged from 0.3 at EUP to 1.0 at LUA (Figure 4). There were no significant differences in either species richness (Permanova, Pseudo-F = 1.006, P = 0.335) or evenness (Permanova, Pseudo-F = 1.028, P = 0.329) among depths. In contrast to species richness and evenness, there were significant differences in incidence of species (Figure 5) among depths (Permanova, Pseudo-F = 7.115, P = 0.005) and species (Permanova, Pseudo-F = 9.779, $P < 0.001$). There was also significant interaction among depth and species (Permanova, Pseudo-F = 6.840, $P < 0.001$). There was a considerable range in the incidence and total number of individuals for each species observed per site across depths. Incidence of the different crab species did not differ between 5 and 10 m depth but both depths had a significantly higher incidence ($P < 0.05$) than 20 m depth. Overall, incidence of *P. conculcata* and *P. echinata* was significantly higher than *P. denticulata*, *P. immaculata* and *P. maculata*. Furthermore, incidence of *P. armata* was significantly higher than *P. denticulata* and *P. maculata.*

The results from MDS reveal no obvious associations between species and sites, but suggest that species distributions are associated with depth. Shallow (5 m) quadrats predominantly occur at low (negative) dimension 1 values, and deeper quadrats (10 and 20 m) at higher (positive) dimension 1 values. The first two axes of the PCA explained 59.2% of the variance, and revealed marked differences among species (Figure 6), which can be explained by site-depth combinations. For example, compared to other species *P. armata* and *Po. patynotus* were more prevalent in shallow habitats at MTB and MWG, *P. conculcata* in shallow habitats at JKB, *P. echinata* in deeper (20 m) habitats at EUP and JKB, and *P. maculata* in the Luichi River delta (KMJ, LUI, MGU).

Stable isotope signatures

Mean stable isotopic signatures ranged from –15.0 to –20.2 ‰ δ^{13}C and from 2.9 to 6.1 ‰ δ^{15}N for the different crab species. There was considerable variability among the mean stable isotope values of potential food resources (Figure 7). Isotopic signatures of endemic Lake Tanganyika gastropods diverged in two separate groups. The first group included *Lavigeria* sp. M, *Paramelania damoni*, *Reymondia horei*, *Spekia zonata*, and *Vinundu guillemei*, with mean isotope values ranging between –16.0 to –19.2 ‰ $\delta^{13}C$, and 0.7 to 1.8 ‰ $\delta^{15}N$. The second group included *L. coronata*, *L. grandis*, *L.* sp. J., *L. nassa*, and *L. paucicostata*, with mean isotope values ranging between–10.7 to –12.3 ‰ $\delta^{13}C$, and –0.5 to –1.7 ‰ $\delta^{15}N$. Mean values for detritus differed between sites, ranging from –9.5 to -15.4 ‰ $\delta^{13}C$ and –1.9 to 1.2 ‰ $\delta^{15}N$. Mean ^{13}C signatures of *P. armata*, *P. conculcata*, *P. echinata*, *P. immaculata* and *Po. platynotus* were depleted by -3.53 to -10.68‰ relative to detritus collected in rocky littoral habitats, and mean ^{13}C signature of *P. maculata* was enriched by 2.3‰ relative to detritus collected in the Luichi River delta. All crab species were enriched in mean $\delta^{13}C$ isotopic signatures relative to bivalves (*Coelatura typica*) aquatic insect larvae (caddisflies, mayflies, midges), algae, and terrestrial-derived plant matter (decomposing leaves and bark collected from the lake floor). With the exception of *P. conculcata*, which showed some overlap with larvae of caddisflies and midges, crabs were consistently enriched in mean $\delta^{15}N$ signatures relative to all putative food resources.

DISCUSSION

Our results provide evidence that crabs are important components of benthic communities in Lake Tanganyika. Although their distribution in benthic littoral zones is patchy, our results show that crabs can be locally abundant (Figure 4). Patchy distribution patterns with local abundance peaks are typical for crabs (e.g. Deudero et al. 2005; Flores et al. 2005; Ribeiro et al. 2005), and might be explained by a combination of predator avoidance behaviour, reproductive aggregation behaviour and/or the patchy distribution of food resources. Marked spatial variability in densities was also observed for potamonautid crabs in African freshwater habitats (e.g. King 1983; Somers & Nel 1998; Abdallah et al. 2004), with local abundance peaks of up to 48 individuals per m^{-2} (Table 1). Our density estimates of crabs in Lake Tanganyika are comparable to those obtained for *Potamonautes perlatus* in similar size classes, which ranged from 2.9 (± 2.1) to 15.6 (± 7.2) individuals m^{-2} between different sites in South African rivers (Somers & Nel 1998).

Several studies have underlined the potential of crabs to dominate invertebrate biomass in tropical freshwater ecosystems (Dobson et al. 2004, 2007a). Studies in East African forest streams have demonstrated that crabs may contribute between 58-94% of the total benthic invertebrate biomass (Abdallah et al. 2004; Dobson et al. 2007b). Invertebrate communities in Lake Tanganyika differ from those in most freshwater systems because they also include a diverse and locally highly abundant gastropod fauna. Mean gastropod densities on rocky littoral substrates in Lake Tanganyika range from 0.1-62.2 individuals m^{-2} (Donohue et al. 2003; Barret et al. 2003; McIntyre et al. 2005), and average biomass (including shell) estimates range from 20-250 g m^{-2} (Barret et al. 2003; Donohue et al. 2003). These numbers indicate that gastropods also contribute significantly to benthic biomass in Lake Tanganyika. The extent to which dominance of invertebrate biomass by crabs and gastropods is alternated or shared between localities remains to be tested. It should be noted that our quadrat surveys probably underestimate densities of the largest-bodied endemic Lake Tanganyika crab species *Platythelphusa armata* and *Potamonautes platynotus.* A significant relationship was demonstrated between crab body size (carapace width) and substrate use of crabs in the lake's rocky littoral areas (this thesis, Chapter 4). Large (carapace width ≥ 40 mm) individuals of *P. armata* and *Po. Platynotus* often occur on large substrates (boulders, rocks) that could not be adequately sampled using quadrats. Unfortunately, we also could not obtain data for the two deep lake dwelling species *P. tuberculata* and *P. praelongata*, which both occur at depths >

40 m (Marijnissen et al. 2004; this thesis, Chapter 4). Additional studies using trapping and/or mark recapture techniques are required to determine the extent to which these species contribute to the total biomass of crabs in benthic habitats of Lake Tanganyika.

The results of our surveys indicate that densities of crabs in the river delta area (KMG, LUI, MGU) were relatively low (Figure 4). The highest densities of crabs in the rocky littoral zone occurred at depths between 5 and 10 m, and rapidly decreased around 20 m depth. These results are similar to patterns observed in Lake Tanganyika for a range of endemic fish species in different trophic guilds (benthic algivores, phytoplanktivores, piscivores), which exhibit the highest densities in rocky littoral areas at depths < 20 m (Alin et al. 1999). Higher densities of crabs in rocky littoral habitats at shallow depths are likely explained by a combination of lower amounts of food resources and higher levels of silt content of the substrate at greater depths (e.g. Alin et al. 1999; Buat et al. 2002). We did not find obvious patterns in species richness or evenness among sites and/or depths (Figure 4). However, our analyses indicated that there are significant differences in species incidence among depths. Interestingly, of the two most common crab species in the rocky littoral zone, *P. echinata* and *P. conculcata*, the former has a higher incidence in deep (20 m) habitats than any of the other species, whereas the latter has the highest incidence at shallow (5 m) depths (Figure 5). These patterns might be driven by interspecific competition, but this remains to be tested experimentally. Although species associations

Functional role of Lake Tanganyika endemic crabs

Understanding the role of the different crab species in lacustrine foodwebs requires insight in their feeding habits and relative trophic position. A longstanding theory is that the high levels of species diversity in the African Rift lakes are to an important extent maintained through competition and niche diversification (e.g. Schluter 2000). From this theory it follows that each individual species occupies a distinctly different functional role in the trophic foodweb. Indeed, there are indications that the dense species packing in these lakes is facilitated by intricate trophic foodwebs comprising many highly derived and stenotopic species, particularly in rocky littoral areas (Hori et al. 1993; Bootsma et al. 1996; Bouton et al. 1997). Other studies demonstrated large overlap of niche components between closely related species (Bouton et al. 1997; Genner et al. 1999; Cohen 2000), and it has been suggested that some taxa are ecologically redundant (Cohen 2000; Martens 2002). Although there are indications of ecological niche divergence among the endemic crab species in Lake Tanganyika based on habitat use and functional morphological differences, gut content analyses revealed considerable overlap of their diets (this thesis, Chapter 3 and 4). Stable isotope analyses provide a potentially powerful method to examine questions of trophic niche width and interspecific differentiation (e.g. Genner et al. 1999; Bearhop et al. 2004). Previous analyses using $\delta^{13}C$ and $\delta^{15}N$ demonstrated that there are significant differences in mean isotopic signatures among endemic Lake Tanganyika crab species, but individuals within species exhibit a range of different foraging strategies (this thesis, Chapter 4). This would suggest that although the different species should not be considered functional equivalents, there might be some ecological redundancy through versatile foraging patterns.

In the present study, we compare crab isotopic signatures with those of putative food sources and we further examine patterns of variability. Following the conventional assumption that $\delta^{13}C$ increases by 0 to 1‰ and $\delta^{15}N$ by 2 to 4‰ between an organism and its diet (e.g. Minegawa & Wada 1984; Vander Zanden & Rasmussen 2001; McCutchan et al. 2003), it becomes clear that the mean signatures of all putative food sources are outside of the range of the mean signatures of the different crab species (Figure 7). Most of this discrepancy is explained by the high mean $\delta^{13}C$ values of the crabs. Unexpectedly high ^{13}C signatures and enrichment factors have also been reported by O'Reilly et al. (2002) and Sarvala et al. (2003) for the pelagic food web of Lake Tanganyika. It was suggested that relatively high metabolic rates and low growth efficiencies caused by tropical temperatures might influence ^{13}C enrichment in Lake Tanganyika (Sarvala et al. 1999, 2003) but this remains to be tested experimentally. Another possibility is that our sampling was not extensive enough, and did not cover a sufficiently broad range of putative food resources. However, our sampling included food resources that were common in gut contents of the crabs as well as in their habitats. An exception is *P. tuberculata*, because this species occurs at depths that were out of reach of our sampling strategies. The observed discrepancy between the mean δ^{13}C and δ^{15}N signatures of the different crab species and their putative food sources is likely to be related to the high variability among individual isotopic signatures. An important factor that can influence variability of consumer stable isotope signatures is the range of trophic levels from which food resources are drawn (Bearhop et al. 2004). Our gut content analyses demonstrated that crabs include primary producers as well as primary and secondary consumers in their diet, which might complicate inferences based on stable isotope analyses.

Although based on our current data, it is not possible to confidently link crabs to individual food sources, the high levels of ^{15}N enrichment relative to other benthic taxa demonstrate that crabs are top invertebrate predators. As such, the relative abundance of crab populations can have important implications for organisms lower in the foodweb. Using nutrient-enrichment and exclosure experiments it was recently shown that grazing has a significant impact on benthic productivity (McIntyre et al. 2006), and it is likely that crabs play a key role in top-down control. Furthermore, it has been shown that crabs form an important component in the diets of several endemic fish species (Coulter 1991; Hori 1983; Hori et. al. 1993). It is thus becoming evident that the crabs are closely linked to lower as well as higher trophic levels, and they are integrated components of Lake Tanganyika's benthic foodweb.

Threats to benthic communities

Lake Tanganyika presents a prominent example of a unique freshwater system that is under pressure of expanding human populations and associated environmental problems (reviewed in Lowe-McConnell 2003). Invasion of the Louisiana crayfish *Procambarus clarkii* Girard is considered a serious threat. This species was introduced in Lake Naivasha in 1970 (Parker 1974), and it subsequently spread throughout Eastern Africa. Expanding populations presently exist in Uganda, Kenya and Zambia (Arrignon et al. 1990), as well as throughout the Nile River basin up to Egypt (G. Howard, pers. comm.). Moreover, it is considered a likely prospect that the Louisiana crayfish will reach the upper Kagera River system in Tanzania and subsequently move into Lake Tanganyika (G. Howard, pers. comm.). Through its resilience to different environmental circumstances, its high dispersal capacity and its opportunistic diet, the Louisiana crayfish is capable of causing dramatic biodiversity shifts (e.g. Smart et al. 2002; Snyder & Evans 2006: Cruz & Rebelo 2007), and it would undoubtedly cause an ecological disaster if this invasive species would manage to establish itself in Lake Tanganyika.

Another imminent threat to benthic communities is caused by ongoing riparian deforestation and associated sediment discharge in the lake (Bizimana & Duchafour 1991; Cohen et al. 1993, 2005; Patterson 1996; Vandelannoote et al. 1996; Alin et al. 1999, 2002). Discharge of sediment and nutrients from deforested watersheds can affect primary producers in Lake Tanganyika through eutrophication, increased turbidity, oxygen stress, and/or blanketing of the substrate (Ellis 1936; Grobbelaar 1985; Bootsma & Hecky 1993; Hecky 1993; Mugidde 1993; Hecky et al. 1999, 2003; O'Reilly 1999; Bellinger et al. 2006).

Furthermore, it is known that increased sediment discharge can negatively affect aquatic organisms through a range of factors including deterioration of habitat quality, reduction of habitat heterogeneity, reduction of food intake, decrease of respiration efficiency, alteration of competitive relationships, decrease of reproductive success, and breakdown of mate recognition systems (Berkman & Rabeni 1986, 1987; Cooper 1987; Borgstrom et al. 1992; Seehausen et al. 1997; Wood & Armitage 1997; Henley et al. 2000; Burkhead & Jelks 2001; Zweig & Rabeni 2001; Airoldi 2003).

Predicting the consequences of increased sedimentation on the endemic crabs in Lake Tanganyika is not straightforward for a number of reasons. The majority of crab species are found in the rocky littoral zone, which is the area that is the most sensitive to the impacts of sediment loading (e.g. Cohen et al. 1993). If sediment impact has a strong influence on crab species composition and/or densities, it can be expected that obvious differences would exist between sites adjacent to deforested areas and those adjacent to areas with relatively natural vegetation. However, our surveys revealed a lack of apparent effects of sedimentation on crab distribution patterns. It could be argued that our sampling strategy was not sensitive enough to test vulnerability of crab species to sediment disturbance. On the other hand, community-level responses of crabs might be relatively resilient to sediment increase compared to other taxa in Lake Tanganyika that exhibit more intimate substrate-associations such as gastropods and ostracods. The pathways through which deforestation related sedimentation will affect crabs are likely to be indirect and subtle.

Gut content analyses demonstrated that crabs include algae, ostracods and gastropods in their diet. Evidence from surveys and *in situ* experiments in Lake Tanganyika has shown that these taxa are sensitive to elevated levels of sediment discharge, although response thresholds might be influenced by temporal and spatial factors (Cohen et al. 1993; Cohen 1995; Alin et al. 1999, 2002; O'Reilly 1999; Wells et al. 1999; Donohue & Irvine 2003, 2004a,b; Donohue et al. 2003; Eggermont & Verschuren 2003; McIntyre et al. 2005). Because Lake Tanganyika endemic crabs are trophically linked to organisms that are vulnerable to the impacts of increased sedimentation, it can be predicted that they will respond by shifting foraging patterns (e.g. McIntyre et al. 2005). However, because the different crab species feed on multiple trophic levels, responses are expected to be complex, and delayed relative to lower trophic levels. Using a theoretical model, it was recently shown that in situations where species exhibit some degree of ecological niche overlap, species loss might be buffered by density compensation following competitive release. However, the same model also suggested a greater tendency for competitive exclusion and cascading extinctions (Petchey et al. 2004).

Conservation implications

Scientific research in Lake Tanganyika should focus on the objective to establish a comprehensive model that links catchment variables with aquatic productivity, benthic and littoral species diversity, and ecosystem functioning on a local- as well as lake-wide scale. We have here highlighted the ecological significance of crabs in benthic lacustrine systems. It is clear that crabs need to be included in trophic interaction models both as prey and as primary and secondary consumers. To predict the impact of environmental perturbations on benthic communities, it is crucial that we have a better understanding of the interactions between crabs and their food resources. Future studies should furthermore focus on determining general patterns of dominance in terms of biomass.

Extensive surveys are required to examine distribution and abundance patterns on a lake-wide scale. A preliminary evaluation in the framework of an assessment of the status and distribution of freshwater biodiversity in Eastern Africa (Darwall et al 2005) considered the endemic Lake Tanganyika species *Po. platynotus, P. armata*, *P. conculcata*, *P. echinata*, and *P. tuberculata* as least concern (LC) under version 3.1 (2001) of the IUCN Red List of Threatened Species, based on their relative abundance during field surveys conducted between 1993-2004 (Cumberlidge & Marijnissen 2004a, b, d, i; also see Cumberlidge et al. 1999). *Platythelphusa maculata* and *P. polita* were also assessed as least concern (LC), based on the argument that although they have low representations in museum collections, historical records suggest that these two species have a lake-wide distribution and they both are assumed to occur in more than 10 locations (Cumberlidge & Marijnissen 2004f, g). However, recent collection efforts yielded only very small numbers of individuals from these two species (Cumberlidge et al. 1999; S.A.E. Marijnissen and G. Kazumbe, pers. obs). *Platythelphusa polita* was absent from sites that we surveyed in Tanzania and Zambia between 2002 and 2004 (S.A.E. Marijnissen and G. Kazumbe, pers. obs.), and our present study demonstrates that *P. maculata* has narrow habitat preferences and occurs in relatively low densities. Based on historical records and the results of our surveys in Tanzania and Zambia, *P. denticulata* and *P. praelongata* were tentatively considered vulnerable (VU D2), and *P. immaculata* was considered near threatened (NT B1ab(i); D1) (Cumberlidge & Marijnissen 2004c, e, h). It is obvious that more extensive surveys are critical to examine present lake-wide distribution- and abundance patterns and to test current conservation assessments of Lake Tanganyika endemic crab species.

At present, there is no consensus on how conservation of biodiversity in Lake Tanganyika can best be achieved. Examples from Lake Malawi National Park, which was gazetted as the world's first freshwater underwater park in 1980 and designated a UNESCO World Heritage Site in 1984 (Bootsma 1992) suggest that assignment of protected areas can be a successful method to protect aquatic diversity on a local scale. Several authors have therefore advocated the concept of assigning conservation areas to protect biodiversity in Lake Tanganyika (Cohen 1992; Coulter & Mubamba 1993; Lowe-McConnell 1993; Coulter 1999; Allison et al. 2000; Coulter et al. 2004; but see Pendleton & van Breda 1994). It was recommended that initial strategies should concentrate on the extension of existing terrestrial reserves (Coulter & Mubamba 1993; Allison et al. 2000; Mölsä et al. 2005). Five national parks border Lake Tanganyika, namely the Rusizi River Natural Reserve and Kigwena Forest in Burundi, Gombe Stream National Park and Mahale Mountains National Park in Tanzania, and Nsumbu National Park in Zambia (Odada et al. 2006). Primary arguments to extend existing reserves are economic (cost effectiveness of maintaining existing parks versus establishing new parks). Ideally, conservation prioritization should be based on lacustrine habitat characteristics as well as information about focal faunal components (e.g. Cohen 1992). Although it could be argued that sites such as those adjacent to Gombe Stream, Mahale Mountains and Nsumbu National park are protected from the negative effects of deforestation-associated sedimentation (Cohen et al. 1993), it has not explicitly been tested if these sites encompass elevated levels of priority taxa for conservation purposes (e.g. Verheyen & Rüber 2000; Darwall & Vié 2005). Without sufficient knowledge on the lake-wide distribution of functional ecological- and evolutionary relevant diversity across taxa, any decision to assign conservation status to aquatic regions adjacent to an existing terrestrial reserve would be arbitrary. Moreover, it is questionable if conservation efforts directed at particular organisms or core areas will be effective enough to ensure sustainability of the key ecological and evolutionary processes that generate and maintain diversity in Lake Tanganyika.

Conservation of aquatic diversity and maintenance of a healthy, functioning lacustrine ecosystem will require a multidimensional, basin wide approach. To ensure that human impact on this unique lake is minimized, it is not only crucial that the link between terrestrial activities and aquatic ecosystem functioning is well-understood, but also that relevant information is adequately disseminated to both national and international policy makers, as well as local communities. This necessitates a strong commitment of the scientific community to focus on the appropriate fundamental and applied research topics, and to actively engage with resource users as well as policy makers (Allison 2002). Moreover, it is becoming clear that conservation of freshwater biodiversity can only be accomplished in a framework that also provides sustainable means of subsistence for riparian human populations (Charles 1994; Coulter 1999; Allison et al. 2000; Mölsä et al. 2005). Increased efforts are required to understand and improve the socio-economic situation of the human populations in the Lake Tanganyika catchment basin. Integrated management of the lake, its catchment basin and its inhabitants on an international level (e.g. West 2001; Reynolds 2006) will be critical to the conservation of its unique aquatic diversity.

Acknowledgements

George Kazumbe, Moniek Kars, Marjolein Kamermans and Kim Bosch are gratefully acknowledged for their help with collecting data in Lake Tanganyika. Special thanks to Pete McIntyre and Linda Grotenbreg for providing valuable insights. We thank the Gombe Stream Research Centre for facilitating surveys along the coastline of Gombe National Park. The Tanzanian Fisheries Research Institute (TAFIRI-Kigoma), the Nyanza Project (NSF Paleoclimates ATM 0223920), and the Institute for Biodiversity and Ecosystem Dynamics/University of Amsterdam are thanked for logistical assistance. This research was supported by grants from the Netherlands Foundation for the Advancement of Tropical Research (WOTRO W84-489), the Schure-Beijerinck-Popping Fund of the Royal Netherlands Academy of Arts and Sciences (SBP/JK/2003-27), and Iso-analytical Limited, UK. We are grateful to the Tanzanian Commission for Science and Technology for permission to conduct research at Lake Tanganyika.

REFERENCES

Abell, R. 2001. Conservation biology for the biodiversity crisis: a freshwater follow-up. Conservation Biology 16:1435-1437.

Abell, R., Allan, J.D. and Lehner, B. 2007. Unlocking the potential of protected areas for freshwaters. Biological Conservation 134:48-63.

Abdallah A.H., de Mazancourt C., Elinge M.M., Graw, B., Grzesiuk, M., Henson, K., Kamoga, M., Kolodziejska, I., Kristersson, M., Kuria, A., Leonhartsberger, P., Matemba, R.B., Merl, M., Moss, B., Minto, C., Murfit, E., Musila, S.N., Ndayishiniye, J., Nuhu, D., Oduro, D.J., Provvedi, S., Rasoma, R.V., Ratsoavina, F., Trevelyan, R., Tumanye, N., Ujoh, V.N., van de Wiel, G., Wagner, T., Waylen, K. and Yonas, M. 2004. Comparative studies on the structure of an upland African stream ecosystem. Freshwater Forum 21:27-47.

Airoldi, L. 2003. The effects of sedimentation on rocky coast assemblages. Oceanography and Marine Biology: an Annual Review 41:161-236.

Alin, S.R., Cohen, A.S., Bills, R., Gashagaza, M.M., Michel, E., Tiercelin, J., Martens, K., Coveliers, P., Mboko, S.K., West, K., Soreghan, M., Kimbadi, S. and Ntakimazi, G. 1999. Effects of landscape disturbance on animal communities in Lake Tanganyika, East Africa. Conservation Biology 13:1017-1033.

Alin, S.R., O'Reilly, C.M., Cohen, A.S., Dettman, D.L., Palacios-Fest, M.R. and McKee, B.A. 2002. Effects of land-use change on aquatic biodiversity: a view from the paleorecord at Lake Tanganyika, East Africa. Geology 30:1143-1146.

Allison, E.H. 2002. Sustainable management of African Great Lakes: science for development? Aquatic Ecosystem Health and Management 5:315-327.

Allison, E.H., Paley, R.G., Ntakimazi, G., Cowan, V.J. and West, K. 2000. Biodiversity assessment and conservation in Lake Tanganyika. BIOSS final technical report. Pollution control and other measures to protect biodiversity in Lake Tanganyika. Lake Tanganyika Biodiversity Project (UNDP/GEF/UNOPS, RAF/92/G32), pp. 1-66. www.ltbp.org

Arrignon, J.C.V., Huner, J.V. and Laurent, P.J. 1990. L'écrevisse rouge des marais. Technicien d'Agriculture Tropicale (France), no. 12. Maisonneuve et Larose, Paris, France, pp 1-87

Barret, M., Bishobibiri, A.B. and Catron, J. 2003. Why do Tanganyikan gastropods have patchy distributions? Abundance, diversity, and species distribution in relation to abiotic and biotic parameters. Nyanza Project Report 2003, pp 1-19. www.geo.arizona.edu/nyanza

Bearhop, S., Adams, C.E., Waldron, S., Fuller, .A. and MacLeod, H. 2004. Determining trophic niche width: a novel approach using stable isotope analysis. Journal of Animal Ecology 73:1007-1012.

Beeton, A.M. 2002. Large freshwater lakes: present state, trends, and future. Environmental Conservation 29:21-28.

Bellinger, B.J., Cocquyt, C. and O'Reilly, C.M. 2006. Benthic diatoms as indicators of eutrophication in tropical streams. Hydrobiologia 537:75-87.

Berkman, H.E. and Rabeni, C.E 1986. Biomonitors of stream quality in agricultural areas: fish versus invertebrates. Environmental Management 10:413-419.

Berkman, H.E. and Rabeni, C.F. 1987. Effect of siltation on stream fish communities. Environmental Biology of Fishes 18:285-294.

Bertness, M.D., Trussell, G., Ewanchuk, P.J. and Silliman, B.R. 2003. Testing for Alternate Stable States on Maine Rocky Shores. Ecology 83: 3434–3448.

Bizimana, M. and Duchafour, H. 1991. A drainage basin management study: The case of the Ntihangwa River Basin. In: Cohen, A. (Ed.). Report on the first international conference on conservation and biodiversity of Lake Tanganyika. Biodiversity Support Program, Washington D.C., U.S.A., pp 43-45.

Bootsma, H.A. 1992. Lake Malawi National Park: An overview. Mitteilungen Internationale Vereinigung für Theoretische und Angewandte Limnologie 23:125-128.

Bootsma, H.A. and Hecky, R.E. 1993. Conservation of the African Great Lakes: a limnological perspective. Conservation Biology 7:644-656.

Bootsma, H.A. and Hecky, R.E., Hesslein, R.H. and Turner, G. 1996. Food partitioning among Lake Malawi nearshore fishes as revealed by stable isotopes analyses. Ecology 77:1286-1290.

Borgstrom, R., Brabrand, A. and Solheim, T.J. 1992. Effects of siltation on resource utilization and dynamics of allopatric brown trout, *Sulmo trutta,* in a reservoir.

Bouton, N., Seehausen, O. and van Alphen, J.J.M. 1997. Resource partitioning among rock-dwelling haplochromines (Pisces: Cichlidae) from Lake Victoria. Ecology of Freshwater Fish 6:225-240.

Bowen, R.E. and Depledge, M.H. 2006. Rapid Assessment of Marine Pollution (RAMP). Marine Pollution Bulletin 53:631-639.

Buat, P., Samlal, P.S. and Guildford, S.J. 2002. The relationship between organic matter, invertebrates, and bacteria in the sediments of Lake Malawi. Aquatic Ecosystem Health and Management 5:307-313.

Burkhead, N.M. and Jelks, H.L. 2001. Effects of suspended sediment on the reproductive success of the tricolor shiner, a crevice-spawning minnow. Transactions of the American Fisheries Society 130:959-68.

Charles, A.T. 1994. Towards sustainability: the fishery experience. Ecological Economics 11:201-211.

Cleary, D.F.R. 2003. An examination of scale of assessment logging and ENSO induced fires on butterfly diversity in Borneo. Oecologia 135:313-321.

Cleary, D.F.R. and Genner. M.J. 2004. Changes in rainforest butterfly diversity following major ENSO-induced fires in Borneo. Global Ecology and Biogeography 13:129-140.

Cleary D.F.R. and Mooers, A.Ø. 2004. Butterfly species richness and community composition in forests affected by ENSO-induced burning and habitat isolation in Borneo. Journal of Tropical Ecology 20:359-367

Cohen, A.S. 1992. Criteria for developing viable underwater natural reserves in Lake Tanganyika. Mitteilungen Internationale Vereinigung für Theoretische und Angewandte Limnologie. 23:109-116.

Cohen, A.S. 1995. Paleoecological approaches to the conservation biology of benthos in ancient lakes: a case study from Lake Tanganyika. Journal of the North American Benthological Society 14:654-668.

Cohen, A.S. 2000 Linking spatial and temporal changes in the diversity structure of ancient lakes: examples from the ecology and paleoecology of the Tanganyikan ostracods. In: Rossiter, A. and Kawanabe, H. (eds.). Ancient lakes: biodiversity, ecology and evolution. Advances in Ecological Research 31521-537.

Cohen A.C., R. Bills, C.Z. Cocquyt, and A.G. Caljon. 1993. The impact of sediment pollution on biodiversity in Lake Tanganyika. Conservation Biology 7: 667-677.

Cohen A.S., Lezzar K.E., Tiercelin J.J. and Soreghan M. 1997. New paleogeographic and lake level reconstructions of Lake Tanganyika: implications for tectonic, climatic, and biological evolution in a rift lake. Basin Research 9/2:107-132.

Cohen, A. S., Palacios-Fest, M. R. Msaky, E. S., Alin, S. A., McKee, B., O'Reilly, C. M. Dettman, D. L., Nkotagu, H. and Lezzar, K. E. 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.

Cooper, C.M. 1987. Benthos in Bear Creek, Mississippi: effects of habitat variation and agricultural sediments. Journal of Freshwater Ecology 4:101-113.

Coulter, G.W. 1991. Lake Tanganyika and its life. Oxford University Press, London, UK, pp 1-354.

Coulter, G.W. 1999. Sustaining both biodiversity and fisheries in ancient lakes. In: Kawanabe, H., Coulter, G.W. and Roosevelt, A.C. (eds.) Ancient lakes: their cultural and biological diversity. Kenobi Productions, Ghent, Belgium, pp. 177-187.

Coulter, G., Langenberg, V.T., Lowe-McConnell, R., Riedel, F., Roest, F., Sarvala, J. and Timoshkin, O. 2004. Survival of ancient lake biodiversity. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 29:1178-1181.

Coulter, G. W. and Mubamba, R. 1993. Conservation in Lake Tanganyika, with special reference to underwater parks. Conservation Biology 7:678-685.

Cruz, M.J. and Rebelo, R. 2007. Colonization of freshwater habitats by an introduced crayfish, *Procambarus clarkii*, in Southwest Iberian Peninsula. Hydrobiologia 575:191-201.

Cumberlidge, N., von Sternberg, R., Bills, I.R. and Martin, H. 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.

Cumberlidge, N. and Marijnissen, S.A.E. 2004a. *Platythelphusa armata*. In 2004 IUCN Red List of Threatened Species. International Union for the Conservation of Nature and Natural Resources. www.redlist.org.

Cumberlidge, N. and Marijnissen, S.A.E. 2004b. *Platythelphusa conculcata*. In 2004 IUCN Red List of Threatened Species. International Union for the Conservation of Nature and Natural Resources. www.redlist.org.

Cumberlidge, N. and Marijnissen, S.A.E. 2004c. *Platythelphusa denticulata*. In 2004 IUCN Red List of Threatened Species. International Union for the Conservation of Nature and Natural Resources. www.redlist.org.

Cumberlidge, N. and Marijnissen, S.A.E. 2004d. *Platythelphusa echinata*. In 2004 IUCN Red List of Threatened Species. International Union for the Conservation of Nature and Natural Resources. www.redlist.org.

Cumberlidge, N. and Marijnissen, S.A.E. 2004e. *Platythelphusa immaculata*. In 2004 IUCN Red List of Threatened Species. International Union for the Conservation of Nature and Natural Resources. www.redlist.org.

Cumberlidge, N. and Marijnissen, S.A.E. 2004f. *Platythelphusa maculata*. In 2004 IUCN Red List of Threatened Species. International Union for the Conservation of Nature and Natural Resources. www.redlist.org.

Cumberlidge, N. and Marijnissen, S.A.E. 2004g. *Platythelphusa polita*. In 2004 IUCN Red List of Threatened Species. International Union for the Conservation of Nature and Natural Resources. www.redlist.org.

Cumberlidge, N. and Marijnissen, S.A.E. 2004h. *Platythelphusa praelongata*. In 2004 IUCN Red List of Threatened Species. International Union for the Conservation of Nature and Natural Resources. www.redlist.org.

Cumberlidge, N. and Marijnissen, S.A.E. 2004i. *Platythelphusa tuberculata*. In 2004 IUCN Red List of Threatened Species. International Union for the Conservation of Nature and Natural Resources. www.redlist.org.

Cumberlidge, N., Marijnissen, S.A.E., Reed, S.K. and Michel, E. 2006. A conservation assessment of the freshwater crabs of Tanzania with special reference to Lake Tanganyika. In: State of Lake Tanganyika, a case study. Climate change, food web alterations, invasive species, and management. International Symposium Changing Great Lakes of the World (GLOW IV), Aquatic Ecosystem Health and Management Society, Canada, pp 73. www.aehms.org/conferences.html

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

Darwall, W.R.T. and Vié, J.-C. 2005. Identifying important sites for conservation of freshwater biodiversity: extending the species-based approach. Fisheries management and Ecology 12:287-293.

Denny, P. 2000. Limnological research and capacity building in Sub-Saharan Africa. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 27:641-654

Denny, P. 2001. Research, capacity building and empowerment for sustainable management of African wetland ecosystems. Hydrobiologia 458:21-31.

Deudero, S., Frau, A., Cerda, M. and Hampel, H. 2005. Distribution and densities of the decapod crab *Percnon gibbesi*, an invasive Grapsidae, in western Mediterranean waters. Marine Ecology Progress Series 285:151-156.

Dobson, M.K., Magana, A., Lancaster, J. and Mathooko, J.M. 2007a. Aseasonality in the abundance and life history of an ecologically dominant freshwater crab in the Rift Valley, Kenya. Freshwater Biology 52:215-225.

Dobson M., Magana A.M., Mathooko J.M. and Ndegwa F.K. 2007b. Distribution and abundance of freshwater crabs (*Potamonautes* spp.) in rivers draining Mt Kenya, East Africa. Fundamental and Applied Limnology - Archiv für Hydrobiologie. 168:271-279.

Dobson, M.K., Magana, A., Mathooko, J.M. and Ndegwa F.K. 2002. Detritivores in Kenyan highland streams: more evidence for the paucity of shredders in the tropics? Freshwater Biology 47:909-919.

Donohue, I. and Irvine, K. 2003. Effects of sediment particle size composition on survivorship of benthic invertebrates from Lake Tanganyika. Archiv für Hydrobiologie 157:131-144.

Donohue, I. and Irvine, K. 2004a. Seasonal patterns of sediment loading and benthic invertebrate community dynamics in Lake Tanganyika, Africa. Freshwater Biology 49:3320-331.

Donohue, I. and Irvine, K. 2004b. Size-specific effects of increased sediement loads on gastropod communities in Lake Tanganyika, Africa. Hydrobiologia 522:337-342.

Donohue, I., Verheyen, E. and Irvine. K. 2003. In situ experiments on the effects of increased sediment loads on littoral rocky shore communities in Lake Tanganyika, East Africa. Freshwater Biology 48:1603-161.

Dudgeon, D. 2000. The ecology of tropical Asian rivers and streams in relation to biodiversity conservation. Annual Review of Ecology, Evolution and Systematics 31:239-263.

Dudgeon, D. 2003. The contribution of scientific information to the conservation and management of freshwater biodiversity in tropical Asia. Hydrobiologia 500:295-314.

Dudgeon, D. Arthington, A.H., Gessner, M.O., Kawabata, Z.I., Knowler, D.J., Lévêque, C., Naiman, R.J., Prieur-Richard, A.H., Soto, D., Stiassny, M.L.J. and Sullivan, C.A. 2005. Freshwater biodiversity: importance, threats, status and conservation challenges. Biological Reviews 81:163-182.

Eggermont, H. and Verschuren, D. 2003. Impact of soil erosion in disturbed tributary drainages on the benthic invertebrate fauna of Lake Tanganyika, East Africa. Biological Conservation 113:99-109.

Ellis, M.M. 1936. Erosion silt as a factor in aquatic environments. Ecology 17:29-42.

Flores, A.A., Abrantes, K.G. and Paula, J. 2005. Estimating abundance and spatial distribution patterns of the bubble crab Dotilla fenestrata (Crustacea: Brachyura). Austral Ecology 30:14-23.

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

Genner, M.J., Seehausen, O., Cleary, D.F.R., Knight, M.E., Michel, E. & Turner, G.F. 2004. How does the taxonomic status of allopatric populations influence species richness within African cichlid fish assemblages? Journal of Biogeography 31:93-102.

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

Gherardi, F., Tarducci, F. and Micheli, F. 1989. Energy maximization and foraging strategies in *Potamon fluviatile*. Freshwater Biology 22:233-245.

Gherardi, F. and Vannini, M. 1989. Spatial behaviour of the freshwater crab *Potamon fluviatile*: a radio-telemetric study. Biology of Behaviour 14: 28-45.

Green, P.T., O'Dowd, D.J. and Lake, P.S. 1997. Control of seedling recruitment by land crabs in rain forest on a remote oceanic island. Ecology 78:2474–2486

Grobbelaar, J. 1985. Phytoplankton productivity in turbid waters. Journal of Plankton Research 7:653-663.

Groombridge, B. and Jenkins, M. 1998. Freshwater Biodiversity: A preliminary global assessment. World Conservation Monitoring Centre (WCMC), World Conservation Press, Cambridge, UK, pp 1-104. www.wcmc.org.uk

Hamilton, S.K. and Lewis, W.M. Jr. 1992. Stable carbon and nitrogen isotopes in algae and detritus from the Orinoco River floodplain, Venezuela. Geochimica et Cosmochimica Acta 56:4237–4246.

Harrison, E.M. 1995. The zonation of freshwater crabs with altitude in a mountain stream in the East Usambara Mountains, Tanzania. Frontier Tanzania Expedition Report TZ943. pp. 1-56.

Hecky, R.E. 1993. The eutrophication of Lake Victoria. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 25:39-48.

Hecky, R.E., Bootsma, H.A. and Kingdon, M.L. 2003. Impact of land use on sediment and nutrient yields to Lake Malawi/Nyasa (Africa). Journal of Great Lakes Research 29: 139-158.

Hecky R.E., Kling, H.J., Johnson, T.C., Bootsma, H.A. and Wilkinson, P. 1999 Algal and sedimentary evidence for recent changes in the water quality and limnology of Lake Malawi/Nyasa. Pages 191-214 In: Bootsma, H.A., and Hecky, R.E. (eds.) Water Quality Report, Lake Malawi/Nyasa/Niassa Biodiversity Conservation Project. SADC/GEF.

Henley, W.W., Patterson, M.A., Neves, R.J. and Lemly, A.D. 2000. Effects of sedimentation and turbidity on lotic food webs: a consice review for natural resource managers. Reviews in Fisheries Science 8:125-139.

Hill, M.P. and O'Keeffe, J. H. 1992. Some aspects of the ecology of the freshwater crab (*Potamonautes perlatus* Milne Edwards) in the upper reaches of the Buffalo River, Eastern Cape Province, South Africa. South African Journal of Aquatic Sciences 18:42-50.

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

IUCN 2001. IUCN Red List categories and criteria: Version 3.1. Species Survival Commission, IUCN. Gland, Switzerland and Cambridge, UK. pp 1-30.

Jenkins, M.J. 2003. Prospects for biodiversity. Science 302:1175-1176.

Jorgensen, S.E., Ntakimazi, G. and Kayombo, S. 2005. Lake Tanganyika: Experience and lessons learned brief. In: Nakamura, M. (ed). Managing lakes and their basins for sustainable use: a report for lake basin managers and stakeholders. International Lake Environment Committee Foundation (ILEC), Kusatsu, Japan, pp 363-375.

King, J.M. 1983. Abundance, biomass and density of benthic macro-invertebrates in a western Cape River, South Africa. Transactions of the Royal Society of South Africa 45:11-34.

Krebs C. J. 1999. Ecological Methodology. Addison Wesley Longman Inc., CA, USA, pp 1-620.

Lee, S.Y. and Kneib, R.T. 1994. Effects of biogenic structure on prey consumption by the xanthid crabs *Eurytium limosum* and *Panopeus herbstii* in a salt marsh. Marine Ecology Progress Series 104:39-47.

Legendre, P. and Gallagher, E.D. 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129:271-280.

Leloup, E. 1950. Lamellibranches. Résultats scientifiques de l'exploration hydrobiologique du Lac Tanganyika (1946-1957). Institut Royal des Sciences Naturelles de Belgique 3:1-153.

Lévêque, C., Balain, E.V. and Martens, K. 2005. An assessment of animal species diversity in continental waters. Hydrobiologia 542:39-67.

Lowe-McConnell, R. 1993. Fish faunas of the African Great Lakes: origins, diversity, and vulnerability. Conservation Biology 7:634-643.

Lowe-McConnell, R. 2003 Recent research in the African Great Lakes: fisheries, biodiversity and cichlid evolution. Freshwater Forum 20: 1-64.

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

Martens, K. 2002. Redundancy and ecosystem stability in the fluctuating environments of long-lived lakes. In: Odada, E.O. and Olago, D.O. (eds.) The East African Great Lakes: limnology, paleolimnology and biodiversity. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 309-319.

McIntyre, P.B., Michel, E., France, K., Rivers, A., Hakizimana, P. and Cohen, A.S. 2005. Individual- and assemblage-level effects of anthropogenic sedimentation on snails in Lake Tanganyika. Conservation Biology 19:171-181.

McIntyre, P.B., Michel, E. and Olsgard, M. 2006. Top-down and bottom-up controls on periphyton biomass and productivity in Lake Tanganyika. Limnology and Oceanography 51:1514-1523.

Meester, de, L. and Declerck, S. 2005. The study of biodiversity in freshwater habitats: societal relevance and suggestions for priorities in science policy. Hydrobiologia 542:1-9.

Michel, E., Todd, J.A., Cleary, D.F.R., Kingma, I., Cohen, A.S., and Genner, M.J. 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.

Minegawa, M. and Wada, E. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between ^{15}N and animal age. Geochimica et Cosmochimica Acta 48:1135-1140.

McCutchan, J.H. Jr., Lewis, W.M. Jr., Kendall, C. and McGrath, C.C. 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos 102:378-390.

Mölsä, H., Reynolds, E.J., Coenen, E.J. and Lindqvist, O.V. 1999. Fisheries research towards resource management in Lake Tanganyika. Hydrobiologia 407:1-24.

Mölsä, H., Sarvala, J., Huttula, T., Salonen, K. and Lindqvist, O.V. 2005. Management of an African Great Lake fishery: Challenges to research and community. In: Hietanen, O. (ed.) University partnerships for international development. Finland Futures Research Centre (FFRC) Publication 6/2005, Helsinki, Finland, pp. 115-142.

Moss, B. 2000. Biodiversity in fresh waters – an issue of species preservation or system functioning? Environmental conservation 27:1-4.

Moss B. 2005. Rapid shredding of leaves by crabs in a tropical African stream. Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie 29:147-150.

Moustakas, A. and Karakassis, I. 2004. How diverse is aquatic biodiversity research? Aquatic Ecology 39:367-375.

Mugidde, R. 1993. The increase in phytoplankton productivity and biomass in Lake Victoria. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 25:846-849.

Odada, E.O., Olago, D.O., Bugenyi, F., Kulindwa, K., Karimumuryango, J., West, K., Ntiba, M., Wandiga, S., Aloo-Obudho, P. and Achola, P. 2003. Environmental assessment of the East African Rift Valley lakes. Aquatic Sciences 65:254-271.

Odada, E.O., Olago, D.O., Kulindwa, K.A.A., Bugenyi, F., West, K., Ntiba, M., Wandiga, S. and Karimumuryango, J. 2004. East African Rift Valley lakes. Global International Waters

Assessment (GIWA) Regional assessment 47, United Nations Environmental Programme (UNEP), University of Kalmar, Kalmar, Sweden, pp 1-114.

Ogutu-Ohwayo, R., Hecky, R.E., Cohen, A.C. and Kaufman, L. 1997. Human impacts on the African Great Lakes. Environmental Biology of Fishes 50:117-131.

Olago, D.O. and Odada, E.O. 2007. Sediment impacts in Africa's transboundary lake/river basins: Case study of the East African Great Lakes. Aquatic Ecosystem Health and Management 10: 23-32.

O'Dowd, D.J. and Lake, P.S. 1990. Red crabs in rain forest, Christmas Island: differential herbivory of seedlings. Oikos 58:289-292.

O'Reilly, C.M. 1999. Benthic algal productivity in Lake Tanganyika and the effects of deforestation. Lake Tanganyika Biodiversity Project (UNDP/GEF/UNOPS, RAF/92/G32), pp 1-17. www.ltbp.org

O'Reilly, C.M., Hecky, R.E., Cohen, A.S. and Plisnier, P.D. 2002. Interpreting stable isotopes in food webs: recognizing the role of time averaging at different trophic levels. Limnology and Oceanography 47:306-309.

Park, L.E. and Downing, K.F. 2000. Implications of phylogeny reconstruction for ostracod speciation modes in Lake Tanganyika. In: Rossiter, A. and Kawanabe, H. (eds.) Ancient lakes: Biodiversity, ecology and evolution. Advances in Ecological Research 31. Academic Press, London, UK, pp 303-330.

Parker, I. S. C., 1974. The status of the Louisiana red swamp crayfish (*Procambarus clarkii* Girard) in Lake Naivasha. Wildlife Services, Nairobi, Kenya, pp 1-45.

Patterson, G. 1996. Sediment discharge and its consequences: baseline review. Pollution control and other measures to protect biodiversity in Lake Tanganyika. Lake Tanganyika Biodiversity Project RAF/92/G32. Natural Resources Institute, UK. www.ltbp.org

Pendleton, L.H. and van Breda, A. 1994. Underwater parks may not be the best conservation tool for Lake Tanganyika. Conservation Biology 8:330-331.

Petchey, O.L., Downing, A.L., Mittelbach, G.G., PErsson, L., Steiner, C.F., Warren, P.H. and Woodward, G. 2004. Species loss and the structure and functioning of multitrophic aquatic systems. Oikos 104:467-478.

Peterson, B.J. and Fry, B. 1987. Stable isotopes in ecosystem studies. Annual Reviews of Ecology and Systematics 18:293-320.

Ramsar 2007. The list of wetlands of international importance. Ramsar Convention Secretariat, Gland, Switserland, pp 1-39. www.ramsar.org

Rao, C.R. 1995. A review of canonical coordinates and an alternative to correspondence analysis using Hellinger distance. Qüestiió 19:23-63

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

Revenga, C., Campbell. I., Abell, R., de Villiers, P. and Bryer, M. 2005. Prospects for monitoring freshwater ecosystems towards the 2010 targets. Philosophical Transactions of the Royal Society B. 360:397-413.

Reynolds, E. 2006. The regional programme for integrated management of Lake Tanganyika. International Symposium Changing Great Lakes of the World (GLOW IV), Aquatic Ecosystem Health and Management Society, Canada, pp 50. www.aehms.org/conferences.html

Ribeiro, P.D., Iribarne, O.O. and Deleo, P. 2005. The relative importance of substratum characteristics and recruitment in determining the spatial distribution of the fiddler crab *Uca uruguayensis* Nobili. Journal of Experimental Marine Biology and Ecology 214:99-111.

Sarvala, J., Badende, S., Chitamwebwa, D., Juvonen, P., Mwape, L., Mölsä, H., Mulimbwa, N., Salonen, K., Tarvainen, M. and Vuorio, K. 2003. Size-fractionated $\delta^{15}N$ and $\delta^{13}C$ isotope ratios elucidate the role of the microbial food web in the pelagial of Lake Tanganyika. Aquatic Ecosystem Health and Management 6:241-250.

Sarvala, J., Salonen, K., Järvinen, M., Aro, E., Huttula, T.,Kotilainen, P., Kurki, H., Langenberg, V., Mannini, P., Peltonen, A., Plisnier, P.D., Vuorinen, I., Mölsä, H. and Lindqvist, O.V. 1999. Trophic structure of Lake Tanganyika: carbon flows in the pelagic food web. Hydrobiologia 407, 155–179.

Schluter, D. 2000. The ecology of adaptive radiation. Oxford University Press, Oxford, NY, USA, pp 1-288.

Scholz, C.A. and Rosendahl, B. 1988. Low lake stands in Lakes Malawi and Tanganyika, delineated with multifold seismic data. Science 240:1645-1648.

Schuwerack, P.M.M., Lewis, J.W. and Jones, P. 2001. The potential use of the South African river crab, *Potamonautes warreni*, as a bioindicator species for heavy metal contamination. Ecotoxicology 10:159-166.

Seehausen, O., van Alphen, J.J.M. and Witte, F. 1997 Cichlid fish diversity by eutrophication that curbs sexual selection. Science 277:1808-1811.

Sherman, P.M. 2003. Effects of land crabs on leaf litter distributions and accumulations in a mainland tropical rain forest. Biotropica 35:365-347.

Silliman, B.R. and Bertness, M.D. 2002. A trophic cascade regulates salt marsh primary production. Proceedings of the National Academy of Sciences of the United States of America 99:10500-10505.

Silliman, B.R., Layman, C.A., Geyer, K. & Zieman, J.C. 2004. Predation by the black-clawed mud crab *Panopeus herbstii*, in Mid-Atlantic salt marches: further evidence for top-down control of march grass production. Estuaries 27:188-196.

Smart, A.C., Harper, D.M., Malaisse, F., Schmitz, S., Coley, S. and Gouder de Beauregard, A.C. 2002. Feeding of the exotic Louisiana red swamp crayfish, *Procambarus clarkii* (Crustacea, Decapoda), in an African tropical lake: Lake Naivasha, Kenya. Hydrobiologia 488:129-142.

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 1880:344-353.

Smith, T.J. III, Boto, K.G., Frusher, S.D. and Giddins, R.L. 1991. Keystone species and mangrove forest dynamics: the influence of burrowing by crabs on soil nutrient status and forest productivity. Estuarine, Coastal and Shelf Science 33:419-432.

Snyder, W.E. and Evans, E.W. 2006. Ecological effects of invasive arthropod generalist predators. Annual Review of Ecology, Evolution, and Systematics 37:95-122.

Somers, M.J. and Nel, J.A.J. 1998. Dominance and population structure of freshwater crabs (*Potamonautes perlatus* Milne Edwards). South African Journal of Zoology 33:31-36.

Strayer, D.L. 2006. Challenges for freshwater invertebrate conservation. Journal of the North American Benthological Society 25:271-287.

Thieme, M.L., Abell, R., Stiassney, M.L.J., Skelton, P., Lehner, B., Teugels, G.G., Dinerstein, E., Kamden Toham, A., Burgess, N. and Olson, D. 2005. Freshwater ecoregions of Africa and Madagascar: A conservation assessment. Island Press, Washington D.C., U.S.A, pp 1-430.

Tiercelin, J.J. and Mondeguer, A. 1991. The geology of the Tanganyika Trough. In: Coulter, G. (ed.) Lake Tanganyika and its life. Oxford University Press, London, UK, pp. 7-48

Trussell, G., Ewanchuk, P.J. and Bertness, M.D. 2002. Field evidence of trait-mediated indirect interactions in a rocky intertidal food web. Ecology Letters 5:241-245.

Turnbull-Kemp, P.St.J. 1960. Quantitative estimations of populations of the river crab *Potamon* (*Potamonautes*) *perlatus* (Milne-Edwards) in Rhodesian trout streams. Nature 13:481.

UNEP 2005. One planet, many people. Africa's lakes: An atlas of environmental change. Division of Early Warning and Assessment (DEWA), United Nations Environment Programme (UNEP), Nairobi, Kenya, pp 1-77. www.earthprint.com

Vandelannoote, A., Robberecht, H., Deelstra, H., Vyumvohore, F., Bitetera, X and Ollevier, F. 1996. The impact of the River Ntahanga, the most polluted Burundian affluent of Lake Tanganyika, on the water quality of the lake. Hydrobiologia 328:161-171.

Vander Zanden, M.J. and Rasmussen, J.B. 2001. Variation in $\delta^{15}N$ and $\delta^{13}C$ trophic fractionation: implications for aquatic food web studies. Limnology and Oceanography 46:2061-2066.

Verheyen, E. and Rüber, L. 2000. Conservation of the endemic cichlid fish of Lake Tanganyika: Implications from population-level studies based on mitochondrial DNA. In: Rossiter, A. and Kawanabe, H. (eds.) Ancient lakes: Biodiversity, ecology and evolution. Advances in Ecological Research 31. Academic Press, London, UK, pp 539-550.

Wells, T.M., Cohen, A.S., Park, L.E., Detmann, D.L. and McKee, B.M. 1999. Ostracode stratigraphy and paleoecology from surficial sediments of Lake Tanganyika, Africa. Journal of Paleolimnology 22:259-276.

West, K. 2001. Lake Tanganyika: Results and experiences of the UNDP/GEF conservation initiative (RAF/92/G32) in Burundi, D. R. Congo, Tanzania, and Zambia. Lake Tanganyika Biodiversity Project (UNDP/GEF/UNOPS, RAF/92/G32), pp 1-137. www.ltbp.org

West, K., Michel, E., Todd, J., Brown, D. and Clabaugh, J. 2003 The gastropods of Lake Tanganyika: Diagnostic key, classification and notes on the fauna. International Association of Theoretical and Applied Limnology SIL, Occasional Publication 2:1-132.

Williams, T.R. 1961. The diet of freshwater crabs associated with *Simulum neavei* in East Africa. I. Crabs from west and east Uganda, collected by the Cambridge East Africa expedition, 1959. Annals of tropical medicine and parasitology 55:128-131.

Williams, T.R. 1962. The diet of freshwater crabs associated with *Simulum neavei* in East Africa. II. The diet of *Potamon berardi* from Mount Elgon, Uganda. Annals of tropical medicine and parasitology 56:362-367.

Wood, P.J, and Armitage, P.D. 1997. Biological effects of fine sediment in the lotic environment. Environmental Management 21:203-17.

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

Zweig, L.D. and Rabeni. C.F. 2001. Biomonitoring for deposited sediment using benthic invertebrates: a test on 4 Missouri streams. Journal of the North American Benthological Society 20:643-657.

Table 1. Density- and biomass estimates for African freshwater crabs in different habitats.

Species Locality and habitat	Density (crabs m^{-2})	Biomass (dry M g m^{-2})	Size (mm)	Sampling method	Reference
Potamonautes perlatus					
Cape province, R	0.3-2.7	< 3.0	n.a.	Net trap (monthly for 1 year)	King (1983)
Cape province, R	1.7-5.3	54.2-136.1	25.0-80.0	Baited traps (2 months)	Hill & O'Keeffe (1992)
Cape province, R	2.9-15.6	n.a.	4.0-44.6	Quadrat surveys (4 collections during 1 year)	Somers & Nel (1998)
Zimbabwe, R	0.1-2.2	n.a.	18.7-39.5	Baited traps (6 months)	Butler & du Toit (1994)
Zimbabwe, R	0.8-1.3	2.2-5.4*	17.3-45.0	Baited traps (sampling period not specified)	Turnbull-Kemp (1960)
Potamonautes sp.					
Tanzania, SF	1.6-48	0.6-11.5	n.a.	Surber sampler and pond net (single collection).	Abdallah et al. (2004)
Potamonautes n.sp.					
Kenya, R	7.2-24.8	2.4-4.6	3.3-27.8	Surber sampler (monthly for 12 months) and hand sampling (single collection)	Dobson et al. (2007a)
Potamonautes ohdneri					
Kenya, R	10.7-16.0	0.3-15.1	3.0-27.0	Surber sampler (single collection)	Dobson et al. (2007b)
Platythelphusa spp. and *Potamonautes platynotus*					
Tanzania, L	2.0-12.2	0.9-21.0	10.0-56.8	Quadrat surveys using SCUBA diving (multiple collections with irregular intervals over 3 years)	This study

L= lake; R = river; SF = forest stream and associated floodplain; n.a. = not available. *Estimated from wet mass data provided in the reference.

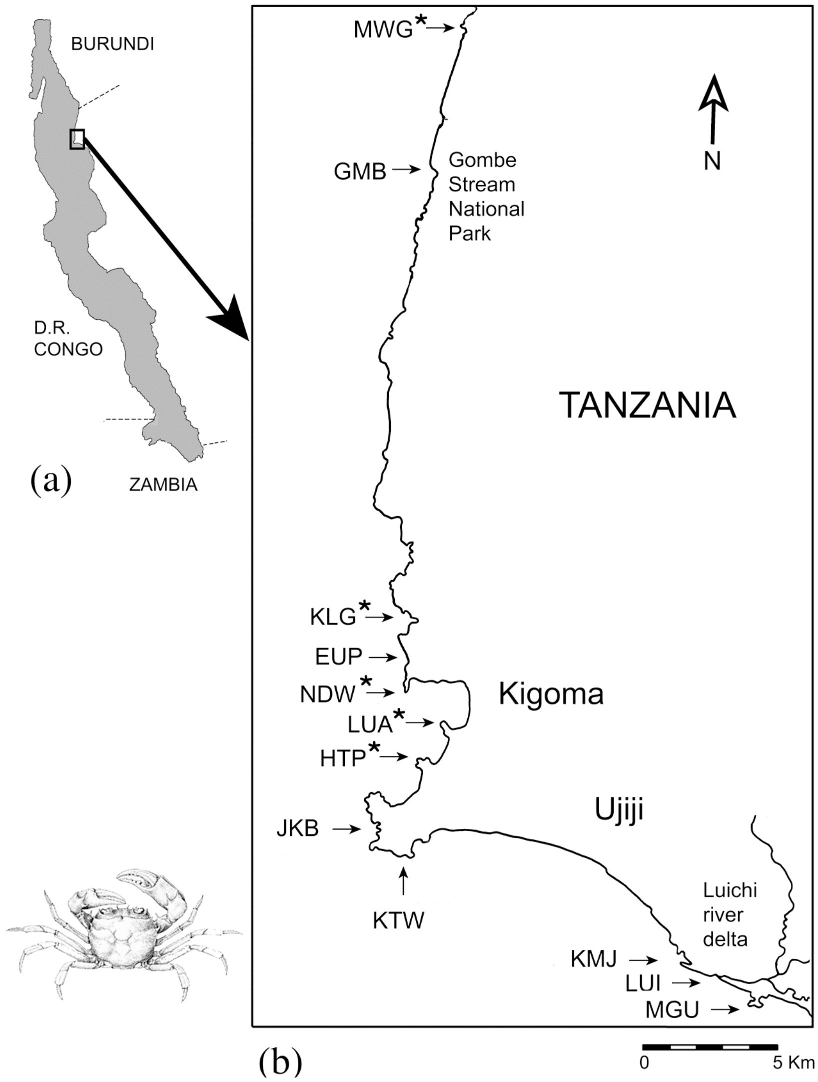

Figure 1. (a) Map of Lake Tanganyika, and (b) study sites. Acronyms (local names in brackets): MWG = Mwamgongo village; GMB = Gombe Stream National Park; KLG = Kalalangabo (Lemba village); EUP = Euphorbia (Kasazi Hill); LUA = Luansa Point (Kigoma Bay); HTP = Hilltop Hotel; JKB = Jakobsen's Beach (Mwamahunga); ZNG = Mzungu; KTW = Kitwe Point; KMJ = Kangamoja; LUI = Luichi river northernmost outlet; MGU = Mgumile. Sites adjacent to deforested areas are denoted with an asterisk.

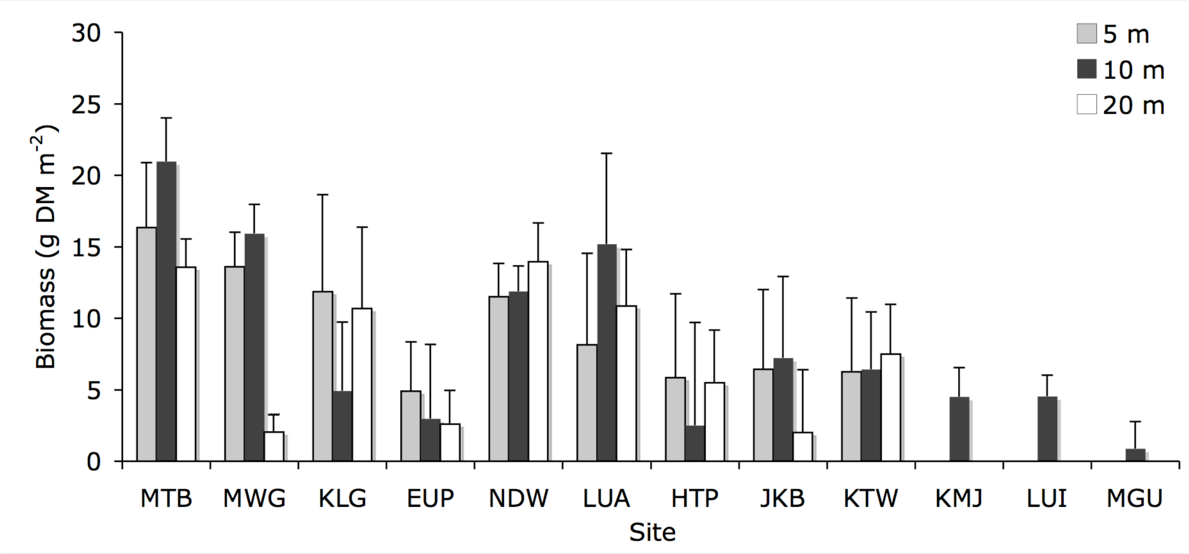

Figure 2. Spatial patterns in biomass of endemic crabs in Lake Tanganyika. Mean (±SE) biomass estimates are based on twenty quadrats at each site and depth combination. DM = dry mass. Site acronyms are explained in Figure 1.

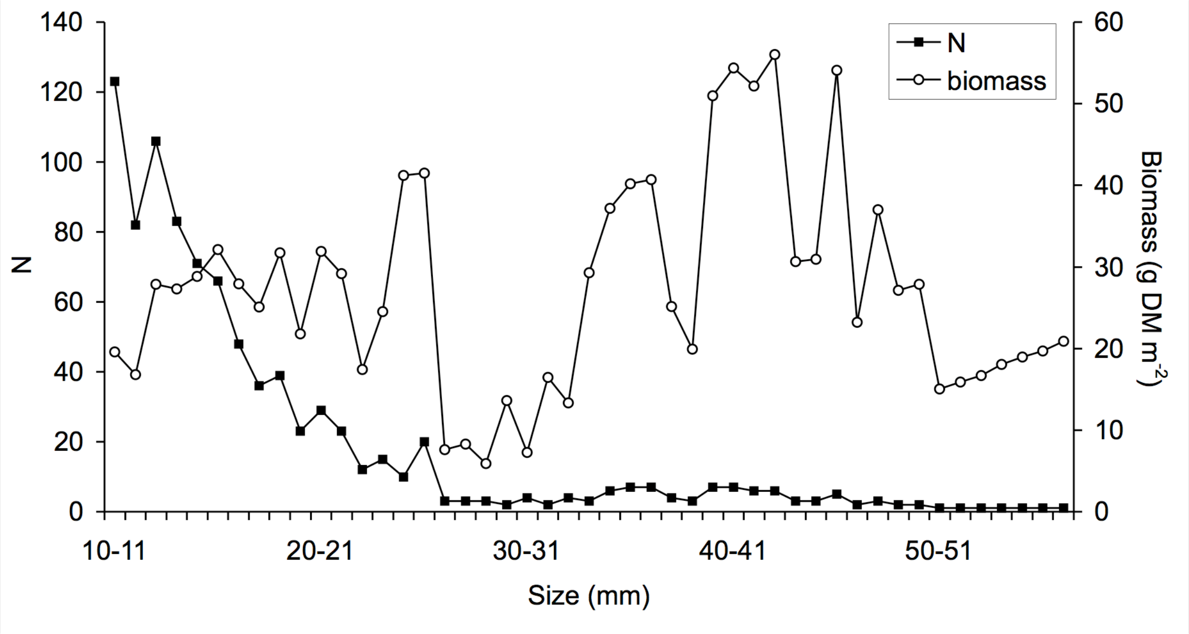

Figure 3. Relationship between the numbers of crabs collected per size class and estimated biomass.

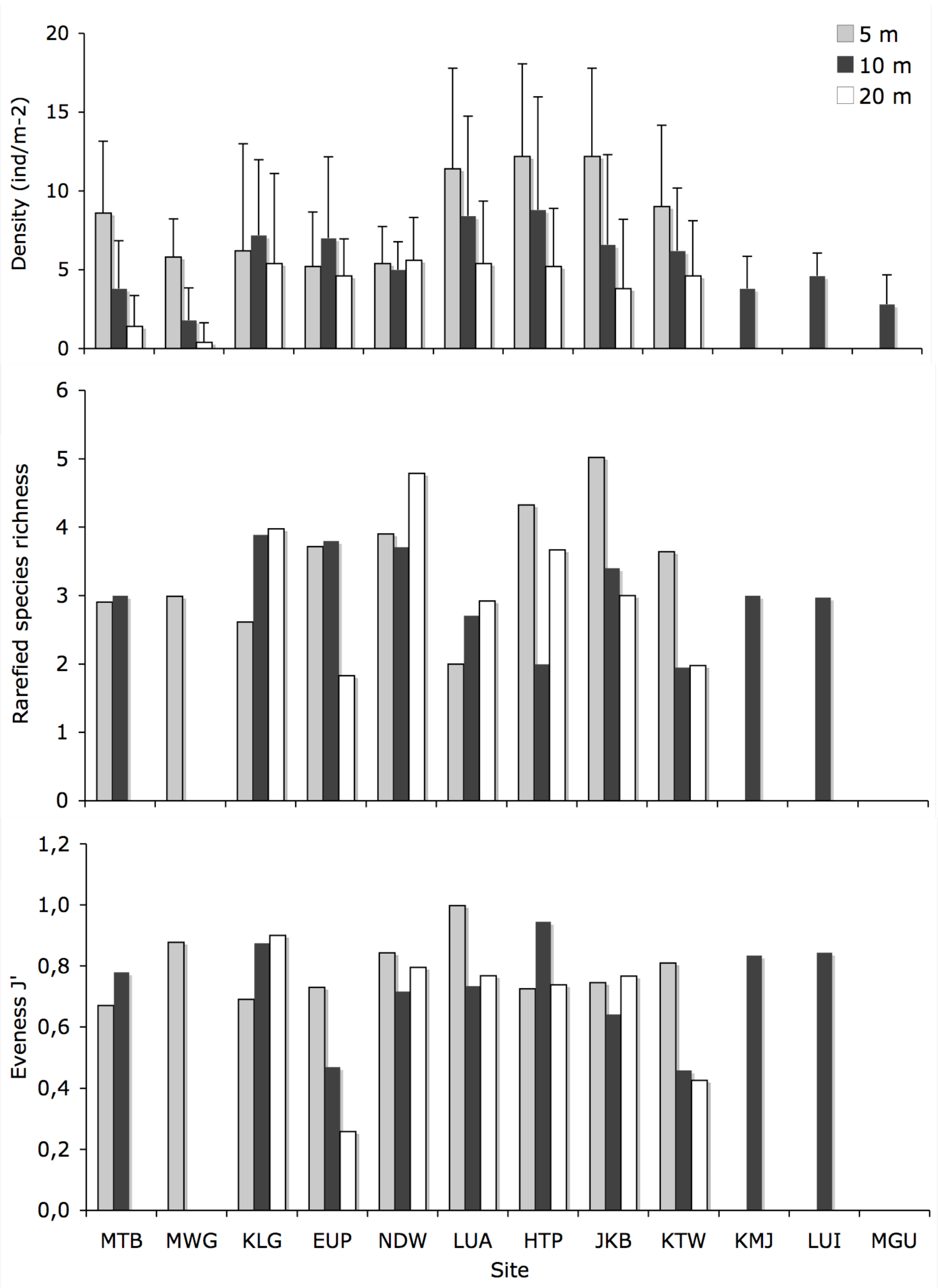

Figure 4. Spatial patterns in (a) densities, (b) rarefied species richness, and (c) evenness of endemic crabs in Lake Tanganyika. Mean (±SE) density is based on twenty quadrats at each site and depth combination. Site acronyms are explained in Figure 1.

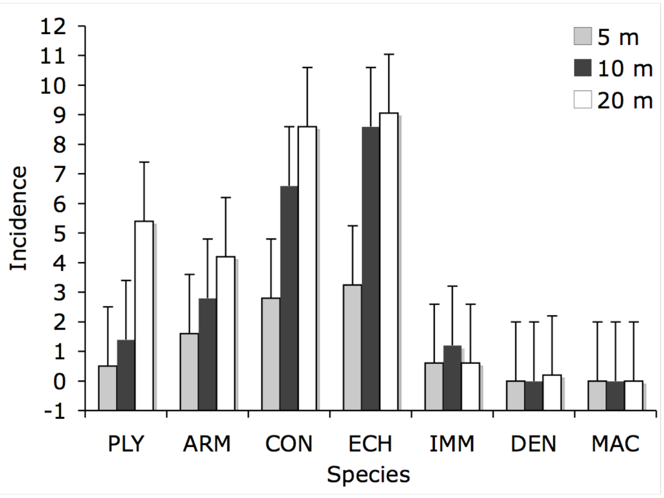

Figure 5. Incidence of crab species across depths. PLY = *Potamonautes platynotus*; ARM = *Platythelphusa armata*; CON = *P. conculcata*; ECH = *P. echinata*; IMM = *P. immaculata*; DEN = *P. denticulata*; MAC = *P. maculata*. Site acronyms are explained in Figure 1.

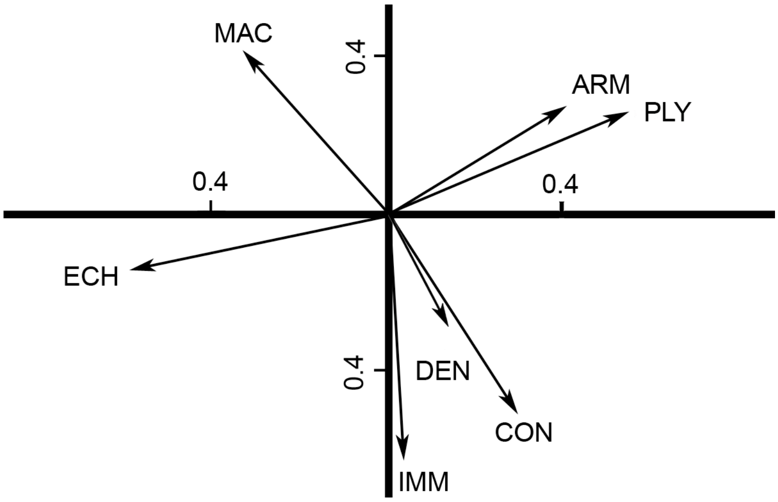

Figure 6. Results of principal component analyses on species distribution, showing the first two axes. PLY = *Potamonautes platynotus*; ARM = *Platythelphusa armata*; CON = *P. conculcata*; ECH = *P. echinata*; IMM = *P. immaculata*; DEN = *P. denticulata*; MAC = *P. maculata*.

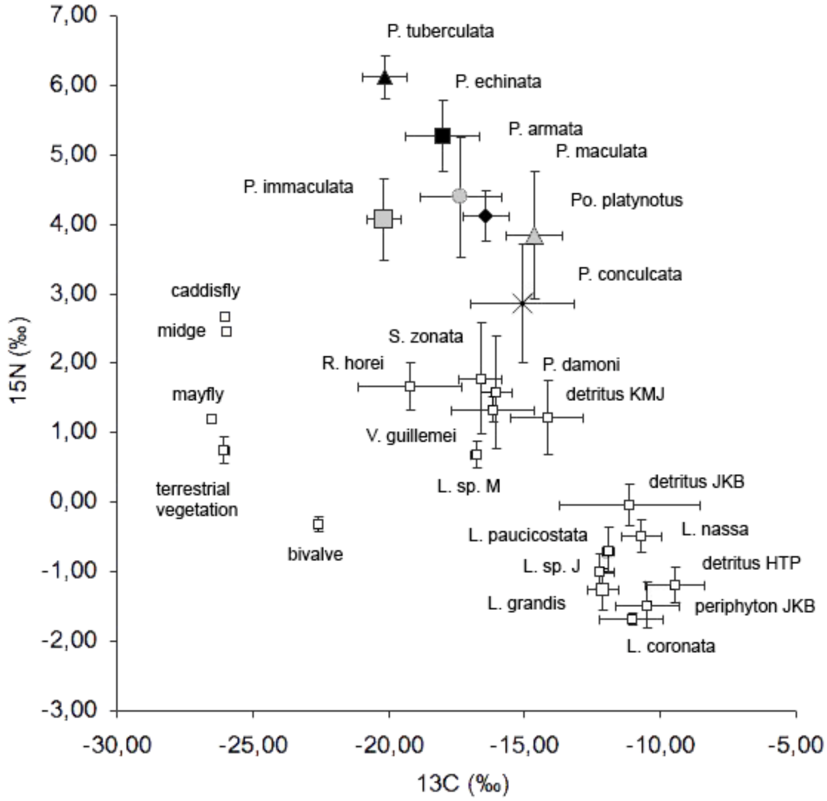

Figure 7. Stable carbon and nitrogen isotope signatures of crabs and putative food resources in Lake Tanganyika benthic littoral habitats. Site acronyms are explained in Figure 1.