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Lake Tanganyika crabs : evolution, ecology, and implications for conservation

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LAKE TANGANYIKA CRABS

Evolution, Ecology, and Implications for Conservation

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Cover: Female *Platythelphusa armata*.

Inside: Endemic crab species from Lake Tanganyika. The specimens shown here are all adult males, with exception of *Platythelphusa praelongata*, which is an adult female. Some of the natural colours of the crabs have faded as a result of preservation procedures.

LAKE TANGANYIKA CRABS

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. D.C. van den Boom

ten overstaan van een door het college voor promoties
 ingestelde commissie,
in het openbaar te verdedigen in de Aula der Universiteit

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S E M P E R A L I Q U I D N O V I A F R I C A A F F E R T

PLINY THE ELDER, ca 77 A.D.

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Chapter 1



Lake Tanganyika as a hotspot of freshwater crab diversity

1

Saskia A.E. Marijnissen

ABSTRACT

Biodiversity in Lake Tanganyika is increasingly at risk from human activities such as pollution, overexploitation, and widespread catchment deforestation resulting in excess sedimentation. In order to predict ecosystem responses to environmental perturbations, it is essential to have an enhanced understanding of the functioning of various key components of the lake ecosystem. Here, we focus on endemic freshwater crabs that have a potentially important function in benthic lacustrine foodwebs. Field surveys showed that crabs are locally abundant in rocky littoral substrates, and densities ranged from 0-28 crabs m⁻². On average, crab densities decreased with depth. Although our sampling area included sites adjacent to deforested areas as well as relatively pristine sites, we found no significant differences in species richness or evenness among sites. Estimates of crab dry mass varied from 0.0-117.7 g m⁻². By comparing stable ¹³C and ¹⁵N isotopes of crabs with those of their putative food resources, we demonstrate that crabs occupy a central position as consumers in benthic foodwebs. Mean ¹⁵N signatures of different crab species were enriched relative to those of endemic snails, bivalves, aquatic insect larvae, plant matter, and detritus. Because crabs occupy multiple trophic levels, and the different species exhibit overlapping ecological niches, we expect that community-level responses of crabs to sedimentation-related disturbances will be delayed relative to other organisms that exhibit narrower ecological niches. Our results emphasize the intricacy of benthic faunal responses to environmental perturbations. We discuss the current conservation status of the endemic crabs, as well as some general implications for strategies aimed at conserving biodiversity in Lake Tanganyika.

INTRODUCTION

The three great East African Rift Valley lakes Malawi, Tanganyika and Victoria¹ are renowned for their outstanding species richness and high levels of endemism, 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 (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 (Agnès & 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 endemism across other taxonomic groups, including gastropods, bivalves, ostracods, leeches, 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 (Table 1). Tragically, not only do the African Rift lakes include spectacular examples of evolutionary diversification, 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;

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.

T a b l e 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
Human population in catchment area	> 10 million	> 10 million	> 30 million
Human population growth rates	2.0-3.2%	2.0-4.7%	~ 6%

Data from Odada et al. (2004), Bootsma & Jorgensen (2005), Jorgensen et al. (2005), Kayombo & Jorgensen (2005).

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 agricultural discharges (Meybeck, 1985; Coulter, 1992; Tweddle, 1992; Vandelanoote et al., 1996; Bailey-Watts et al., 2000), overexploitation of 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 watershed deforestation. Conversion of forests to agricultural crops causes changes in watershed hydrological regimes, 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 & Duchaour, 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 associated nutrients can have direct as well as indirect detrimental effects on aquatic organisms. Evidence from the African Rift lakes has shown that high levels of sediment discharge negatively affect species assemblages of fish and benthic invertebrates (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

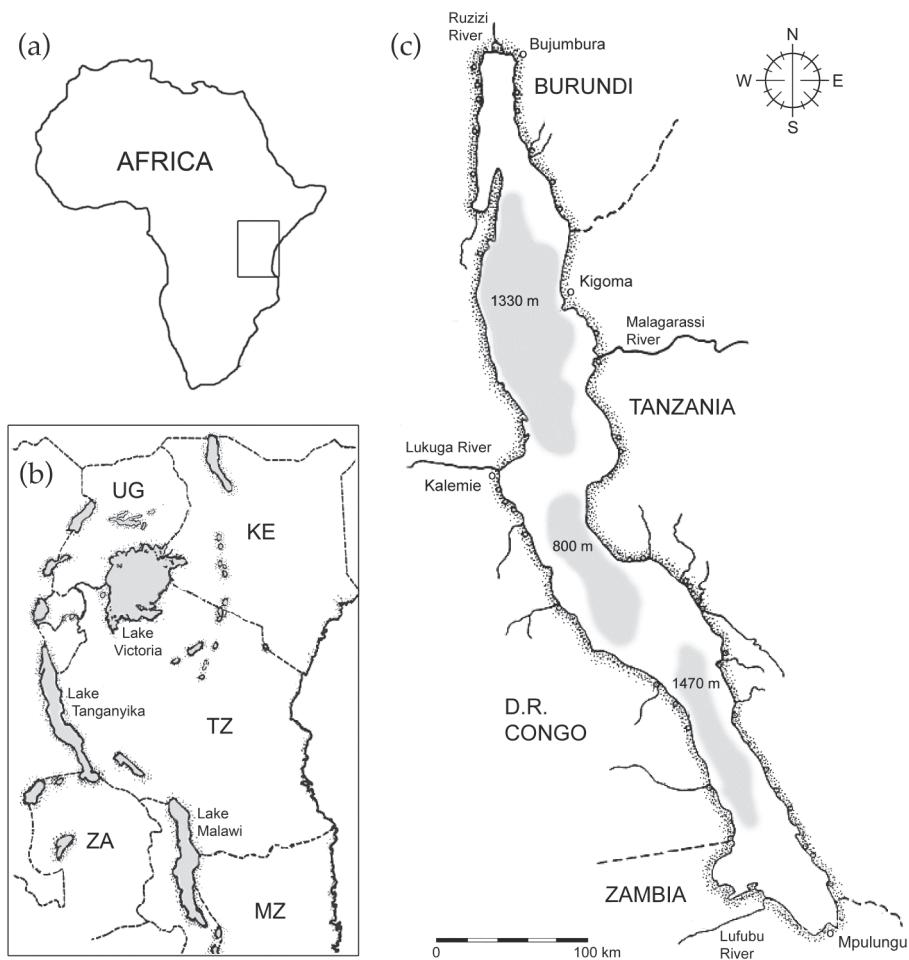


Figure 1. (a) Location of the three great African Rift Lakes. (b) Western branch of the East African Rift Valley, showing Lakes Victoria, Tanganyika, and Malawi (c) Lake Tanganyika showing the approximate area of three paleo-lakes that follow the present 600 meter depth contour. For each paleo-lake, the present maximum depth is shown (Tiercelin & Mondeguer 1991). KE, Kenya; MZ, Mozambique; TZ, Tanzania; UG, Uganda; ZA, Zambia.

(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 need for conservation interventions in these lakes. Several international projects have therefore been initiated since the early 1990s 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 caused by human activities. This requires (i) an understanding of the processes that are causal to 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).

EXPLAINING ELEVATED LACUSTRINE ENDEMICITY

The question of what has caused the high levels of diversity and endemism in the 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 to pinpoint the dominant causes of elevated endemism, and to understand 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 ($\pm 110,000$) or 89,000 ($\pm 74,000$) years ago (Genner et al., 2007). The onset of divergence in the Lake Malawi cichlid radiation was dated to either 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 also differ widely (Meyer et al., 1990; Sturmbauer et al., 1994; Duftner et al., 2005; Koblmüller et al., 2005; Won et al.,

T a b l e 2. Geological history of the Tanganyika Trough

Epoch	Event	Date ¹	Reference
MIOCENE 5.3-2.3 ma	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 Ma.	20-12 Ma	Tiercelin & Mondeguer (1991), Cohen et al. (1993)
	Transformation of the proto-Malagarassi-Congo River in a swampy area with a mosaic of shallow lakes.	12-8	Tiercelin & Mondeguer (1991), Cohen et al. (1993)
PLIOCENE 1.8-0.3 ma	Initiation of tectonic activity in northern Lake Tanganyika region (~7.8-5 Ma). Formation of the northern basin.	8-7	Lezzar et al. (1996), Cohen et al. (1997)
	Establishment of a truly lacustrine habitat. Subsidence of the graben produces progressively deeper lakes. Closing of the drainage system at the Lukuga outlet to the Congo river.	6-5	Tiercelin & Mondeguer (1991)
PLIOCENE 1.8-0.3 ma	Formation of the southern basin. Pliocene regional aridification in East and Central Africa (~3-2 Ma).	4-2	Cohen et al. (1997)
	Strong tectonic activity on the Kivu-Ruzizi Volcanic Dome (~1.9 Ma). Major lake level decline (~650-700 m bpl). Separation of the northern, middle and southern basin. Small and probably saline lakes in the northern basin.	1.1	Lezzar et al. (1996), Cohen et al. (1997), Scholz & Rosendahl (1988) ²
PLEISTOCENE 1.0 ka -1.8 ma	Rise of lake levels in the northern basin, evidence of sedimentation from the Proto-Ruzizi 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)
PLEISTOCENE 1.0 ka -1.8 ma	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 ³), followed by transgression in the northern basin between ~170-40 ka.	190-170	Cohen et al. (1997), Scholz et al. (2003)
PLEISTOCENE 1.0 ka -1.8 ma	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)
PLEISTOCENE 1.0 ka -1.8 ma	Continued lowering of lake levels, probably associated with a cooler and drier climate resulting	19-14	Gasse et al. (1989), Johnson (1996),

Table 2. (Continued)

HOLocene present-10 ka	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.		Guiot & Tiercelin (1993), Cohen et al. (1997), Scholz et al. (2003), Gasse (2000)
	Rising water levels. Increased waterflow through the Ruzizi river caused by upfolding of the Virunga volcanoes north of Lake Kivu. Establishment of post-glacial climatic conditions by ~12 ka, with increasing temperatures and humidity.	12-9	Gasse et al. (1989), Tiercelin & Mondeguer (1990), Guiot & Tiercelin (1993), Johnson (1996)
	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 & Mondeguer (1990), Nicholson (1999)

¹Note that these are all approximate numbers that are subject to discussion and must be interpreted with caution.
²Scholz & 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 & Mondeguer (1991) estimated a minimum of 200,000 years based on a rate of 0.5 mm/year sedimentation that was calculated for marine sediments. ³Scholz 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.

2005, 2006; Genner et al., 2007). Estimates for the onset of marked divergence in Lake Tanganyika *Synodontis* catfish range between 2.6 (\pm 0.9) and 2.0 (\pm 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 Lake 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 climatic fluctuations. Both of these forces have led 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 indicate 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 shown numerous fluctuations in Lake Malawi (Owen et al., 1990; Nicholson, 1998; Johnson et al., 2001, 2002), as well as in Lake Tanganyika (Table 2), 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 have been to a high degree isolated from riverine habitats. Furthermore, by dividing larger bodies of water into smaller ones, lake level drops have caused temporary geographic isolation between populations of formerly interbreeding individuals. If a period in which the lake level is low 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 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; Schlüter, 1996, 2000). Adaptive radiation is defined as the evolution of ecological and phenotypic diversity within a rapidly multiplying lineage (Schlüter, 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 (Schlüter, 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 endemism 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 (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 & Kocher, 2006). 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; Rüber et al., 1999; 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

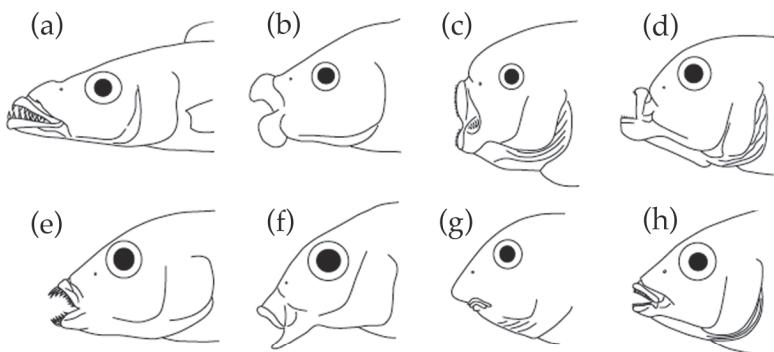


Figure 2. Diversity in trophic morphologies among cichlid species. (a) *Rhamphochromis macrourus*, a piscivore; (b) *Haplochromis euchilus*, a sand-digger; (c) *Petrotilapia tridentiger*, a rock scraper; (d) *Genyochromis mento*, a scale eater; (e) *Labidochromis vellicans*, a picker of small arthropods; (f) *Lethrinops brevis*, a sand-digger; (g) *Labeotropheus fuelleborni*, an algivorous rock scraper; (h) *Haplochromis similis*, a leaf chopper (from Mabuchi et al., 2007).

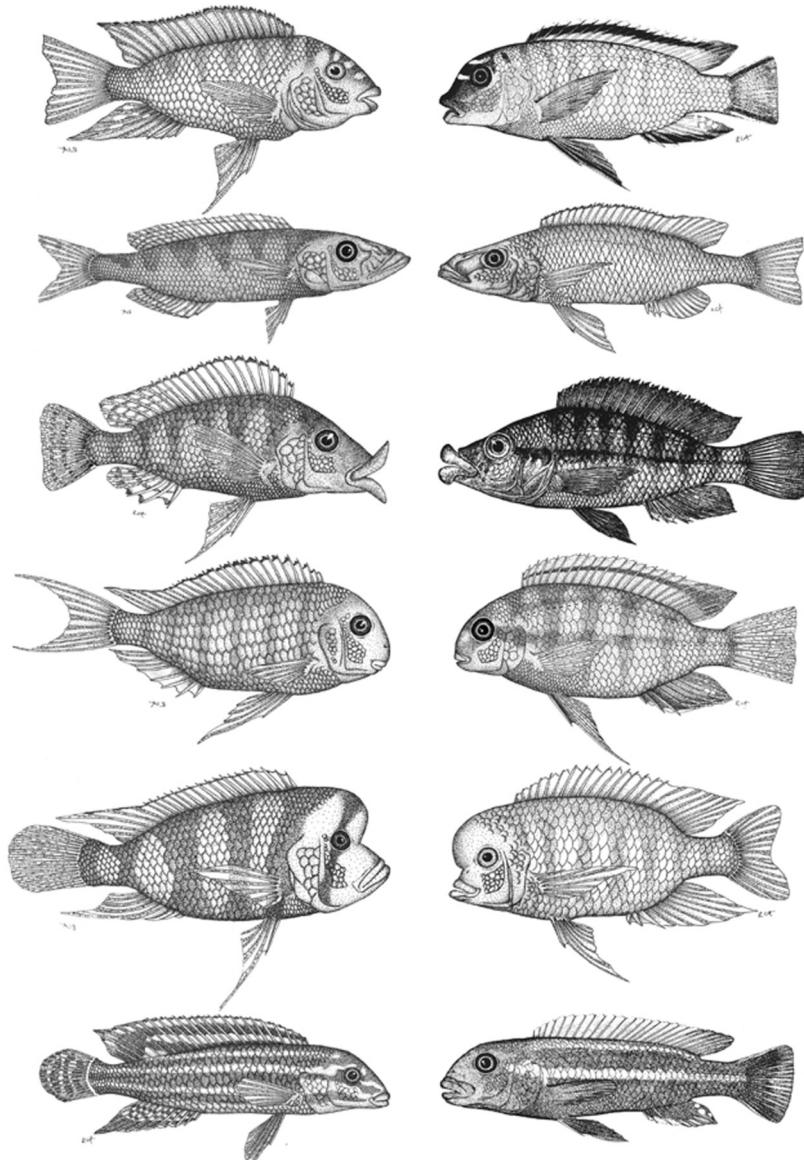


Figure 3. Convergence of body shapes among cichlid species from two African Rift Valley Lakes. Left column shows species from Lake Tanganyika, and the right column shows cichlid species from Lake Malawi (from Albertson & Kocher, 2006).

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 propensity 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 the traits that are under natural selection, or on recruitment of other isolating traits through the 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 indicates that this is not necessarily 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 can 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 THE 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 are 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; Takamur,a 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 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 adult 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*², 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 Cunningham (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 the literature and museum material with newly collected specimens from Lake Tanganyika, I found several discrepancies. This resulted in comments on the taxonomic position of *Platythelphusa denticulata*, and the description of the new species *Platythelphusa immaculata* and *Platythelphusa praelongata* in CHAPTER 2. This chapter

² The genus name *Platythelphusa* is derived from a combination of the Greek 'platy', which means flat or broad, and 'thelphusa', which refers to a spring that plays a role in Greek mythology.

furthermore provides a taxonomic key to the species of *Platythelphusa*. With the description of two new species, and the removal of *P. denticulata* from synonymy with *P. conculcata*, the total number of platyhelphusid species from Lake Tanganyika was raised to nine. Although this might seem like a small number compared to 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; Reed & Cumberlidge, 2006), 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 of what has caused the morphological diversity and elevated endemism 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 abri³”, A. Milne-Edwards (1887, p. 146) provided the very first 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’*Eriocheirus 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 courantes⁴.” 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 4). Freshwater crab hatchlings are miniature crabs complete with an abdomen folded underneath the sternum in the sternoabdominal cavity, four pairs of walking legs and two claws. Female freshwater crabs protect their 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 crabs in Lake Tanganyika are derived from freshwater crab ancestors. However, Moore (1903) questioned this. He

³ “The abdomen of this female is enormous, 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 abdomen and the absence of metamorphosis in the juveniles, which makes it certain that it should be assigned to a freshwater genus.

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 of whether the ‘marine habitus’ of the Lake Tanganyika platyhelphusids 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 analysis of the platyhelphusid crabs using representatives of six different families as outgroups. Their study did not support the idea that the platyhelphusids emerged from a relict population of a grapsid or grapsid-like taxon. Instead, cladistic analyses supported the idea that the platyhelphusids evolved from freshwater ancestors (von Sternberg & Cumberlidge, 1999). However, no consensus was achieved about their closest relatives (compare Cumberlidge & von Sternberg, 1999; von Sternberg et al., 1999; von Sternberg & Cumberlidge, 1999, 2001), and consequently the evolutionary history of the platyhelphusids remained enigmatic. Therefore, I examined the phylogenetic relationships of the Lake Tanganyika endemic crabs using sequences of 12S and 16S rRNA mitochondrial DNA in CHAPTER 3. Mitochondrial phylogenies generally provide very reasonable working hypotheses. Assuming that the patterns described in this chapter are accurate, the following conclusions can be drawn: (i) it is likely that the platyhelphusids are derived from East African freshwater ancestors (see also Daniels et al., 2006); (ii) the platyhelphusids are more closely related to each other than to other African freshwater lineages; (iii) branches within the platyhelphusid clade are short, and (iv) platyhelphusid species are relatively young. This indicates that the endemic crab radiation

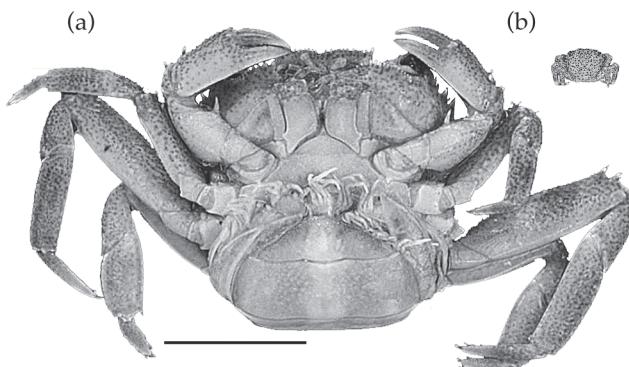


Figure 4. (a) *Platylephusa conculcata* with hatchlings in its brood pouch. (b) Juvenile *P. conculcata* at approximately the size of release from the brood pouch. Scale bar represents 10 mm. Pictures taken by Louis van der Laan.

shows great potential to serve as an invertebrate model for studies on speciation in Lake Tanganyika.

CHAPTER 4 focuses on two major processes that might have been important in contributing to the divergence of the endemic Lake Tanganyika crabs: ecological niche partitioning and sexual selection. The approach that I took in this chapter was to first provide a more extensive mitochondrial phylogenetic framework based on sequences of 16S rRNA and cytochrome oxidase II mtDNA, and then to use this framework to examine 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). Morphological comparisons between the claws of *P. armata* and other freshwater crabs, in combination with a series of shell-crushing- and predation experiments provided strong support for the hypothesis that the unusual morphological derivation of the Lake Tanganyika gastropods is the result of lacustrine coevolutionary interactions with specialised molluscivores (West et al., 1991; West & Cohen, 1994, 1996; also see Soccia, 2001; Rosales, 2002). I discuss similarities and differences between *P. armata* and *Potamonautes platynotus*, which is also endemic to Lake Tanganyika (see Cunningham, 1907). I then compare claw performance properties of *Platythelphusa tuberculata* that exhibit strong indications of sexual selection. I subsequently focus on divergence of claw functional morphological traits within the platyhelphusid clade as a whole. The results of these analyses indicate that both ecological niche partitioning as well as sexual selection interact to generate diversity in Lake Tanganyika endemic crabs.

CHAPTER 5 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 a 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 6, and infer their level of vulnerability to environmental perturbations. Finally, I discuss general implications for the conservation of biodiversity in Lake Tanganyika.

Chapter 2



Two new species of *Platythelphusa*
A. Milne-Edwards, 1887 (Decapoda,
Potamoidea, Platythelphusidae) and
comments on the taxonomic position
of *P. denticulata* Capart, 1952

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Crustaceana 77:513-532

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 plathyhelphusid species reported from Lake Tanganyika to nine. A key is provided to separate the species of *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 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 the lake. 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; Cunningham, 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* Cunningham, 1899, *P. concilcata* Cunningham, 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. concilcata* (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 platyhelphusid 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, Belgium.

TAXONOMY

Family PLATYTHELPHUSIDAE Colosi, 1920

Platythelphusa A. Milne-Edwards, 1887

Platythelphusa immaculata n. sp. (Figure 1 a-d)

MATERIAL EXAMINED

Holotype, 1 male, cw 18.22 mm (ZMA De.204594), Lake Tanganyika, Cape Mpimbwe near Katondo Point, Tanzania ($7^{\circ}05.59'S$ $30^{\circ}30.00'E$), 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 ($4^{\circ}55.05'S$ $29^{\circ}35.73'E$), 10 m depth, cobbles and sand, coll. S.A.E. 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 ($4^{\circ}54.730'S$ $29^{\circ}35.901'E$), 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.A.E. 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 ($4^{\circ}54.73'S$ $29^{\circ}35.90'E$), 2-20 m depth, rocks and cobbles, coll. S.A.E. 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 ($8^{\circ}45.23'S$ $31^{\circ}05.14'E$), 7 m depth, rocks and sand, coll. S.A.E. 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 (Figure 1a). Suborbital margin lined with small tooth-like tubercles; medial end of margin with narrow, pointed tooth (Figure 1c). Lateral, superior, and inferior margins of merus of cheliped granulate. Inner margin of carpus of cheliped with two large subequal

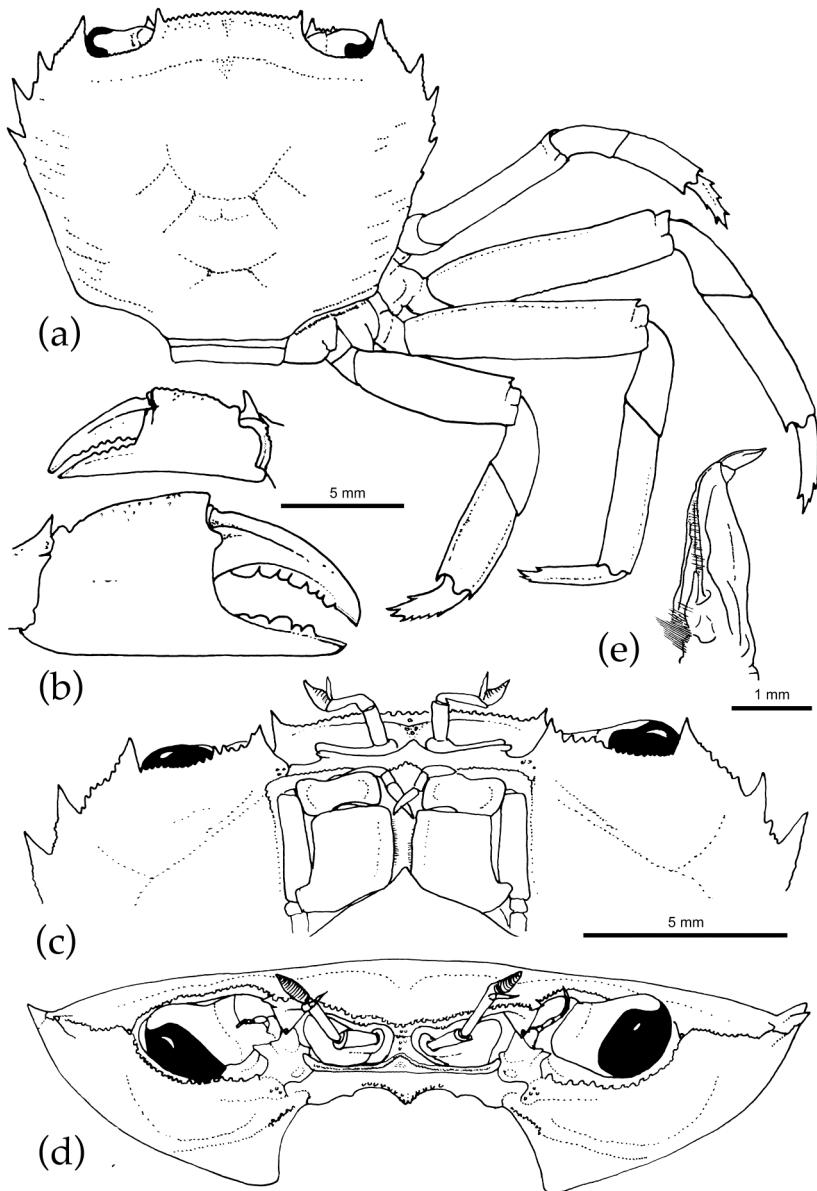


Figure 1. *Platythelphusa immaculata* n. sp., male, CW 18.22 mm, holotype (ZMA De.204594). (a) dorsal view of carapace and pereiopod 2-5; (b) frontal view of left (above) and right (below) cheliped; (c) ventral view of anterior area of carapace showing suborbital margin and 3rd maxillipeds; (d) frontal view of carapace; (e) ventral view of right gonopod 1.

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 (Figure 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. Terminal article of Go1 directed outward at a 60° angle to the vertical; slim cone-shaped article tapering strongly to pointed tip (Figure 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 (Figure 1a). Triangular descending process of front produced into a small tooth. Occlusal (sub-ocular) tooth in orbital hiatus well developed (Figure 1d). Suborbital margin with a prominent shelf, lined with irregular shaped, tooth-like tubercles (Figure 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 ($0.66 \times$ merus length), robust ($0.33 \times$ ischium width); distinct distal medial process of exopod, exopod with long flagellum. Epimeral sulcus present on sidewall of the 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. Epsisternal 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. conculkata*, *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. conculkata* and *P. echinata*. *Platythelphusa immaculata* is distinguished from *P. conculkata* by differences in the relative height and width of the carapace; in the frontal margin, which is fringed with pronounced tooth-like tubercles in *P. conculkata*, 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. conculkata* (Table 1 and 2). Finally, the angle of the terminal article of gonopod 1 differs between *P. conculkata* and *P. immaculata* (Table 1). *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 1).

Platythelphusa praelongata n. sp. (Figure 2 a-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 with several irregularly shaped small teeth and one large broad tooth lateral to mesogastric region (Figure 2a). Suborbital margin lined with large granules; broad low tooth at medial end (Figure 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 (Figure. 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 (Figure 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 (Figure 2d). Suborbital margin with a prominent shelf, lined with small tooth-like tubercles (Figure 2c). First antennal segment oval, fused into epistome; proximal-most 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 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 x merus

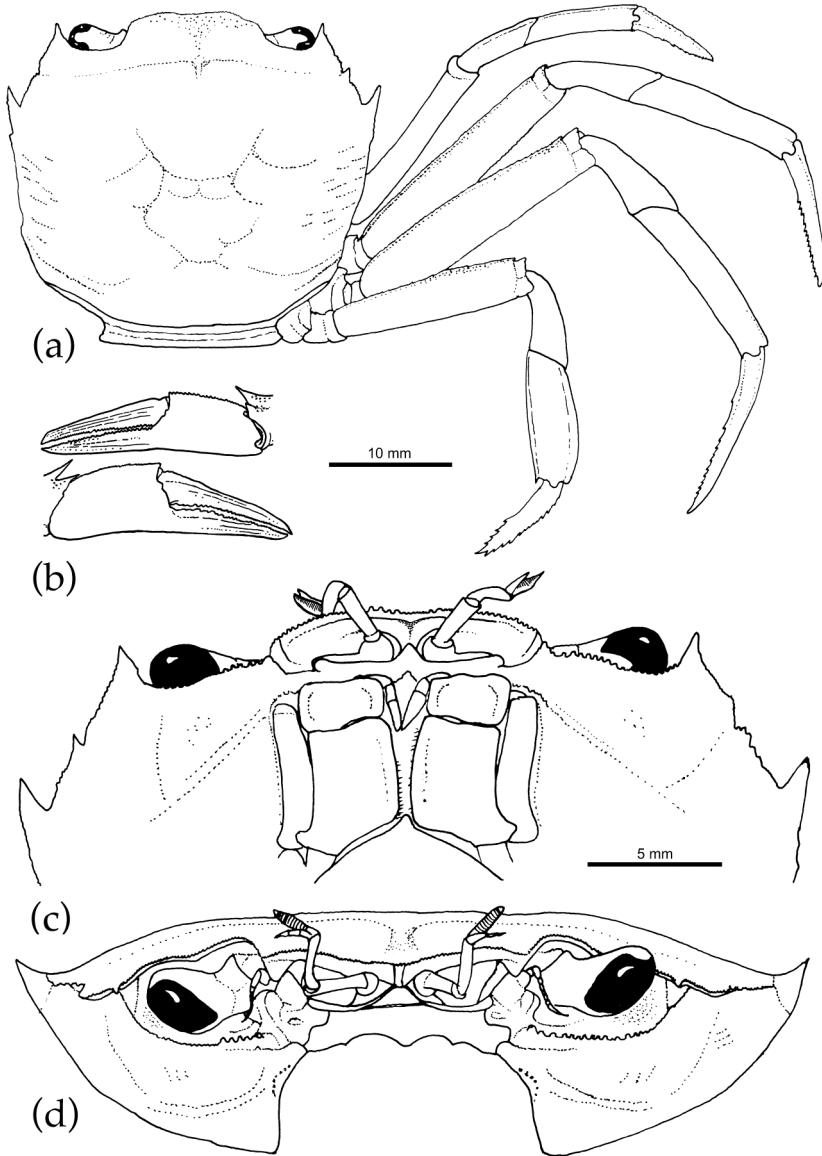


Figure 2. *Platythelphusa praelongata* n. sp., female (gravid), CW 28.76 mm, holotype (ZMA De.204595). (a) dorsal view of carapace and pereiopod 2-5; (b) frontal view of left (above) and right (below) cheliped; (c) ventral view of anterior area of carapace showing suborbital margin and 3rd maxillipeds; (d) frontal view of carapace.

length), robust ($0.33 \times$ ischium width); with distinct distal medial process and long flagellum.

Carapace with epimeral sulcus on the sidewall of the carapace, 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 (bouton 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 ($CW = 3.02 \pm 0.08$ mm, $CL = 2.83 \pm 0.12$ 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 by only 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 1 and 2).

DISCUSSION

The platyhelphusid 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, Cunningham (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* Cunningham, 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 Cunningham (1899) acknowledged lacked sufficient information to determine the exact relationships between the two genera. In a later paper, Cunningham (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 Potamoniidae (Rathbun, 1904, 1905; Alcock, 1910; Bouvier, 1917a, b, 1921; Cunningham, 1920; Capart, 1952; Bott, 1955; Balss, 1957), the Plathyhelphusinae (Colosi, 1920), and the Potamonautidae (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

Table 1. Morphological comparison of the nine species of *Platythelphusa* recognized herein.

	<i>P. armata</i> A. Milne-Edwards, 1887	<i>P. denticulata</i> Capart, 1952	<i>P. maculata</i> Cunnington, 1899	<i>P. praelongata</i> n. sp.	<i>P. tuberculata</i> 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	finely 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 teeth	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	2 or 3 teeth, tooth lateral of mesogastric region
Suborbital margin	small regular shaped, tooth-like tubercles	irregular tooth-like tubercles	minute regular shaped, tooth-like tubercles	small regular shaped, tooth-like tubercles	always the largest minute regular shaped,
Suborb. margin, medial end	large, pointed tooth	narrow, pointed tooth	broad, low tooth	broad, low tooth	tooth-like tubercles broad, pointed tooth
3 rd Maxillipeds	gape absent	gape absent	gape absent	gape absent	slight gape
medial margins	slightly raised	slightly raised	slightly raised	not raised	pronouncedly raised
Epibranchial lobes					

Table 1. (Continued).

	<i>P. immaculata</i> n. sp.	<i>P. conculcata</i> Cunnington, 1907	<i>P. echinata</i> Capart, 1952	<i>P. polita</i> Capart, 1952
Frontal margin	almost horizontal, indented granular	almost horizontal, indented tuberculated	slightly deflexed, slightly indented finely granular	deflexed, slightly indented minutely granular
Frontal margin	square, with sharp tooth	square, with sharp tooth	square, with small low tooth, sometimes lacking tooth	square, without tooth
Front, external angles				
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
3 rd Maxillipeds	gape absent	gape absent	gape absent	gape absent
medial margins				
Epibranchial lobes	not raised	not raised	not raised	not raised

Table 1. (Continued).

	<i>P. armata</i>	<i>P. denticulata</i>	<i>P. maculata</i>	<i>P. praelongata</i>	<i>P. tuberculata</i>
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,	granular,	granular,
Cheliped merus, superior margin	finely granular	granular, sometimes with small distal tooth	finely granular	large distal tooth	large distal tooth
Ischium P1-P5, inferior margin	smooth	granular	granular	finely granular	granular
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
Propodus P3-P4, inferior margin	smooth	smooth	smooth	smooth	smooth
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 1. (Continued).

	<i>P. immaculata</i>	<i>P. concavata</i>	<i>P. echinata</i>	<i>P. polita</i>
Intersexual dimorphism between chelipeds	present	present	present	present
Cheliped dactyls, 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	smooth, small distal tooth	smooth, small distal tooth
Cheliped merus, superior margin	granular	granular, smaller distal tooth	granular, large distal tooth, sometimes with several unequal teeth	finely granular
Ischium P1-P5, inferior margin	granular	sometimes minute distal spine	posterior to distal tooth	finely granular
Merus P2-P4, subdistal tooth	small spine	pointed spine	granular	finely granular
Merus P2-P4, distal tooth	small spine, sometimes no spine	pointed spine	pointed spine	no spine
Merus P2-P4, inferior margin	minutely serrated	minutely serrated	small spine, sometimes no spine	no spine
Propodus P2, inferior margin	smooth	smooth	row of spines	minutely serrated
Propodus P3-P4, inferior margin	smooth	smooth	row of spines	several minute spines
Dactylus P3-P4, superior margin	smooth, with several distal spines	smooth	row of spines	several minute spines
Dactylus P3-P4, inferior margin	smooth, with several distal spines	smooth, with several distal spines	smooth, with several distal spines	row of spines
Gonopod 1, angle of terminal segment	60°	90°	90°	60°

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 platyhelphusid species flock (Cumberlidge, 1999; Cumberlidge & Von Sternberg, 1998; 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 has a smooth, short, strongly tapering to 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 x 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. conculkata*, 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. conculkata* and considered Cunningham's (1907) type to be a junior synonym of either *P. armata* or *P. maculata*. Cumberlidge et al. (1999) recognized the validity of *P. conculkata* 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. conculkata* 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. conculkata* is flat and the pereiopods lack a distal meral spine. Bott (1955) recognized only one species of platyhelphusid (*P. armata*), which he considered to be a subgenus of *Potamonautes*, treating *P. maculata* as a junior synonym of *P. armata*, and *P. conculkata* 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. conculkata*.

Cumberlidge et al. (1999) tentatively treated *P. denticulata* as a junior synonym of *P. conculkata* on the basis of the figure of *P. denticulata* provided by Capart (1952: Figure 2), which clearly shows characters that are characteristic of *P. conculkata*, 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 ($6^{\circ}30.00'S$ $29^{\circ}55.00'E$). 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 1 and 2). 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 1 and 2).

T a b l e 2. Carapace proportions (\pm SD) 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	CW/FW	CL/FW	Merus P5/FW	Moult of Puberty (CW mm)	CW max ¹ (mm)
<i>P. polita</i>	1.13 ± 0.05	2.38 ± 0.10	1.94 ± 0.08	0.76 ± 0.03	11.4 – 13.0	18.0 ²
<i>P. tuberculata</i>	1.08 ± 0.12	2.82 ± 0.27	2.29 ± 0.22	1.43 ± 0.09	17.8 – 18.5	39.9
<i>P. armata</i>	1.07 ± 0.13	2.75 ± 0.20	2.34 ± 0.16	1.07 ± 0.08	35.7 – 38.3	60.0
<i>P. maculata</i>	1.02 ± 0.05	2.34 ± 0.10	2.06 ± 0.09	0.92 ± 0.05	11.0 – 12.9	17.9
<i>P. denticulata</i>	0.93 ± 0.04	2.49 ± 0.09	2.12 ± 0.09	1.01 ± 0.04	18.4 – 21.4	46.0
<i>P. praelongata</i> n. sp.	0.90	2.72	2.37	1.05	?	28.9
<i>P. immaculata</i> n. sp.	0.87 ± 0.05	2.70 ± 0.14	2.24 ± 0.22	1.09 ± 0.06	16.9 – 21.2	31.0
<i>P. echinata</i>	0.79 ± 0.09	2.41 ± 0.17	1.92 ± 0.10	0.95 ± 0.14	12.6 – 17.7	39.0
<i>P. conculcata</i>	0.78 ± 0.05	2.45 ± 0.11	2.20 ± 0.12	1.11 ± 0.14	11.3 – 17.8	30.3

¹Carapace width of the largest known specimen. ²Data from Cumberlidge et al. (1999). Numbers of specimens examined for each species: *Platythelphusa polita* n=8; *P. tuberculata* n=92; *P. armata* n=241; *P. maculata* n=31; *P. denticulata* n=1; *P. praelongata* n=1; *P. immaculata* n=25; *P. echinata* n=45; *P. conculcata* n=81.

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 width5
- 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* Cunningham, 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* Cunningham, 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.

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Chapter 3



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

3

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ABSTRACT

The freshwater crab family Platythelphusidae encompasses a taxonomically modest, but morphologically diverse radiation of nine species endemic to Lake Tanganyika. Several platythelphusid species exhibit morphological characters that are reminiscent of marine ancestry, which prompted the hypothesis that the platythelphusids are among the most primitive of the extant species of African freshwater crabs. An alternative hypothesis is that the unusual morphological features of these crabs are the result of convergent evolution. We use 12S and 16SRNA mtDNA to test hypotheses on the origin of morphological disparity of the platythelphusid crabs. The phylogenetic patterns recovered by our analyses offer evidence for common ancestry of the Platythelphusidae, and provide support for a recent radiation.

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 (Kornfield and Smith, 2000; Kocher, 2004). 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, pers. comm.). Of the ten 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 Potamonautilidae. 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 plathyhelphusids 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 (Cunnington, 1899; Moore, 1903; Bott, 1955). Alternatively, it was suggested that convergent evolution caused the unusual appearance of plathyhelphusids (Cunnington, 1920; von Sternberg and Cumberlidge, 1999). These two hypotheses lead to fundamentally different predictions regarding (a) the phylogenetic placement of plathyhelphusids with respect to other freshwater crabs, and (b) the position of the most derived plathyhelphusid within its own clade.

So far, only morphological characters have been used to infer evolutionary relationships of the plathyhelphusid 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; Daniels et al., unpublished). 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.

MATERIALS AND METHODS

Platyhelphusid 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 *Platyhelphusa*. For seven of these we included multiple representatives, however a single individual of *P. praelongata* was available (see Marijnissen et al., 2004). Extensive efforts to collect *P. polita* were unsuccessful at the sites surveyed. Crabs were collected either by hand through SCUBA diving, or obtained from local fishermen (*P. 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 *Platyhelphusa* 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 *Potamonautes 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 reactions contained 14.9 µl millipore water, 3 µl of 25 mM MgCl₂, 2.5 µl of 10 x Mg²⁺ 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.

Sequences were aligned in CLUSTAL X 1.81 (Thompson et al., 1997) under default settings and optimized manually (Page & 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,

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

Species	Code	Locality	Latitude, longitude	12S	16S
<i>Platyhelphusa armata</i> (A. Milne-Edwards, 1887)	JKB	Jakobsen	LT, TZ 29°35.85'E	DQ203187	DQ203213
<i>Platyhelphusa armata</i>	MBT	Mbita	LT, ZM 31°05.14'E	DQ203188	DQ203214
<i>Platyhelphusa armata</i>	UJJ	Ujiji	LT, TZ 29°41.82'E	DQ203189	DQ203215
<i>Platyhelphusa conculcata</i> Cunnington, 1907	HTP	Hilltop	LT, TZ 29°36.90'E	DQ203190	DQ203216
<i>Platyhelphusa conculcata</i>	JKB	Jakobsen	LT, TZ 29°35.90'E	DQ203191	DQ203217
<i>Platyhelphusa conculcata</i>	KIG	Kigoma	LT, TZ 29°37.21'E	DQ203192	DQ203218
<i>Platyhelphusa denticulata</i> Capart, 1952	KAB	Kabwe	LT, TZ 30°33.00'E*	DQ203194	DQ203220
<i>Platyhelphusa denticulata</i>	MZG	Mzungu	LT, TZ 29°35.73'E	DQ203193	DQ203219
<i>Platyhelphusa echinata</i> Capart, 1952	HTP	Hilltop	LT, TZ 29°35.80'E	DQ203196	DQ203222
<i>Platyhelphusa echinata</i>	MPL	Mpulungu	LT, ZM n.a.	DQ203197	DQ203223
<i>Platyhelphusa echinata</i>	UJJ	Ujiji	LT, TZ 29°43.27'E	DQ203195	DQ203221
<i>Platyhelphusa immaculata</i> Marijnissen et al., 2004	JKB	Jakobsen	LT, TZ 29°35.90'E	DQ203199	DQ203225
<i>Platyhelphusa immaculata</i>	KTB	Katabe	LT, ZM 29°35.67'E	DQ203200	DQ203226
<i>Platyhelphusa immaculata</i>	MBT	Mbita	LT, TZ 31°05.14'E	DQ203198	DQ203224
<i>Platyhelphusa maculata</i> (Cunnington, 1899)	KAS	Kasanga	LT, TZ 31°08.60'E*	DQ203201	DQ203227
<i>Platyhelphusa maculata</i>	KMJ	Kangamoja	LT, TZ 29°41.20'E	DQ203202	DQ203228
<i>Platyhelphusa maculata</i>	MPL	Mpulungu	LT, ZM 31°06.40'E	DQ203203	DQ203229
<i>Platyhelphusa praelongata</i> Marijnissen et al., 2004	MPL	Mpulungu	LT, ZM 31°05.14'E	DQ203204	DQ203230
<i>Platyhelphusa tuberculata</i> Capart, 1952	UJJ	Ujiji	LT, TZ 29°30.00'E*	DQ203206	DQ203232
<i>Platyhelphusa tuberculata</i>	MBT	Mbita	LT, ZM 31°05.34'E	DQ203205	DQ203231
<i>Potamonautes emini</i> (Hilgendorf, 1892)	GMB	Gombe	LT, TZ 29°37.81'E	DQ203207	DQ203233
<i>Potamonautes emini</i>	KIV	Ruzizi	LK, DC n.a.	DQ203208	DQ203234
<i>Potamonautes niloticus</i> (H. Milne-Edwards, 1837)	SRD	n.a.	n.a.	AY 803496	AY 803536
<i>Potamonautes lirrangensis</i> (Rathbun, 1904)	KIV	Ruzizi	LK, DC n.a.	DQ203210	DQ203236
<i>Potamonautes lirrangensis</i>	MAL	Thumbi West	LM, MW n.a.	DQ203209	DQ203235

T a b l e 1. (Continued)

<i>Potamonautes lirrangensis</i>	ZAM	Uazua	LT, ZM	n.a.	DQ203211	DQ203237
<i>Potamonautes platynotus</i> (Cunnington, 1907)	KAL	Kalemie	LT, DC	5°55.60'S, 29°11.60'E*	DQ203212	DQ203238
<i>Potamonautes clarus</i> Gouws et al., 2000	OLI	Oliviers- hoekpas	KZ, SA	n.a ^a	AY042320	AY042241
<i>Potamonautes brincki</i> (Bott, 1960)	FER	Fernkloof	WC, SA	n.a ^a	AY042322	AY042244
<i>Potamonautes depressus</i> (Krauss, 1843)	COL	Coleford	KZ, SA	n.a ^a	AY042325	AY042247

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 (Posada 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*4 b10 under default settings. Maximum likelihood and parsimony analyses were performed using heuristic searches and TBR branch swapping with ten 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 & Huelsenbeck, 2003). Bayesian inference of phylogeny (BI) was performed using eight Markov chains, ten 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 platyhelphusid 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*4 b10 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).

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 variable 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 Akaike Information Criterion (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 platyhelphusids 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 Platytelphusidae. Average 12S rRNA and 16S rRNA sequence divergence (uncorrected *p*-distances) between *Platyhelphusa* 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 platyhelphusid lineage separated from Potamonautidae approximately 9.0–6.5 Myr ago, while divergence of the platyhelphusid 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 Platytelphusidae (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).

DISCUSSION

The platyhelphusids 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 Platylhelphusidae is an unequivocal genetic clade, with surprisingly short internal branches. The endemic Tanganyikan potamonatid *Potamonautes platynotus* does not cluster with the platylhelphusids, 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 Platylhelphusidae 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 (Schubart et al., 1998a; Daniels et al., 2003; Bossuyt et al., 2004). The limited sequence divergence (0.4–2.7%) between the platylhelphusid taxa indicates that their lineages might have diverged too recently for the 12S rRNA and 16S rRNA 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 (Moran and Kornfield, 1993; Albertson et al., 1999; Takahashi et al., 2001).

A study of morphologically almost indistinguishable allopatric populations of *Potamonautes 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 (Sturmbauer et al., 1996; Schubart et al., 1998b), the major cladogenetic events between *Potamonautes 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 platylhelphusid 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 platylhelphusid 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 platylhelphusids underlines that the unusual morphologies of these crabs are not a reflection of retained plesiomorphies. This is corroborated by (a) cladistic analyses (von

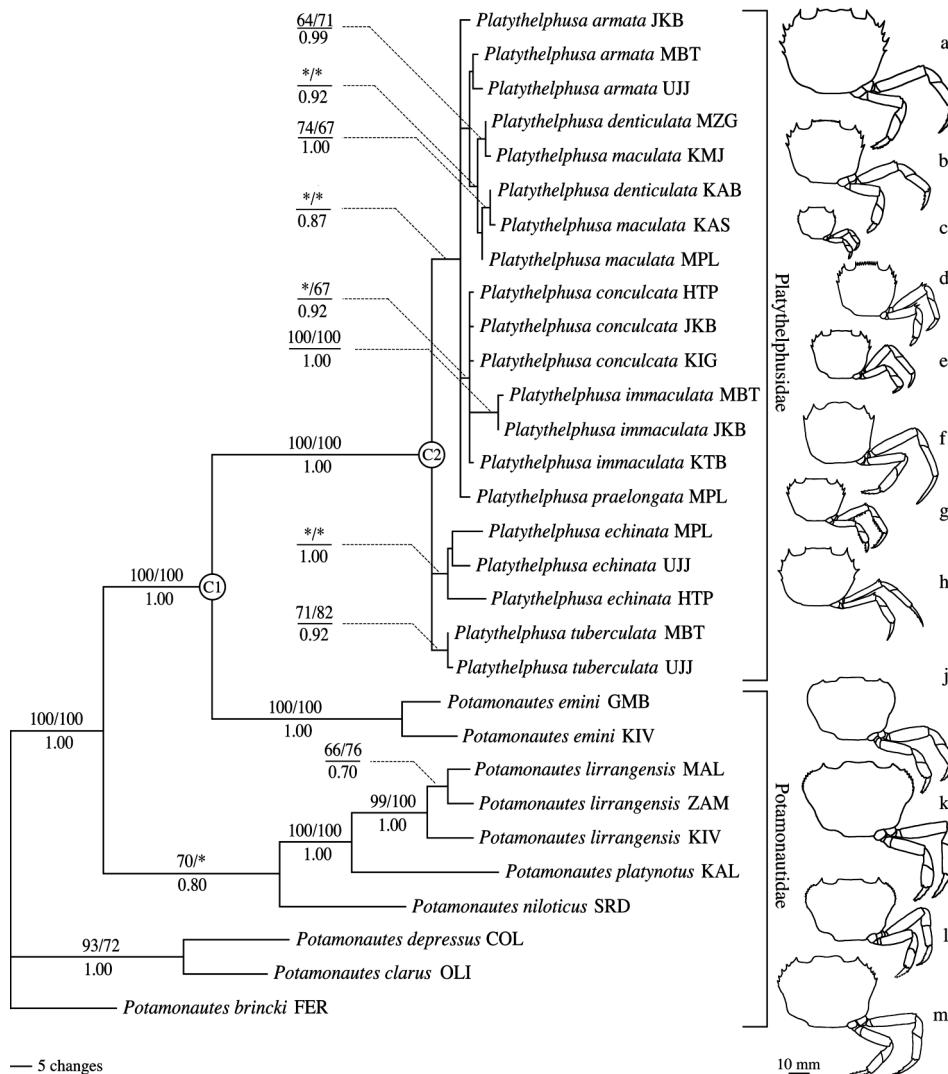


Figure 1. Maximum likelihood tree of combined 12S and 16S rRNA mtDNA sequences, with branch lengths proportional to number of changes. Taxon labels indicate morphological species diagnosis and locality acronym (see Table 1). Numbers above nodes denote maximum likelihood and parsimony bootstrap support values, followed by Bayesian posterior probabilities. *Indicates support less than 60% in otherwise supported branches. Node C1 represents the origin of the plathyhelphusid lineage, estimated 9–6.5 Myr ago; C2 was estimated at 3.3–2.5 Myr (see Methods). a, *Platyhelphusa 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*; m, *P. niloticus*. a-h and l, endemic to Lake Tanganyika; j, k, and m, East African riverine species.

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 platyhelphusid clade. There are several factors that can be causal to the morphological disparity of platyhelphusids. 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 (Scholtz and Rosendahl, 1988; Tiercelin and Mondeguer, 1991; Cohen et al., 1993)). 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 (Verheyen et al., 1996; Sturmbauer et al., 2001). Platypelphusids 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. *Platythelphusa maculata* has a small, rounded body and shows a preference for living in empty gastropod shells (Cunnington, 1899; Capart, 1952), whereas *P. tuberculata* shows affinity for deep lake floor habitats (Coulter, 1991; Marijnissen et al., 2004). *Platythelphusa 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*, *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 platyhelphusids 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.

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Chapter 4



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

4

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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 claw 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). 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 marine crabs that have planktonic larvae, freshwater crabs lack larval stages and brood their young. Therefore, freshwater crabs have a lower dispersal capacity and possibly a higher speciation potential than their marine relatives. The platyhelphusid 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 into 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 platyhelphusid, *Platyhelphusa 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, *Platyhelphusa 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 morphology that are related to sexual selection. We subsequently focus on divergence of claw functional traits within the platyhelphusid 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 were recorded during systematic habitat surveys using 50*50 cm quadrats (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 (Table 1). 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).

Table 1. Specimens included in the phylogenetic analyses. Column labels indicate codes used in figures, and localities where crabs were collected.

Species	Code	Locality
<i>Platythelphusa armata</i> (A. Milne-Edwards, 1887)	JKB01	Jakobsen
<i>Platythelphusa armata</i>	JKB02	Jakobsen
<i>Platythelphusa armata</i>	MBT01	Mbita
<i>Platythelphusa armata</i>	UJJ14	Ujiji
<i>Platythelphusa conculcata</i> Cunningham, 1907	HTP03	Hilltop
<i>Platythelphusa conculcata</i>	JKB02	Jakobsen
<i>Platythelphusa conculcata</i>	KIG01	Kigoma
<i>Platythelphusa denticulata</i> Capart, 1952	KAB23	Kabwe
<i>Platythelphusa denticulata</i>	MZG22	Mzungu
<i>Platythelphusa denticulata</i>	MPL24	Mpulungu
<i>Platythelphusa echinata</i> Capart, 1952	HTP03	Hilltop
<i>Platythelphusa echinata</i>	KGM23	Kigoma
<i>Platythelphusa echinata</i>	KGM24	Kigoma
<i>Platythelphusa echinata</i>	MPL02	Mpulungu
<i>Platythelphusa echinata</i>	MPL03	Mpulungu
<i>Platythelphusa echinata</i>	MPL25	Mpulungu
<i>Platythelphusa echinata</i>	UJJ05	Ujiji
<i>Platythelphusa immaculata</i> Marijnissen et al., 2004	HTP14	Hilltop
<i>Platythelphusa immaculata</i>	JKB13	Jakobsen
<i>Platythelphusa immaculata</i>	MBT12	Mbita
<i>Platythelphusa maculata</i> (Cunnington, 1899)	KAL22	Kalemie
<i>Platythelphusa maculata</i>	UJJ02	Ujiji
<i>Platythelphusa praelongata</i> Marijnissen et al., 2004	MPL16	Mpulungu
<i>Platythelphusa tuberculata</i> Capart, 1952	UJJ17	Ujiji
<i>Platythelphusa tuberculata</i> Capart, 1952	UJJ18	Ujiji
<i>Platythelphusa tuberculata</i>	MPL19	Mpulungu

T a b l e 1. (Continued)

<i>Potamonautes emini</i> (Hilgendorf, 1892)	GOM04	Gombe	LT, TZ
<i>Potamonautes emini</i>	GOM05	Gombe	LT, TZ
<i>Potamonautes emini</i>	MWG26	Mwamongo	LT, TZ
<i>Potamonautes niloticus</i> (H. Milne-Edwards, 1837)	RPF01	Rippon Falls	LV, UG
<i>Potamonautes niloticus</i>	RPF02	Rippon Falls	LV, UG
<i>Potamonautes niloticus</i>	RPF03	Rippon Falls	LV, UG
<i>Potamonautes lirrangensis</i> (Rathbun, 1904)	KIV28	Ruzizi	LK, DC
<i>Potamonautes lirrangensis</i>	KIV48	Ruzizi	LK, DC
<i>Potamonautes lirrangensis</i>	MAL27	Thumbi West	LM, MW
<i>Potamonautes lirrangensis</i>	MAL33	Lake Malawi	LM, MW
<i>Potamonautes lirrangensis</i>	UVZ30	Uvinza	MR, TZ
<i>Potamonautes lirrangensis</i>	ZAM01	Uazua	LT, ZM
<i>Potamonautes platynotus</i> (Cunnington, 1907)	CRO25	Crocodile Island	LT, TZ
<i>Potamonautes platynotus</i>	HTP01	Hilltop	LT, TZ
<i>Potamonautes platynotus</i>	JKB43	Jakobsen	LT, TZ
<i>Potamonautes platynotus</i>	KAL30	Kalemie	LT, DC
<i>Potamonautes platynotus</i>	KAL23	Kalemie	LT, DC
<i>Potamonautes raybouldi</i>	AMA01	Amani	US, TZ
<i>Potamonautes raybouldi</i>	USB20	Usambara	US, TZ
<i>Potamonautes raybouldi</i>	USB21	Usambara	US, TZ

DC, Democratic Republic Congo; MW, Malawi; LK, Lake Kivu; LM, Lake Malawi; LT, Lake Tanganyika; LV, Lake Victoria; MR, Malagarassi River; TZ, Tanzania; UG, Uganda; US, Usambara Mountains; ZM, Zambia. N.a., not available. *Indicates location not verified with GPS.

GENETIC ANALYSES

A list of specimens included in this study and collection localities is provided in Table 1. 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 (S.A.E. Marijnissen, unpublished data). Genomic DNA was extracted from muscle tissue of each crab, and isolated using Qiagen DNeasy™. 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.

Double-stranded PCR amplifications of 16S rRNA mtDNA were performed in 25.4 μ l solutions containing 14.9 μ l millipore water, 3.3 μ l of 25 mM MgCl₂, 2.5 μ l of 10 x Mg²⁺ free buffer, 2.5 μ l of a 10 mM dNTP solution, and 1 μ l of each primer set (at 10 μ M each), 0.2 μ l of Taq polymerase, and 1 μ l template DNA. PCR conditions were as follows: 3 min at 95°C, then 30 cycles of 94°C for 30 s, 56°C or 48°C for 50 s, 72°C for 40 s, followed by 56°C or 48°C for 5 min, 72°C for 10 min, and 20°C for 5 min. Double-stranded PCR amplifications of COII mtDNA were performed in 25.5 μ l solutions containing 17.9 μ l millipore water, 2.5 μ l of 10 x Mg²⁺ free buffer, 2.9 μ l of a 10 mM dNTP solution, and 1 μ l of each primer set (at 10 μ M each), 0.2 μ l of Taq polymerase, and 1 μ l template DNA. PCR conditions were as follows: 3 min at 95°C, then 30 cycles of 94°C for 30 s,

58°C for 50 s, 72 °C for 40 s, followed by 58°C for 5 min, 72°C for 10 min, and 20°C for 5 min.

Before sequencing, the PCR products were run on a 1% agarose gel, sliced out and purified using a QIAquick™ PCR purification kit (Qiagen, Basel, Switzerland). Sequencing reactions were performed with ABI PRISM Dye Terminator Cycle Sequencing Ready Reaction Kit (Perkin Elmer Rotkreuz, Switzerland). Cycle sequencing was performed in 4.25 µl millipore water, 2 µl purified PCR product, 1 µl ABI PRISM fluorescent dye terminators, and 1 µl of a 10 µM primer solution. All samples were sequenced using an ABI 3700 automated DNA Sequencer.

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) (Figure 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 (Figure 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.

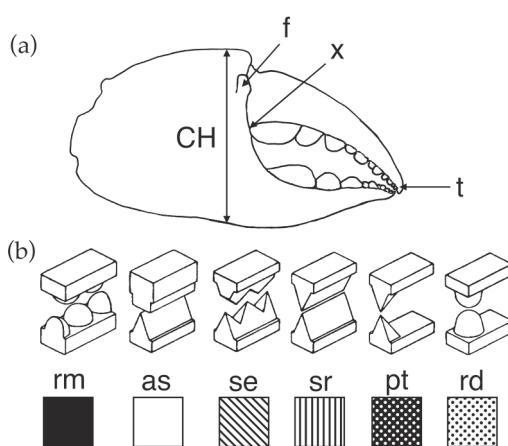


Figure 1. (a) Claw illustrating morphometric measurements and dimensions for force calculations. CH, claw height; L_0 , distance from the fulcrum (f) to the site of force generation at the insertion of the dactyl closer muscle apodeme (x); L_1 , distance from the fulcrum to the site of force application 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 dactylus 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).

CLAW PERFORMANCE

Adult, intermolt male and female specimens of *P. armata* ($n = 39$ and 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

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

Table 2. 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 Figure 1). Taxa are ordered approximately conforming to phylogenetic affinity (see Figure 2)¹. 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.

¹*Platythelphusa polita* was not included in the phylogenetic analyses; however, cladistic analyses suggest a basal position (Sternberg and Cumberland 1999). *Platythelphusa denticulata* exhibits an extensive level of variability and is not included here.

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 One Way ANOVA and Tukey's HSD post-hoc pairwise comparisons. Statistical analyses were performed with $\alpha=0.05$ 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 platyhelphusids from Lake Tanganyika formed a well-supported clade in all analyses (Figure 2), with *Potamonautes niloticus* and *P. emini* as sister taxa. The Tanganyikan endemic *Po. platynotus* was part of a separate clade together with *Po. lirrangensis* and *Po. raybouldi*. Average 16S rRNA and COII mtDNA sequence divergence (uncorrected *p*-distances) was 1.59% (range 0.11-3.46%) between *Platyhelphusa* 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 2). 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 the MA of males and females was significantly different in all species except *P. armata* (Tukey's HSD, $P<0.05$). The

MA of male *P. conculkata*, *P. immaculata*, *P. maculata*, *P. polita*, and *Po. platynotus* did 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 occlusion in *P. conculkata*, *P. immaculata*, and *P. maculata*, to predominantly serrated occlusion in *P. praelongata* and *P. tuberculata* (Table 2). Clear differences also existed in the amount of asymmetry in size between major and minor claws 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. conculkata*, *P. praelongata* and *P. tuberculata* were near symmetrical ($AIF \leq 1.1$). *Platythelphusa denticulata* exhibited extensive variability in AIF as well as in the 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) decreased in the following order: *P. tuberculata* > *P. maculata* > *P. conculkata*, *P. immaculata* > *P. echinata*, *P. polita* > *P. armata* (Table 2). Low SDI in *P. armata* and *P. polita* was related to the enlargement of the female claw (AIF 1.8 and 1.6 respectively), whereas in *P. echinata* it was related to the limited expression of male dimorphism (AIM 1.4).

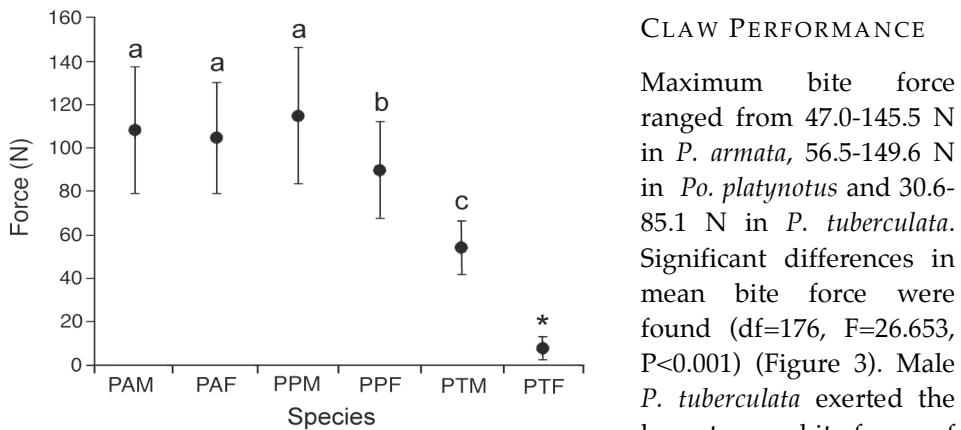


Figure 3. Comparison of major claw biting force (in Newtons). Means with different letters are significantly different (Tukey's test: $P < 0.05$). PAM, *Platythelphusa armata* male ($n = 39$); PAF, *P. armata* female ($n = 38$); PPM, *Potamonautes platynotus* male ($n = 40$); PPF, *Po. platynotus* female ($n = 42$); PTM, *P. tuberculata* male ($n = 37$); PTF, *P. tuberculata* female ($n = 36$). *Female *P. tuberculata* were noncooperative, and therefore they were not included in the statistical analyses.

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 N in *P. tuberculata*. Significant differences in mean bite force were found ($df=176$, $F=26.653$, $P<0.001$) (Figure 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 $P>0.05$).

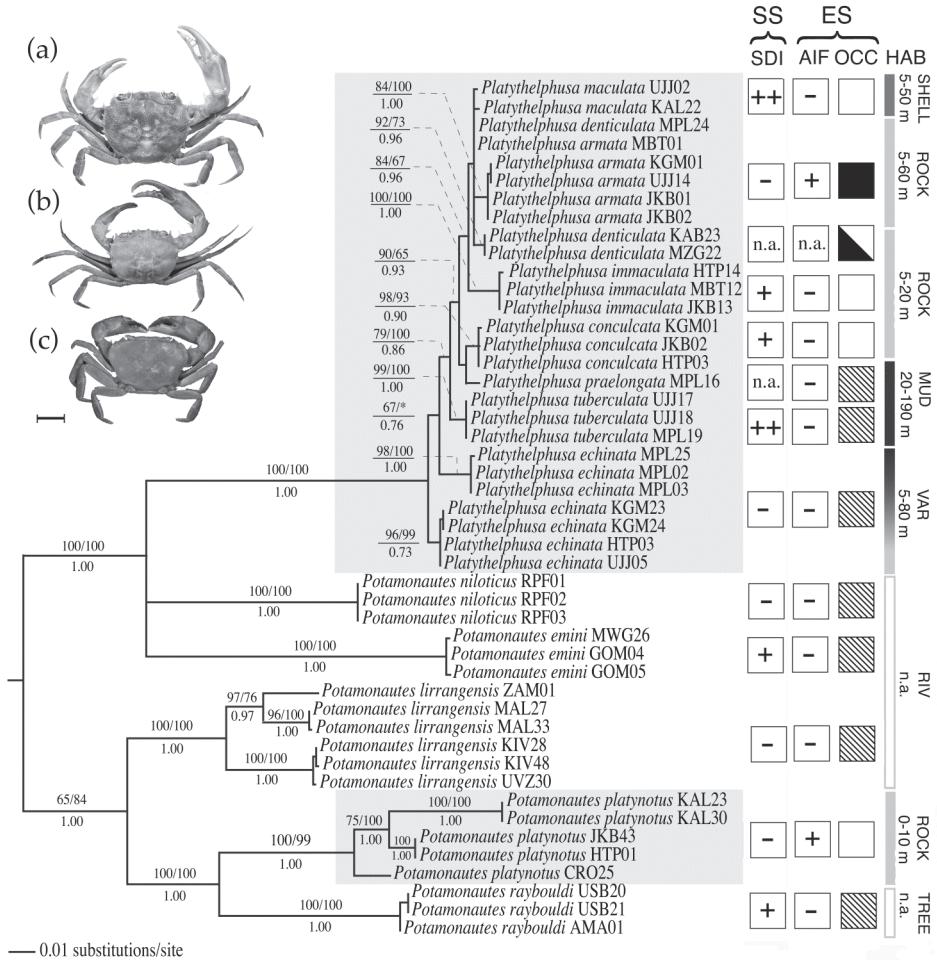


Figure 2. Maximum likelihood tree of Lake Tanganyika endemic crabs and outgroup taxa based on combined 16S rRNA and COII mtDNA sequences, with branch lengths proportional to the number of changes. Numbers above nodes denote maximum likelihood and parsimony bootstrap values, followed by Bayesian posterior 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) *Platyhelphusa 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 Figure 1, Table 2); HAB = principal habitat information of adults; SHELL, empty *Neothauma tanganyicense* 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.

DISCUSSION

PHYLOGENETIC FRAMEWORK

Our analyses of 16S rRNA and COII mtDNA confirm that the platyhelphusids from Lake Tanganyika form a single, well-supported clade, and that the endemic *Potamonautes platynotus* is derived from a lineage that invaded the lake separately (Figure 2). The level of resolution between platyhelphusid species is low in comparison to the level of sequence divergence and resolution exhibited by the outgroup taxa and by *Po. platynotus*. The limited phylogenetic signal within the platyhelphusid 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* (Figure 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; Riesenbergs 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 prevent us from testing this hypothesis. While we recognize there may be some discussion about whether morphologically distinct forms of platyhelphusid 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 platyhelphusid clade is currently undergoing speciation, and that the patterns observed here are consistent with those that characterize recent radiations in other groups (Freeland & Boag 1999; Seehausen 2004, 2006; Parchman et al. 2006). Diversification within *Platyhelphusa* 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 (*Platyhelphusa* and *Potamonautes*) that have independently acquired functional morphological traits that are indicative of molluscivorous adaptations. Both *P. armata* and *Po. platynotus* exhibit marked

dimorphism of claw height in both sexes, as well as molariform dentition (Table 2). The combination of these traits is lacking in most 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 a 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 (Figure 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; Mitchell et al. 2003). These forces are low compared with the load strength of Lake Tanganyika gastropod shells reported in the 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 for a lack of shell crushing strength by 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 2). *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 (Figure 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 the 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 (Figure 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 2, Figure 2, see below).

SUPPORT FOR ECOLOGICAL DIVERGENCE

Species in the plathyhelphusid 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 plathyhelphusid 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 (Le, 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 platyhelphusids (Table 2) 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 2, Figure 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 platyhelphusid crabs (Schluter 2000). Other habitat-phenotype associations exhibited by platyhelphusid 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). *Platyhelphusa maculata* has a small, rounded body and shows a preference for living in empty *Neothauma* gastropod shells (Capart 1952; Cunnington 1899). *Platyhelphusa conculcata* and *P. immaculata* inhabit narrow spaces under rocks and boulders and both have extremely flattened carapaces (Cumberlidge 1999; Cumberlidge et al. 1999; Marijnissen et al. 2004; S.A.E. 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 (Schlute, 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 ($AIF \leq 1.2$) and markedly asymmetric ($AIF \geq 1.5$) 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 platyhelphusid 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 platyhelphusid species, some coexist without showing apparent evidence of ecological differentiation. *Platyhelphusa conculcata* and *P. immaculata*, as well as *P. praelongata* and *P. tuberculata* exhibit similar claw functional traits and overlapping habitat distributions (Table 2, Figure 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 2) suggests that sexual selection plays 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 2). In spite of enlargement and the presence of molariform dentition, the major claw of male *P. tuberculata* has a low mechanical advantage (Figure 3a). 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 (Figure 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 platyhelphusid 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 (Figure 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 (Figure 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 to those seen in 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 platyhelphusid 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

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Chapter 5



5

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 & 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; S.A.E. Marijnissen & A.J. Pereira-Pagarete, 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 (Duftnér 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 (Schlüter, 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* Cunningham, 1899, and *P. polita* Capart, 1952, may be advantageous for living inside empty gastropod shells. *Platythelphusa concilcata* Cunningham, 1907, *P. immaculata* Marijnissen et al. 2004, and *P. echinata* Capart, 1952 each have a markedly flattened carapace (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 platyhelphusid 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 platyhelphusid species, indicating a considerable level of trophic partitioning (Chapter 4). Although there are thus several phenotypic clues to differentiation in resource use, it is still unknown to which extent platyhelphusid 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 included *P. denticulata*, although its taxonomic status is uncertain, and it has been proposed that this might be a hybrid taxon (Chapter 4). We also included another endemic Lake Tanganyika species, *Potamonautes platynotus* (Cunnington, 1907), to determine if its ecological niche is different from that of the platyhelphusid 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; Darwall 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 because it implies a high sensitivity to habitat disturbance. 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 platyhelphusid 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 ZNG) was composed of boulders, cobbles, pebbles, and/or aggregations of empty shells of the freshwater mussel *Pleiodon spekii* (Woodward, 1859), 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 shell hash of the bivalve *Coelatura burtoni* (Woodward, 1859).

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). A fixed surface area of the underlying sediment and periphyton was

brought ashore for analysis by firmly emplacing a sealed cover over the upward face of a flat lying cobble. All material surrounding the cover was scrubbed away and carefully discarded. This provided 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 & Hallegraaff, 1978). Another subsample was dried to a constant mass at 60°C, weighed, combusted at 500°C 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,

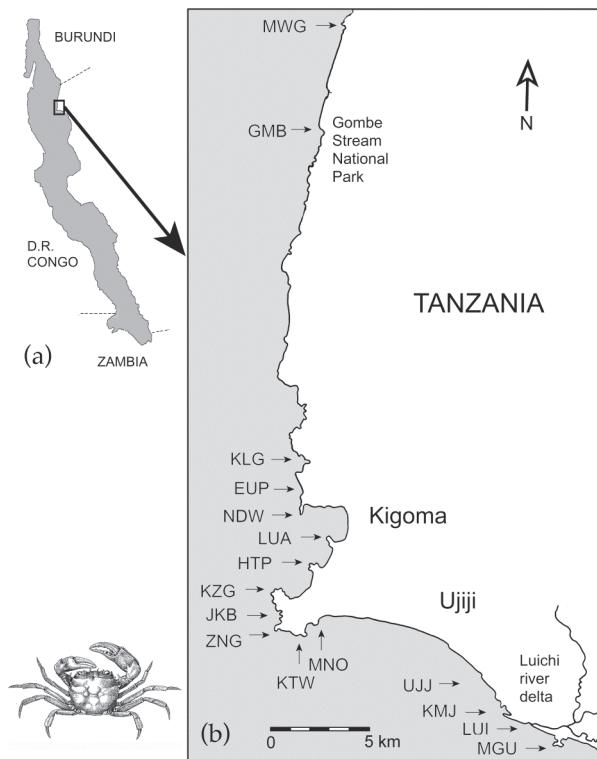


Figure 1. (a) Map of Lake Tanganyika, and (b) study sites that were surveyed for crab habitat specificity. Acronyms: MWG, Mwamongo; GMB, Gombe Stream National Park; KLG, Kalalangabo; EUP, Euphorbia; NDW, Nondwa; LUA, Luansa; HTP, Hilltop; KZG, Kazanga; JKB, Jakobsen's Beach; ZNG, Mzungu; KTW, Kitwe; MNO, Meno; UJJ, Ujiji; KMJ, Kangamoja; LUI, Luichi River outlet; MGU, Mgumile.

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 include many overlaying PCO scores that cannot be distinguished using standard biplots, we applied two-dimensional binning to effectively visualise different scores. The scores were displayed by symbols, the size of which was 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 $\geq 50\%$ 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 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. To examine patterns of trophic segregation between species, a dual-isotope plot $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ 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

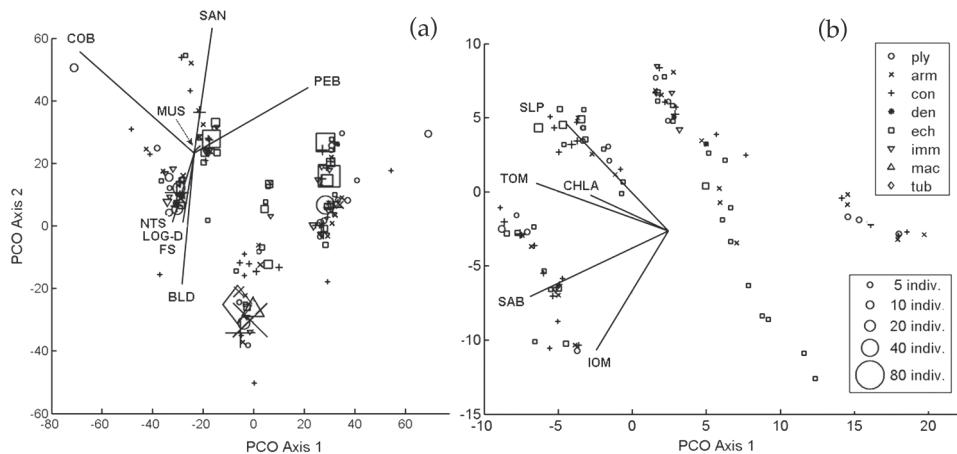


Figure 2. Principal coordinate ordination (PCO) plot of the two first axes of crab species habitat specificity in Lake Tanganyika based on (a) random surveys of different substrate types across depths (0-30 m) and; (b) stratified random quadrat sampling at 5 m depth within the rocky littoral zone at 5 m depth. The relative size of the symbols is proportional for the number of individual observations per species for each habitat type (see text). Abbreviations: arm, *Platythelphusa armata*; con, *P. conculkata*; den, *P. denticulata*; ech, *P. echinata*; imm, *P. immaculata*; mac, *P. maculata*; tub, *P. tuberculata*; ply, *Potamonautes platynotus*; 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 shells of the freshwater mussel *Pleiodon spekii*; NTS, *Neothauma tanganyicense* shells; Log-D, log-transformed depth; SLP, slope of the substrate; CHLA, chlorophyll a; TOM, total organic matter; IOM, total inorganic matter; SAB, relative snail abundance.

Table 1a. 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 1b. 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

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 conculkata* (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 2a. The first two PCO axes explain 39.9 % and 35.1 % of the variation in the dataset (Table 1a). Substrate types with the highest vector loadings were boulders, cobbles, pebbles and sand. With the exception of *P. tuberculata* and *P. maculata*, all species are associated with these four vectors. Although species distributions along the axes thus show considerable overlap, the frequency of the observations within each substrate type differs for each species. Significant differences were found in the similarity of substrate specificity among species (Pseudo- $F_{5,321}=10.029$, $P<0.001$). Significant pairwise differences between species that coexist within the rocky littoral included *P. armata* and *P. conculcata* ($P=0.002$), *P. armata* and *P. echinata* ($P < 0.001$), *P. armata* and *P. immaculata* ($P=0.044$), *P. conculcata* and *P. echinata* ($P=0.010$), *P. conculcata* and *Po. platynotus* ($P < 0.001$) as well as *P. echinata* and *Po. platynotus* ($P < 0.001$). Other pairwise comparisons were not significant ($P > 0.05$).

Additional information on species habitat specificity was obtained from the quadrat surveys at 5 m depth within the rocky littoral zone. The first two axes of the PCO explained 64.2 % and 24.6 % respectively of the total variance in the species dataset (Figure 2b, Table 1b). Influential habitat variables were slope, total organic matter, chlorophyll *a*, 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 chlorophyll *a*. Significant differences were found among species (Pseudo- $F_{7,1463}=108.680$, $P < 0.001$). Pairwise tests between species showed that all comparisons between species were significant ($P < 0.006$) with the exception of the comparisons between *P. denticulata* and *P. conculcata* ($P=0.18$), *P. denticulata* and *P. immaculata* ($P=0.490$), and *P. denticulata* and *Po. platynotus* ($P = 0.554$). Both the mean body size 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

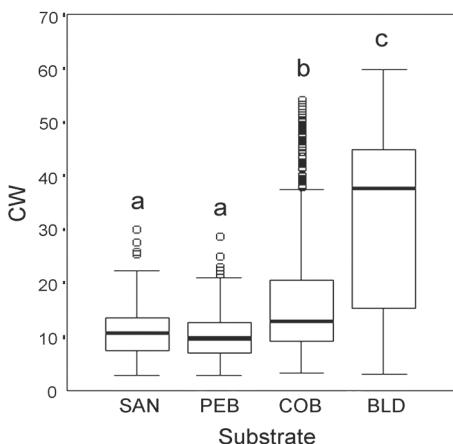


Figure 3. Distribution of crab size classes among various substrate types in the rocky littoral zone in Lake Tanganyika. Box plots represent CW median, and interquartile range with whisker ends corresponding to the first and the last decile. Individual observations beyond these limits are plotted as circles. Different letters above box plots indicate significant differences at $\alpha=0.05$ (Tukey's test: $P < 0.001$). CW, carapace width (mm). SAN, sand; PEB, pebbles; COB, cobbles, BLD, boulders.

(*Encyonema* sp., *Rhopalodia* sp., *Nitzschia* sp., *Surirella* sp.), as well as green algae (*Oocystis* sp., *Ulothrix* sp.) and cyanobacteria (*Anabaena* sp., *Chroococcus* sp., *Oscillatoria* sp.). Ostracods included species of Cyprididae and Cyclocypridae (*Mecynocypria* sp.) as well as 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.

size classes are found in all rocky littoral substrate types, cobbles and boulders harbour larger crabs than sand and pebbles (Figure 3).

DIET COMPOSITION

We collected a total of 574 adult crabs for dietary analyses, of which 386 had $\geq 50\%$ full foreguts. Figure 4 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

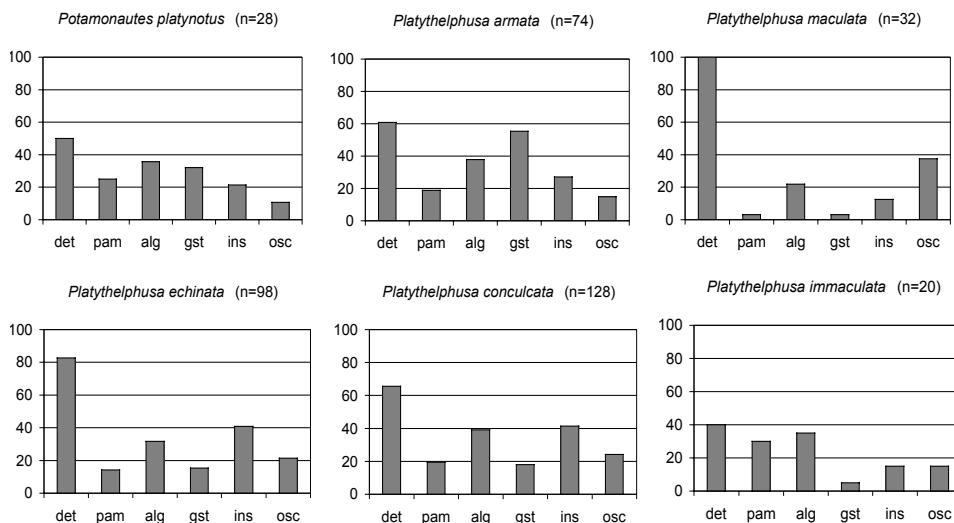


Figure 4. Percentage occurrence of the various food categories in the six species analysed. Numbers of specimens analysed per species are shown in brackets. Det, detritus; pam, vascular plant matter; alg, algae; gst, gastropods; ins, aquatic insect larvae; osc, ostracods.

STABLE ISOTOPE ANALYSES

Crab isotopic signatures ranged from -12.4 to -21.2 ‰ $\delta^{13}\text{C}$ and from 3.6 to 6.4 ‰ $\delta^{15}\text{N}$. 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 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ is presented in Figure 5. The deep, muddy substrate dwelling *P. tuberculata* is segregated from other platylephusid species by its high mean $\delta^{15}\text{N}$ signature. Within the rocky substrate species complex, *P. conculcata* exhibits the lowest $\delta^{15}\text{N}$ values. Pairwise tests showed significant differences between mean $\delta^{13}\text{C}$ and/or $\delta^{15}\text{N}$ between species, with the exception of the comparison between *P. armata* and *P. maculata*, which overlap in both mean $\delta^{13}\text{C}$ as well as $\delta^{15}\text{N}$ values (Table 2).

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

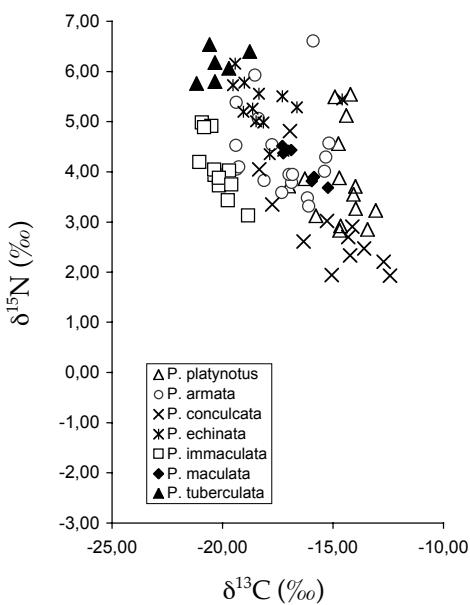


Figure 5. Stable carbon and nitrogen isotope signatures of Lake Tanganyika endemic crab species. Each data point represents an individual organism.

P. maculata (Cumberlidge et al., 1999, and references therein). The following six species were found to 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 platyhelphusid crabs, which all 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 2a and b). 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 platyhelphusid 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

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 indicate a marked preference of *P. maculata* 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

similarity in habitat specificity. Differentiation in habitat specificity within the rocky littoral appears to be mainly a function of substrate size (Figure 3). Adults of small-bodied species such as *P. conculkata*, *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 revealed marked differences among the endemic Lake Tanganyika crab species, indicating a considerable level of trophic divergence (Chapter 4). In contrast, our gut content analyses showed no clear evidence of specialization (Figure 4). 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; Chapter 4; Michel et al., unpublished data). Detritus comprised an important component in the guts of all species that were

Table 2. Pairwise distances (Tukey's test) of mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope composition among adult individuals of Lake Tanganyika endemic crab species.

	Species	<i>P. tuberculata</i>	<i>P. conculkata</i>	<i>P. immaculata</i>	<i>P. maculata</i>	<i>P. echinata</i>	<i>P. armata</i>
$\delta^{13}\text{C}$	<i>P. conculkata</i>	5.05*				ns	
	<i>P. echinata</i>	2.12*	2.92*	2.16*	ns		ns
	<i>P. immaculata</i>	ns	5.08*				
	<i>P. maculata</i>	3.73*	ns	3.76*			
	<i>P. armata</i>	2.79*	2.25*	2.83*	ns	ns	
	<i>Po. platynotus</i>	5.48*	ns	5.51*	ns	3.35*	2.68*
$\delta^{15}\text{N}$	<i>P. conculkata</i>	3.25*					
	<i>P. echinata</i>	ns	2.41*	1.20*	1.16*		
	<i>P. immaculata</i>	2.04*	1.21*				
	<i>P. maculata</i>	1.99*	1.25*	ns			
	<i>P. armata</i>	1.72*	1.52*	ns	ns	0.89*	
	<i>Po. platynotus</i>	2.27*	0.98*	ns	ns	1.43*	ns

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

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 $\delta^{13}\text{C}$ and / or $\delta^{15}\text{N}$ values between our focal taxa revealed that signatures of individual specimens showed considerable overlap. However, there were significant differences in mean $\delta^{13}\text{C}$ and / or $\delta^{15}\text{N}$ 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 platyhelphusid 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; Chapter 4). 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 platyhelphusid 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 platyhelphusid 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 platyhelphusid speciation (Chapter 4), 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 platyhelphusid 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.

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Chapter 6



6

Conservation of freshwater biodiversity in Lake Tanganyika: focus on the endemic crab fauna

ABSTRACT

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Manuscript in preparation

Biodiversity in Lake Tanganyika is increasingly at risk from human-induced perturbations. An enhanced understanding of the functioning of various key components of the lake ecosystem is essential to predict ecosystem responses to environmental changes. Here, we focus on endemic freshwater crabs that have a potentially important function in benthic foodwebs. Surveys showed that crabs are locally abundant in rocky littoral substrates, and densities ranged from 0-28 crabs m⁻². On average, crab densities decreased with depth. Although our sampling area included sites at the depositional base of deforested areas as well as relatively pristine sites, we found no significant differences in species richness or evenness among sites. Estimates of crab dry mass varied from 0.0-117.7 g m⁻². By comparing stable ¹³C and ¹⁵N isotopes of crabs with those of their putative food resources, we demonstrate that crabs occupy a central position as consumers in benthic foodwebs. Mean ¹⁵N signatures of different crab species were enriched relative to those of snails, bivalves, aquatic insect larvae, plant matter, and detritus. Because crabs occupy multiple trophic levels, and the different species exhibit overlapping ecological niches, we expect that community-level responses of crabs to sedimentation-related disturbances will be delayed relative to other organisms that exhibit narrower ecological niches. Our results emphasize the intricacy of benthic faunal responses to environmental perturbations. We discuss the current conservation status of the endemic crabs, as well as general implications for strategies aimed at conserving biodiversity in Lake Tanganyika.

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 endemism (Groombridge & Jenkins, 1998). Estimates suggest that the lake contains at least 1500 species (Coulter, 1991), although species numbers vary according to taxonomic authority and many taxa are under-systematized. Approximately 600 species are currently considered endemic to Lake Tanganyika, including 245 cichlid species and 44 non-cichlid fish species (Snoeks, 2000; but see Genner et al., 2004), an estimated 190 ostracod species (Martens, 1994; K. Martens, pers. comm.), over 90 gastropod species (West et al., 2003; E. Michel & J. Todd, unpublished data), 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/Democratic Republic of Congo, and the Malagarasi-Muyovozi Wetlands in Tanzania (Ramsar, 2007). Moreover, Lake Tanganyika contains approximately 17% of the world's surface freshwater resources. 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). 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; Lévéque 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.

Here, we 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. 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 systems 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'Keefe, 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).

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 (Cumberlidge et al., 2006). An evaluation based on museum collection data and pilot surveys (Cumberlidge & Marijnissen, 2004c,e,h) tentatively listed two out of 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. It is thus becoming clear that it is relevant to include the crabs in efforts to obtain data for conservation purposes in Lake Tanganyika. To obtain insight in their level of vulnerability to habitat perturbations, we not only need data on the lake-wide distribution patterns and local densities of the different endemic crab species, but also on their ecology. In return, more knowledge on the functional role of

the crabs in Lake Tanganyika's foodwebs will help to increase 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 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). Much of the lake's shoreline is rocky and steeply sloped, and consists of a narrow fringe that rapidly drops to > 50 m depth over distances of < 500 m. Extensive gently sloping deltas consisting predominantly of sand, mud or shell beds have developed at the outlet of large rivers such as the Malagarasi in Tanzania, and the Rusizi in Burundi. We selected 12 study sites along approximately 50 km of the lake shoreline near Kigoma, Tanzania (Figure 1), where we conducted surveys between 2001 and 2004. Nine sites (MWG to ZGU) were situated in rocky littoral areas where the substrate is composed of boulders, cobbles, and/or pebbles interspersed with sand, and occasionally with aggregations of shells from the large bivalve *Pleiodon spekii* (Woodward, 1859). 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 near a river delta (Luichi River, see Figure 1), where the substrate consists of mud alternated with extensive shell beds of the large gastropod *Neothauma tanganyicense* Smith, 1880, and shell hash of the small bivalve *Coelatura burtoni* (Woodward, 1859).

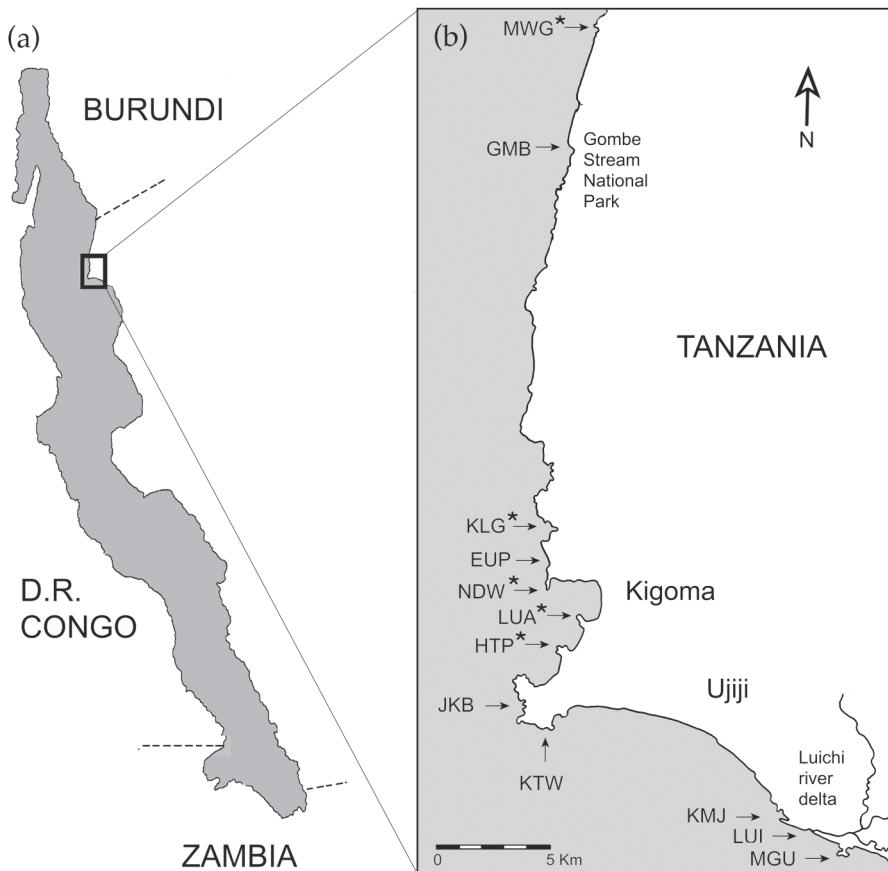


FIGURE 1. (a) Map of Lake Tanganyika, and (b) study sites. Sites adjacent to deforested areas are denoted with an asterisk. MWG, Mwamgongo ($4^{\circ}36.597'S$, $29^{\circ}38.329'E$); GMB, Gombe Stream National Park ($4^{\circ}38.153'S$, $29^{\circ}37.811'E$); KLG, Kalalangabo ($4^{\circ}49.701'S$, $29^{\circ}36.202'E$); EUP, Euphorbia ($4^{\circ}51.003'S$, $29^{\circ}36.537'S$); LUA, Luansa ($4^{\circ}52.521'S$, $29^{\circ}37.168'S$); HTP, Hilltop ($4^{\circ}53.455'S$, $29^{\circ}35.804'E$); JKB, Jakobsen's Beach ($4^{\circ}54.875'S$, $29^{\circ}35.856'E$); ZNG, Mzungu ($4^{\circ}55.052'S$, $29^{\circ}35.737'E$); KTW, Kitwe ($4^{\circ}55.375'S$, $29^{\circ}36.777'S$); KMJ, Kangamoja ($4^{\circ}57.925'S$, $29^{\circ}41.205'E$); LUI, Luichi River northernmost outlet ($4^{\circ}58.003'S$, $29^{\circ}41.825'E$); MGU, Mgumile ($4^{\circ}58.759'S$, $29^{\circ}43.278'S$).

ABUNDANCE AND SPECIES DISTRIBUTIONS

To determine a sampling strategy, a preliminary study was conducted in 2002 at two sites (HTP and JKB). SCUBA divers randomly established 20 replicate 50*50 cm quadrats at each of four depths (5, 10, 20, 30 m), and collected all crabs within each quadrat. The results indicated that crabs were absent from entirely sandy substrates (i.e. not interspersed with cobbles, boulders, or rocks). Mean densities of crabs below 20 m depth at these two sites were ≤ 0.7 (± 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 depths. 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), we focused our sampling efforts on areas with *Neothauma tanganyicense* shell beds. All 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): $\log(\text{dry mass}) = -3.75 + 2.89\log(\text{CW})$, where mass is measured in grams and CW (carapace width) in millimetres.

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 R¹. 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 (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 CRAN³ package 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, UK) with depth as a fixed factor and site as a random factor. Variation in the incidence of species (number of quadrats 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.

¹<http://www.r-project.org> ²<http://cc.oulu.fi/~jarioksa/softhelp/vegan.html>

³<http://pbil.univ-lyon1.fr/ADE-4>

STABLE ISOTOPE ANALYSES

To determine the trophic position of crabs in benthic foodwebs, stable isotope analyses were conducted. Values of $\delta^{15}\text{N}$ are typically used to characterize relative trophic positions of focal organisms, while $\delta^{13}\text{C}$ values can be useful to determine the source and flow of carbon in a food web (Post 2002). Crabs as well as samples of potential food resources were collected between August and November 2002 from three sites (HTP, JKB and KMJ; Figure 1), at depths between 5 and 15 m. The deep-lake dwelling species *Platythelphusa tuberculata* was obtained from 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 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 burtoni* (Woodward, 1859). At least four individuals were collected for each gastropod and bivalve species, with exception of *L. new sp. M* ($n=1$). After each shell was measured a piece of muscle tissue was dissected from the mollusc 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, which were combined into a single sample. Periphyton was scrubbed from the top of cobbles, and samples of filamentous algae were purified using a colloidal silica separation technique (Hamilton et al., 2005).

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 (C) and nitrogen (N) 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 (PDB carbonate for C and atmospheric N₂ for N). Average reproducibility based on replicate measurements was within approximately 0.1 ‰ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. To examine patterns of trophic segregation between species, both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were compared.

RESULTS

ABUNDANCE AND SPECIES DISTRIBUTIONS

A total of 892 individual crabs with a carapace width ≥ 10 mm (range 10.0-56.8 mm, average $17.8 \text{ mm} \pm 8.9 \text{ SD}$) were collected in a total of 600 quadrats. The following seven species were found in Lake Tanganyika during our surveys in the Kigoma area (Figure 1): *Po. platynotus*, *P. armata*, *P. conculcata*, *P. denticulata*, *P. echinata*, *P. immaculata* and *P. maculata*. We did not find *P. polita* and *P. praelongata*. 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 (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} . In general, densities decreased with depth (Figure 4).

Crab dry mass estimates ranged from 0.0-117.7 g m^{-2} . Mean biomass estimates of quadrats pooled for each depth ranged from 0.9 to 21.0 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

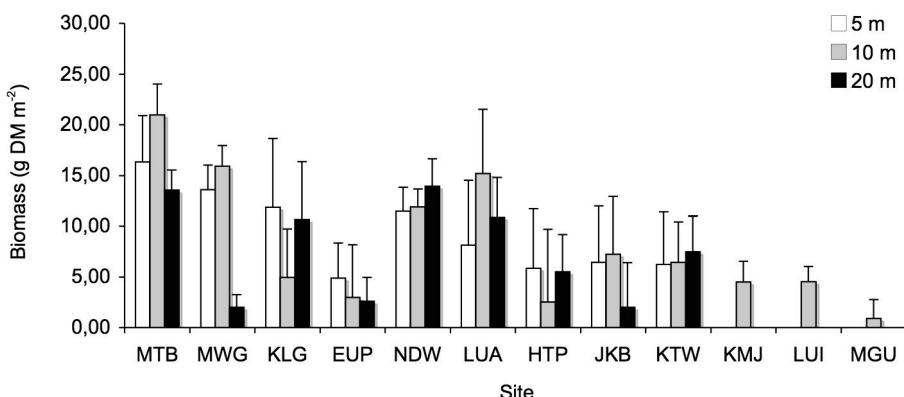


FIGURE 2. Spatial patterns in crab biomass. Mean ($\pm \text{SD}$) dry mass (DM) estimates are based on twenty quadrats at each site and depth combination. Site acronyms are explained in Figure 1.

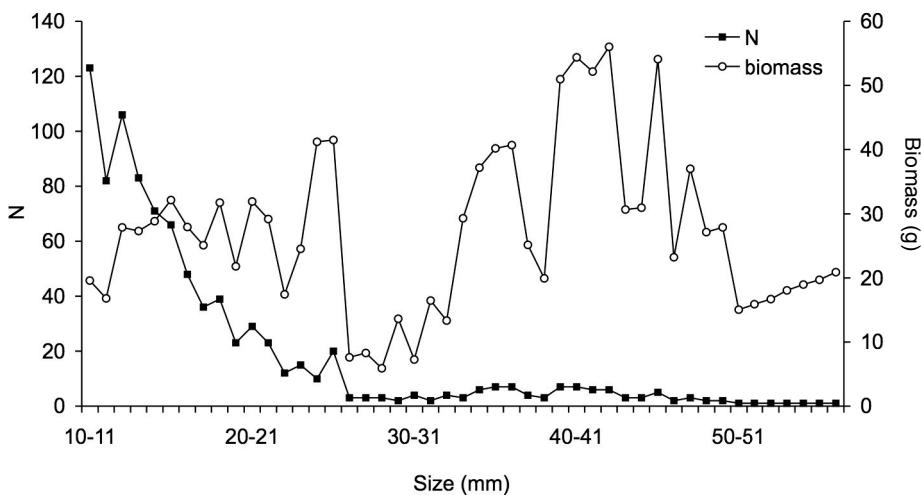


FIGURE 3. Relationship between the numbers of crabs collected per size class and estimated biomass (in grams dry mass).

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 suggest that species distributions were 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).

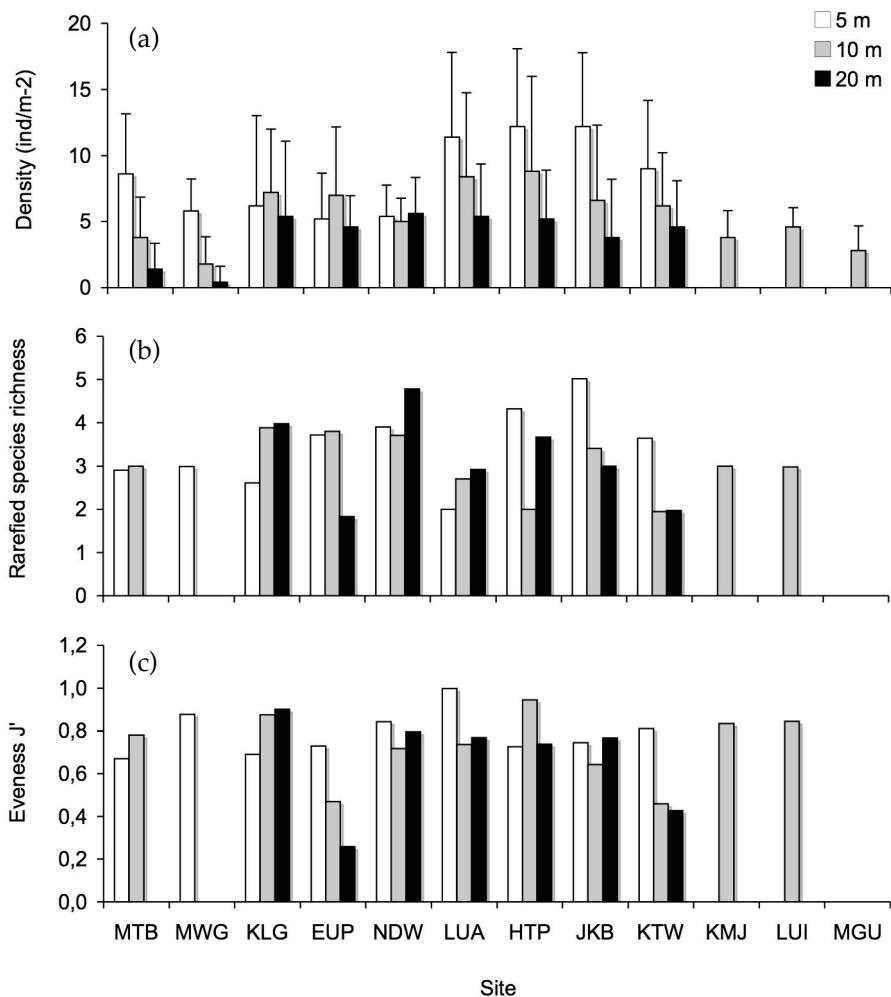


FIGURE 4. Spatial patterns in (a) crab densities, (b) rarefied species richness, and (c) evenness. Mean (\pm SD) density is based on twenty quadrats at each site and depth combination. Site acronyms are explained in Figure 1.

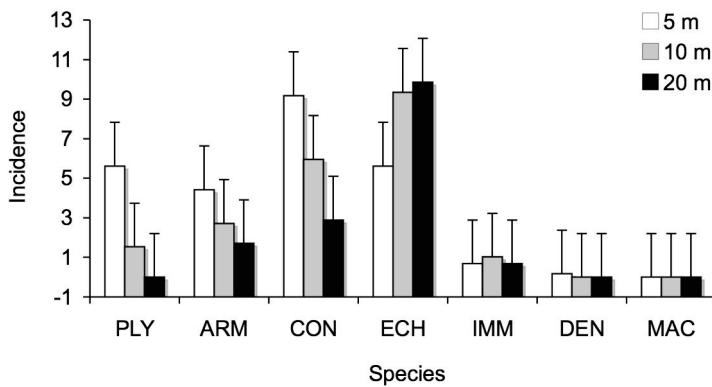


FIGURE 5. Incidence of crab species across depths. PLY, *Potamonautes platynotus*; ARM, *Platythelphusa armata*; CON, *P. conculkata*; ECH, *P. echinata*; IMM, *P. immaculata*; DEN, *P. denticulata*; MAC, *P. maculata*. Site acronyms are explained in Figure 1.

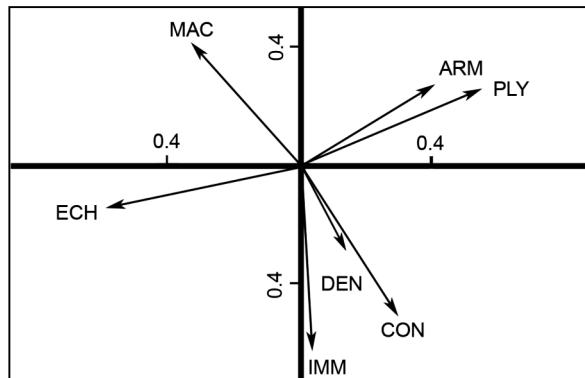


FIGURE 6. Results of principal component analyses on species distribution, showing the first two axes. PLY, *Potamonautes platynotus*; ARM, *Platythelphusa armata*; CON, *P. conculkata*; ECH, *P. echinata*; IMM, *P. immaculata*; DEN, *P. denticulata*; MAC, *P. maculata*.

STABLE ISOTOPE ANALYSES

Mean stable isotopic signatures ranged from -15.0 to -20.2 ‰ $\delta^{13}\text{C}$ and from 2.9 to 6.1 ‰ $\delta^{15}\text{N}$ 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, *Paramelanbia damoni*, *Reymondia horei*, *Spekia zonata*, and *Vinundu guillemei*, with mean isotope values ranging between -16.0 to -19.2 ‰ $\delta^{13}\text{C}$, and 0.7 to 1.8 ‰ $\delta^{15}\text{N}$. 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 ‰ $\delta^{13}\text{C}$, and -0.5 to -1.7 ‰ $\delta^{15}\text{N}$.

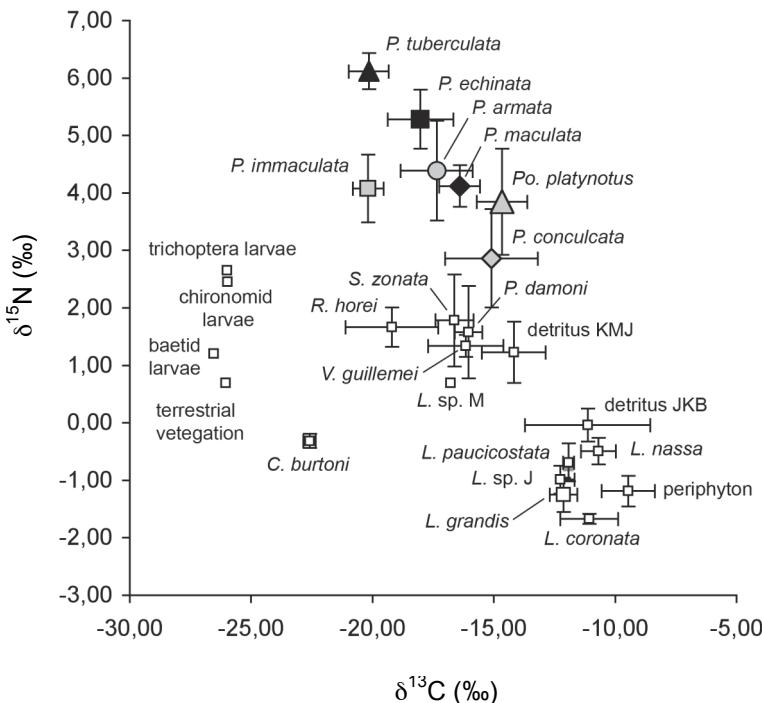


FIGURE 7. Mean stable carbon and nitrogen isotope signatures ($\pm \text{SD}$) of crabs and putative food resources in Lake Tanganyika benthic littoral habitats. Site acronyms are explained in Figure 1.

Mean values for detritus differed between sites, ranging from -9.5 to -15.4 ‰ $\delta^{13}\text{C}$ and -1.9 to 1.2 ‰ $\delta^{15}\text{N}$. 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 $\delta^{13}\text{C}$ 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 $\delta^{15}\text{N}$ 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 in general (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 suitable habitats or food resources. Marked spatial variability in densities was also observed for potamonautilid crabs in other African freshwater habitats (King, 1983; Somers & Nel, 1998; Abdallah et al., 2004), with local abundance peaks of up to 48 individuals per m⁻² (Table 1).

Several studies have underlined the potential of crabs to dominate invertebrate biomass in tropical freshwater ecosystems (Dobson 2004, Dobson et al 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). Our estimates, with dry mass maxima of up to 118 g m⁻² (Figure 2 and 3) suggest that crabs also contribute significantly to the benthic invertebrate biomass in Lake Tanganyika. It should be noted, however, that invertebrate communities in this lake differ from those in many other 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; Barrett et al., 2003; McIntyre et al., 2005), and average biomass (including shell) estimates range from 20-250 g m⁻² (Barrett et al., 2003; Donohue et al., 2003). These numbers indicate that gastropods 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. Our quadrat surveys probably underestimated the 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 by crabs in the lake's rocky littoral areas (Chapter 4). Large (carapace width \geq 40 mm) individuals of *P. armata* and *Po. Platynotus* often occur on large substrates (boulders, rocks) that could not be adequately sampled using quadrats. Because the biomass estimates presented here do not include these large individuals, they represent a conservative minimum. 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; Chapter 4). Additional studies using trapping or mark recapture techniques are

T A B L E 1. Density- and biomass estimates for African freshwater crabs.

Species Locality and habitat	Density (crabs m ⁻²)	Biomass (dry M g m ⁻²)	Size (mm)	Sampling method	Reference
<i>Potamonautes perlatus</i>					
Western Cape Province, R	0.3-2.7	< 3.0	n.a.	Net trap (monthly for 1 year)	King (1983)
Western Cape Province, R	1.7-5.3	54.2-136.1	25.0-80.0	Baited traps (2 months)	Hill & O'Keeffe (1992)
Western Cape Province, R	2.9-15.6	n.a.	4.0-44.6	Quadrat surveys (4 times 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)
<i>Potamonautes</i> sp.					
Tanzania, FS	1.6-48	0.6-11.5	n.a.	Surber sampler and pond net (1 collection).	Abdallah et al. (2004)
<i>Potamonautes</i> 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 (1 collection)	Dobson et al. (2007a)
<i>Potamonautes odhneri</i>					
Kenya, R	10.7-16.0	0.3-15.1	3.0-27.0	Surber sampler (1 collection)	Dobson et al. (2007b)
<i>Platythelphusa</i> spp. and <i>Potamonautes platynotus</i>					
Tanzania, L	2.0-12.2	0.9-21.0	10.0-56.8	Quadrat surveys using SCUBA (multiple collection efforts with irregular intervals over a 3 year period)	This study

L= lake; R = river; FS = forest stream and associated floodplain; n.a. = not available.

*Estimated from wet mass data provided in the reference.

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 inhabiting *Neothauma tanganyicensa* shell beds 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 a decrease in food resources and higher levels of silt content 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.

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 hypothesis is that the high levels of species diversity in the African Rift lakes are principally maintained through competition and niche diversification (Schluter, 2000). This would suggest 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). However, other studies demonstrated an 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 (Chapter 3 and 4). Stable isotope analyses provide a potentially powerful method to examine questions of trophic niche width and interspecific differentiation (Genner et al., 1999; Bearhop et al., 2004). Previous analyses using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ 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 (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 compared crab isotopic signatures with those of putative food sources and we further examined patterns of variability. Following the conventional assumption that $\delta^{13}\text{C}$ increases by 0 to 1‰ and $\delta^{15}\text{N}$ by 2 to 4‰ between a consumer and its diet (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). Part of this discrepancy is explained by the broad distribution of $\delta^{13}\text{C}$ values of both crabs and putative food resources. 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 methods. The observed discrepancy between the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of the different crab species and their putative food sources is likely to be related to the high variability among individual isotopic signatures. Our gut content analyses demonstrated that crabs include primary producers as well as primary and secondary consumers in their diet. Experimental studies have shown that the amount of trophic fractionation can vary between different trophic levels, and the range of trophic levels from which food resources are drawn can influence variability of consumer stable isotope signatures (Vander Zanden & Rasmussen, 2001; Bearhop et al., 2004).

Based on our current data it is not possible to confidently link crabs to individual food sources. However, 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 enclosure 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 are included in the diet of numerous endemic fish species, including

Mastacembelus plagiostomus (spiny eel), *Synodontis dhonti* (catfish), *Chrysichthys brachynema* and *C. stappersi* (bagrid catfish), as well as the cichlids *Boulengerochromis microlepsis* and *Lamprologus lemarii* (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 increasingly under pressure of environmental problems that are generated by growing human populations (reviewed in Lowe-McConnell, 2003). Invasion of the non-native Louisiana crayfish *Procambarus clarkii* Girard into the lake is considered a serious threat. This species was introduced in Lake Naivasha in 1970 (Parker, 1974), and it has subsequently spread throughout East Africa. Expanding populations presently exist in Uganda, Kenya and Zambia (Arrignon et al., 1990), as well as throughout the Nile River basin as far north as Egypt (G. Howard, IUCN, pers. comm.). 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, IUCN, 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 could cause an ecological disaster if this invasive species established 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; McIntyre et al., 2005; 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; Airolidi, 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 expected to be the most sensitive to the impacts of sediment loading. 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 might 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 they are thus trophically linked to organisms that are vulnerable to the impacts of increased sedimentation, it can be predicted that Lake Tanganyika's endemic crabs will respond by shifting foraging patterns (e.g. McIntyre et al., 2005). However, responses are expected to be complex and possibly delayed relative to lower trophic levels, because the different crab species occupy multiple positions within the trophic foodweb. Considering the evidence presented here, as well as in Chapter 4, it is becoming clear that considerable amount of overlap exists among the ecological niches of the different Lake Tanganyika crab species. 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 establishing 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. 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.

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 Lake Tanganyika endemic crab 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 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, pers. obs.). *Platythelphusa polita* was absent from sites that we surveyed in Tanzania and Zambia between 2002 and 2004 (S.A.E. Marijnissen, pers. obs.), and our present study suggests that *P. maculata* has rather 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. Several authors have advocated the concept of assigning core 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). Although a large-scale survey conducted specifically for conservation purposes confirmed that high species diversity of fish and molluscs exists in aquatic habitats adjacent to terrestrial reserves such as Mahale Mountains National Park in Tanzania and Nsumbu National Park in Zambia (Allison et al., 2000), the feasibility of preserving lacustrine biodiversity

in general by directing conservation efforts at these core areas remains questionable.

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. Lacustrine taxa with high levels of endemism often exhibit limited dispersal abilities and high genetic population differentiation (Michel et al., 2004; Sefc et al., 2007, and references therein), which has major implications for conservation decisions. Furthermore, there is evidence that the distribution patterns of some taxa in Lake Tanganyika are consistent with a stochastic metapopulation model (Cohen, 2000; Michel et al., 2004). Because such populations are naturally subject to frequent fluctuations in size and local extinction events, patterns of temporal assemblage variability should also be taken into account when designing conservation strategies.

The largest problem with aquatic conservation is that the entity in need of protection is not necessarily defined by the lake itself, but by the entire catchment from which its water is drawn. Although the concept of assigning core aquatic reserves might seem attractive from a local point of view, coherent conservation of aquatic diversity and maintenance of a healthy, functioning lacustrine ecosystem will more likely be achieved by means of a basin wide approach. To ensure that human impact on this unique lake is minimized, it is crucial that not only 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). Long-lasting environmental education and outreach programs are essential to achieve an enhanced involvement of local communities in freshwater biodiversity conservation efforts. 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.

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Chapter 7



7

Het Tanganyikameer: Bron van diversiteit

Saskia A.E. Marijnissen

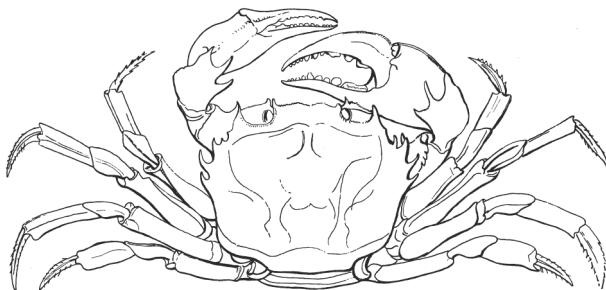
INLEIDING

Het Oostafrikaanse Tanganyikameer is in veel opzichten één van de opmerkelijkste zoetwatergebieden ter wereld. Het meer herbergt een ongekende rijkdom aan endemische soorten. Het meest bekend zijn de soortenzwermen van cichlide vissen, die vaak gebruikt worden als model voor evolutionaire studies. Maar het Tanganyikameer bevat ook vele andere endemische soorten, waaronder meervallen, stekelalen, schelpdieren, ostracoden, garnalen, bloedzuigers en sponzen. Het is bovendien het enige meer in de wereld dat een soortenzwerm van endemische krabben herbergt. Omdat de biodiversiteit in het Tanganyikameer onder steeds grotere druk komt te staan door menselijke activiteiten, is het van groot belang om inzicht te krijgen in de vraag hoe de endemische diversiteit in het meer is ontstaan. Misschien nog belangrijker is het om te weten hoe de enorme soortenrijkdom in het meer zich in stand kan houden. Met andere woorden, er is inzicht nodig in zowel de evolutie als de ecologie van de vele soorten in het meer. Hierbij zijn de krabben vooral belangrijk omdat ze een waardevol modelsysteem kunnen zijn voor soortsvorming in andere diergroepen en omdat ze waarschijnlijk een belangrijke rol spelen in bentische voedselketens. In dit proefschrift volg ik daarom een multidisciplinaire aanpak waarbij ik mij richt op het onderzoeken van zowel de evolutionaire geschiedenis als de ecologie van de endemische krabben in het Tanganyikameer. Ook lever ik een bijdrage aan het beantwoorden van de vraag of de krabben gevoelig zijn voor verstoring van hun leefomgeving. Tot slot filosofeer ik over het behoud van diversiteit in het Tanganyikameer.

DIVERSITEIT VAN ENDEMISCHE KRABBEN

Om biodiversiteit te kunnen bestuderen is taxonomische informatie essentieel. De taxonomie deelt soorten in op basis van gemeenschappelijke eigenschappen. Taxonomie wordt meestal bedreven door gebruik te maken van morfologische kenmerken. In 1887 beschreef de carcinoloog Alphonse Milne-Edwards de eerste krabbensoort uit het Tanganyikameer, aan de hand van een vrouwelijk exemplaar dat door Franse missionarissen naar het Muséum National d'Histoire Naturelle in Parijs was gezonden. Ongetwijfeld geïnspireerd door de sterk vergrootte schaar en de vervaarlijke stekels waarmee deze krab bewapend was, noemde Milne-Edwards de soort *Platythelphusa armata* (Figuur 1). Hierna volgden al snel ontdekkingen van meer krabbensoorten uit het Tanganyikameer. De taxonomie van de krabben is vervolgens een aantal malen grondig

herrangschikt. Zelf heb ik mij afzijdig gehouden van discussies over de hogere taxonomie van deze krabben, maar ik raakte wel geboeid door een aantal opmerkelijke inconsistenties op het niveau van de soort. Zo ontdekte ik al vrij snel tijdens mijn onderzoek het bestaan van twee, tot dan toe onbeschreven krabbensoorten uit



Figuur 1. Het type exemplaar van de soort die in 1887 door A. Milne-Edwards werd beschreven als *Platythelphusa armata*, hier op sierlijke wijze getekend door J.E.S. Moore in zijn boek 'The Tanganyika Problem' uit 1903.

het meer. In HOOFDSTUK 2 beschrijf ik deze soorten als *Platythelphusa immaculata* en *Platythelphusa praelongata*. Ik bespreek daarnaast de taxonomische positie van *Platythelphusa denticulata*, die eerder als synoniem van *Platythelphusa conculcata* was aangezien. Op basis van een aantal morfologische verschillen stel ik vast dat *P. denticulata* en *P. conculcata* niet één en dezelfde soort zijn. Tegelijk zet ik een kanttekening bij het feit dat er opvallende overeenkomsten bestaan tussen *P. denticulata* en *P. armata*. De onzekerheid rondom de taxonomische status van *P. denticulata* zal mij tijdens de loop van mijn gehele onderzoek blijven achtervolgen. Toch blijft hij voorlopig bekend staan als geldige soort. Daardoor zijn er nu in totaal 10 endemische krabbensoorten bekend uit het Tanganyikameer, waaronder 9 soorten in het endemische genus *Platythelphusa* alsmede de soort *Potamonautes platynotus*.

HET ONTSTAAN VAN DIVERSITEIT

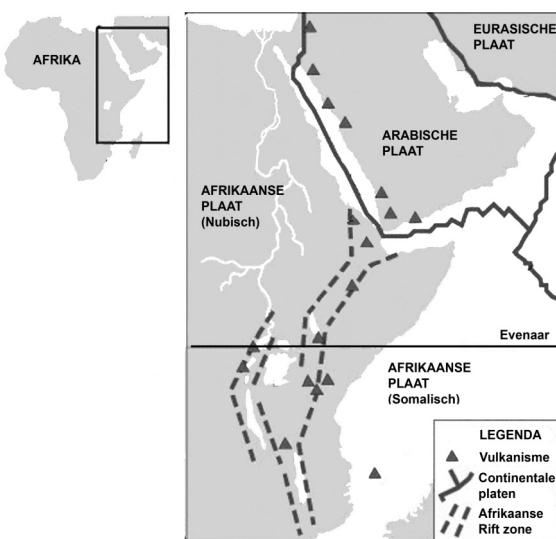
Naar aanleiding van enkele opvallende morfologische overeenkomsten met mariene krabbensoorten suggereerden een aantal wetenschappers aan het begin van de vorige eeuw dat de krabben uit het Tanganyikameer oorspronkelijk uit de zee kwamen. De hypothese luidde dat het Tanganyikameer een gunstige omgeving bood, waardoor de van oorsprong mariene krabben miljoenen jaren in het meer konden blijven voortbestaan. Een alternatieve hypothese is dat de opvallende morfologische kenmerken van deze krabben het resultaat zijn van convergente evolutie. In HOOFDSTUK 3 laat ik zien dat de eerste hypothese zeer onwaarschijnlijk is. Analyses gebaseerd op sequenties van twee verschillende delen van het mitochondriale genoom, de 12S en 16S ribosoomaal RNA genen, duiden erop dat de Tanganyika krabben evolutionair gerelateerd zijn aan andere Afrikaanse zoetwaterkrabben. De resultaten tonen aan dat alle *Platyhelphusa* soorten zeer nauw verwant zijn aan elkaar en samen een monofyletische groep vormen. De fylogenetische stamboom van de *Platyhelphusa* soortenzwerm vertoont zeer korte takken, wat erop duidt dat de soorten vrij recent zijn ontstaan. Uitgaande van de aannames dat mutatiefrequenties redelijk constant zijn en dat 16S rRNA 0.65-0.9% divergentie vertoont per miljoen jaar, kunnen op basis van mijn analyses twee voorzichtige conclusies worden getrokken: (1) de splitsing tussen de voorouder van de huidige *Platyhelphusa* soortenzwerm en zijn naaste verwanten vond ongeveer 9-6.5 miljoen jaar geleden plaats; en (2) ongeveer 3.3-2.5 miljoen jaar geleden begon een periode van elkaar snel opvolgende soortsvormingsepisodes binnen deze soortenzwerm.

Het feit dat er in een relatief korte periode negen krabbensoorten in het Tanganyikameer zijn ontstaan is vooral opvallend wanneer je dit vergelijkt met wat er tot nu toe bekend is van andere Afrikaanse zoetwaterkrabben. Veel van de fylogenetische stambomen van deze krabben laten vaak vrij lange takken zien, maar weinig morfologische diversiteit. Dit betekent dat deze krabben morfologisch weinig verandering ondergaan gedurende lange evolutionaire periodes. De stamboom van de *Platyhelphusa* soortenzwerm is precies omgekeerd: korte takken, maar veel diversiteit. Er is dus blijkbaar iets speciaals aan de hand in het Tanganyikameer.

Er zijn verschillende theorieën die zouden kunnen verklaren waarom er zoveel endemische soorten zijn ontstaan in het meer. Om dit te kunnen begrijpen is eerst een stukje geologische geschiedenis nodig. Het Tanganyikameer maakt deel uit van de Afrikaanse Riftvallei, waar het Nubische- en het Somalische gedeelte van de continentale plaat zich langzaam maar zeker in tweeën aan het splitsen is (Figuur 2). De Riftvallei wordt daardoor steeds dieper. Ongeveer 12-9 miljoen jaar geleden begon zich tussen het stroomgebied van de tegenwoordige Kongo- en Malagarassi-rivier een

verzakking in de Riftvallei te ontwikkelen. Deze verzakking veranderde van een moerasachtig gebied in drie afzonderlijke meren, die ongeveer 6-5 miljoen jaar geleden door verdere verdieping van de Riftvallei overstroomden en daardoor één groot geheel vormden. Het Tanganyikameer was geboren. Tegenwoordig heeft het een maximum diepte van 1470 meter en het is daarmee het allerdiepste meer in Afrika. De plaattektoniek in de Riftvallei blijft echter constant in beweging, waardoor er voortdurend verschuivingen in het Oostafrikaanse gebied plaatsvinden. Daarnaast hebben er de afgelopen miljoenen jaren dramatische klimaatveranderingen in dit gebied plaatsgevonden. Door de combinatie van deze twee factoren heeft het waterpeil in het meer enorme fluctuaties gekend. Tijdens enkele van deze fluctuaties zakte het waterpeil enkele honderden meters, waardoor het Tanganyikameer weer werd opgesplitst in de afzonderlijke delen waaruit het oorspronkelijk bestond.

Door het ontstaan van deze afzonderlijke meren ontstond het klassieke scenario voor soortsvorming. Doordat geografisch gescheiden populaties geen erfelijk materiaal kunnen uitwisselen gaan ze in de loop van de tijd verschillen van elkaar. Hier is geen speciale evolutionaire druk voor nodig; de



Figuur 2. Kaart van Oost Afrika met de twee delen van de continentale plaat (Nubisch en Somalisch) waartussen de Riftvallei is ontstaan. Het Tanganyikameer bevindt zich in de meest westelijke arm van de Riftvallei.

veranderingen kunnen plaats vinden als gevolg van willekeurige mutaties in de genen van de gescheiden populaties. Als de individuen uit deze populaties lang genoeg van elkaar gescheiden blijven, bestaat de kans dat ze niet meer met elkaar kunnen paren. Op dat moment heeft er allopatrische soortsvorming plaatsgevonden. Het ontstaan van nieuwe soorten door geografische barrières is een algemeen geaccepteerde evolutie-theorie. Dankzij de fluctuaties van het waterpeil in het Tanganyikameer zijn er de afgelopen miljoenen jaren dus aardig wat kansen geweest voor allopatrische soortsvorming.

Toch lijkt het onwaarschijnlijk dat het bestaan van honderden endemische soorten in het meer volledig te verklaren valt door dergelijke soortvormings-

processen. Het feit dat een groot aantal soorten opmerkelijke ecologische verschillen vertoont is een aanwijzing dat er naar een alternatieve verklaring gezocht moet worden. Het is mogelijk dat een belangrijk deel van de diversiteit in het Tanganyikameer verklaard kan worden door de theorie van sympatrische soortsvorming. Volgens deze theorie kunnen soorten ontstaan binnen een enkele populatie, zonder dat er sprake is van enige geografische scheiding. Dit is bijvoorbeeld mogelijk wanneer een populatie zich vestigt in een gebied waar zich een aantal lege ecologische niches bevinden, zoals het geval kan zijn geweest nadat het waterpeil in het Tanganyikameer een aanmerkelijke fluctuatie had ondergaan. Door het bestaan van natuurlijke variatie in erfelijke eigenschappen kan het ene deel van een populatie zich makkelijker in de ene niche vestigen dan de andere. Dit kan het begin zijn van het opsplitsen van een populatie in één of meerdere ecologisch verschillende soorten. Biologisch kun je echter pas van verschillende soorten spreken als deze zich onderling niet meer voortplanten. Het ontstaan van reproductieve isolatie kan een toevallige bijkomstigheid zijn van ecologische aanpassingen, of het kan een gevolg zijn van selectieve partnerkeuze. Sympatrische soortsvorming is mogelijk, maar het is moeilijk aan te tonen onder natuurlijke omstandigheden.

KRABBENSCHAREN ALS AANWIJZINGEN

Krabbenscharen vormen multifunctionele gereedschappen. Ze bieden de krab niet alleen bestek om mee te eten, maar ook een sterk wapen om mee te vechten en eventueel een aantrekkelijk signaal om vrouwtjes mee te verleiden. De morfologie van elke schaar vertelt zijn eigen verhaal. Hierdoor zijn krabbenscharen bijzonder interessante studieobjecten voor een evolutiebioloog. In HOOFDSTUK 4 onderzoek ik of de functionele morfologie van scharen mij aanwijzingen kan geven over de evolutionaire processen die bij hebben gedragen aan het ontstaan van diversiteit bij de krabben uit het Tanganyikameer.

Allereerst heb ik een nieuwe fylogenetische boom gegenereerd, op basis van sequenties uit zowel het 16S rRNA als het Cytochrome Oxidase II (COII) mitochondriaal gen. Deze combinatie geeft een iets beter beeld van de fylogenetische verhoudingen binnen de *Platythelphusa* soortenzwerm, maar vooral bovenin de boom zijn de soortsverhoudingen moeilijk te bepalen. Ik twijfel wederom aan de status van *P. denticulata*. Door zijn variabele morfologische kenmerken laat dit taxon zich moeilijk in een hokje stoppen. Ik postuleer de hypothese dat *P. denticulata* wellicht het gevolg is van hybridisatie. Helaas kan ik deze hypothese niet empirisch toetsen met de genetische data die ik tot nu toe gegenereerd heb. In de evolutiebiologie wordt er vanuit gegaan dat mitochondriaal DNA normaal gesproken uitsluitend via de vrouwelijke lijn overerft, waardoor het ongeschikt is om hybridisatie aan te tonen. Om te testen

of er sprake is van hybridisatie zou DNA uit de celkern beter geschikt zijn, dus daar ligt een onderwerp voor een vervolgstudie. Onderzoek aan veelbestudeerde soortenzwermen zoals de Darwinvinken en Afrikaanse cichliden, duiden aan dat hybridisatie een veelvoorkomend fenomeen is bij recent gevormde soorten dat wellicht bijdraagt aan de verhoogde morfologische en ecologische diversiteit van deze groepen. Het lijkt mij geen eigenaardige gedachte dat dit ook het geval is bij de *Platythelphusa* soortenzwerm.

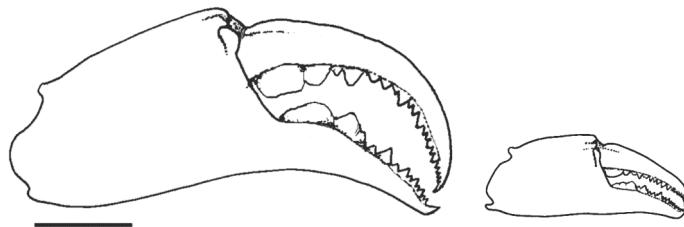
Terug naar de krabben scharen. Er bestaat een markante verscheidenheid aan schaar-morfologien bij endemische krabben uit het Tanganyikameer. *Platythelphusa armata* heeft door zijn sterk vergrootte schaar veel bekendheid vergaard onder wetenschappers. De relatieve grootte en de kiesvormige tanden van deze schaar doen denken aan mariene krabben die gespecialiseerd zijn in het eten van schelpdieren. Opmerkelijk genoeg vertonen de schelpen van endemische slakken uit het Tanganyikameer vaak verdikkingen en uitstulpingen die ook voorkomen als verdediging bij mariene slakken tegen predatie door vissen en krabben. Dit heeft geleid tot de hypothese dat de diversiteit van de slakken uit het Tanganyikameer wordt gedreven door een evolutionaire wapenwedloop met *P. armata*.

Mijn functioneel morfologische analyses bevestigen dat deze soort inderdaad sterk gespecialiseerde schaarkenmerken vertoont, maar het blijkt dat *P. armata* niet de enige is die zich heeft aangepast aan het eten van schelpdieren. Ook de scharen van *Potamonautes platynotus* vertonen aanwijzingen die duiden op regelmatige schelpdierconsumptie, zij het in mindere mate dan *P. armata*. Bij zowel *P. armata* als *Po. platynotus* hebben mannetjes én vrouwtjes een vergrote schaar. Bij een derde soort uit het Tanganyikameer, *P. tuberculata*, hebben alleen de mannetjes een sterk vergrootte schaar. Gemiddeld is de schaar van de mannetjes 1.9 keer groter dan die van de vrouwtjes en het verschil in grote en vorm tussen de schaar van de mannetjes en die van de vrouwtjes is frappant (Figuur 3). Dit is een teken dat er iets bijzonders aan de hand is.

Met behulp van een speciaal aangepaste krachtmeter toon ik aan dat de vergrote schaar van *P. tuberculata* mannetjes veel zwakker is dan die van *P. armata* en *Po. platynotus*. De grootte van de schaar van *P. tuberculata* mannetjes is dus niet direct gericht op het kunnen uitoefenen van kracht. De schaar is daarentegen wél zo gevormd dat hij snel kan bewegen. De vorm doet denken aan die van sommige *Uca* soorten, ook wel wenkkrabben genoemd. Daar is aangegetoond dat de mannelijke scharen door hun vorm en snelheid goed functioneren bij gevechten met mannelijke rivalen. Daarnaast heeft de vorm een meer symbolische functie bij het imponeren en verleiden van vrouwtjes. De specifieke rol van mannelijke rivaliteit versus vrouwelijke voorkeur moet nog onderzocht worden bij de krabben uit het Tanganyikameer. Het is echter zeer waarschijnlijk dat hier seksuele selectie aan het werk is geweest.

Nadat ik de scharen van *Po. platynotus*, *P. armata* en *P. tuberculata* met elkaar had vergeleken, heb ik ook die van de overige endemische krabbensoorten onderzocht. De diversiteit in functionele schaarmorfologie van de vrouwtjes suggerert dat er verschillen in trofische ecologie bestaan tussen de soorten. Dit is bijvoorbeeld duidelijk als de scharen van *P. conculcata* vrouwtjes worden vergeleken met die van *P. praelongata*. De verschillen tussen de scharen van sommige *Platythelphusa* soorten zijn zeer subtiel. Er is echter bij een aantal mariene krabbensoorten aangetoond dat zelfs kleine verschillen al invloed kunnen hebben op het eetgedrag. Verschillen in de relatieve grootte van de scharen van de mannetjes en vrouwtjes leveren bewijs dat ook seksuele selectie van invloed is geweest. Dit is niet alleen duidelijk bij *P. tuberculata*, maar bijvoorbeeld ook bij *P. maculata* waar de mannetjes een schaar hebben die gemiddeld 1.8 keer groter is dan die van de vrouwtjes.

Wanneer de resultaten van de functioneel morfologische analyses worden bekeken in een fylogenetische context, dan blijkt dat de aanwijzingen voor zowel ecologische- als seksuele selectie tijdens de gehele evolutionaire geschiedenis van de *Platythelphusa* soortenzwerm aanwezig zijn. Het zou daarom kunnen dat sympatrische soortsvorming een belangrijke rol heeft gespeeld bij het ontstaan van de diversiteit bij deze soortenzwerm. Om dit aan te tonen is echter veel meer nodig dan alleen morfologische aanwijzingen. Gedragsobservaties in het laboratorium zouden kunnen helpen om inzicht te krijgen in de manier waarop partnerkeuze bij deze krabben werkt, maar dat is een bijzonder lastige opgave. Ecologische soortsvorming laat zich onder natuurlijke omstandigheden ook moeilijk onderzoeken, maar er kan een begin worden gemaakt door te testen of verschillende krabbensoorten inderdaad verschillende ecologische niches bezetten in het Tanganyikameer.



Figuur 3. Schaar van *Platythelphusa tuberculata* mannetje (links) en vrouwje (rechts). Schaal geeft 1 centimeter aan.

ECOLOGIE VAN ENDEMISCHE KRABBENSOORTEN

In HOOFDSTUK 5 ben ik op zoek gegaan naar een antwoord op de vraag of er verschillen te ontdekken zijn tussen de ecologische niches die de endemische krabbensoorten in het Tanganyikameer bezetten. Behalve verschillen in

functionele schaarmorfologiën zijn er nog een aantal morfologische aanwijzingen en veldobservaties die erop duiden dat sommige soorten ecologisch van elkaar gescheiden zijn doordat ze in verschillende habitats voorkomen. In vergelijking tot de andere krabbensoorten hebben *P. tuberculata* en *P. praelongata* vrij lange en dunne looppoten. Het lijkt erop dat beide soorten voornamelijk op diepgelegen modderige bodems voorkomen, waar de lange dunne poten wellicht voordeel opleveren. *Platythelphusa maculata* en *P. polita* hebben beiden een kleine, tamelijk bolle carapax en ze lijken zich voornamelijk te verschuilen in lege schelpen van de endemische slakkensoort *Neothauma tanganyicense* (Figuur 4). De drie middelgrote soorten *P. concilcata*, *P. echinata* en *P. immaculata* hebben zeer platte carapaxen en komen vaak voor in rotsachtige habitats, waar ze zich prima kunnen verschuilen in nauwe nissen. Het kan op basis van deze aanwijzingen worden aangenomen dat er sprake is van enige ecologische scheiding tussen de soorten. Tegelijk lijkt het erop dat de ecologische niches van een aantal soorten overlappen.

Om te onderzoeken in welke mate de ecologische niches verschillende endemische soorten verschillen of overlappen heb ik een aantal methodes gebruikt. Allereerst heb ik een serie inventarisaties uitgevoerd om te bekijken of soorten een consequente voorkeur tonen voor bepaalde habitatvariabelen. Daarvoor heb ik langs ongeveer 50 kilometer kustlijn met behulp van duik- of snorkelapparatuur herhaaldelijk inventarisaties uitgevoerd op 16 locaties, waarbij ik het habitattype noteerde waarin krabben gevonden werden. Op 10 locaties nam ik monsters om de chlorofyl *a* concentratie van het substraat te kunnen bepalen, alsmede de hoeveelheid organisch en anorganisch materiaal. Ook bekeek ik of het voorkomen van bepaalde krabbensoorten gerelateerd kan worden aan dichtheden van schelpdieren. Daarnaast bekeek ik de maaginhoud van een aantal krabbensoorten en verrichtte ik stabiele isotopen analyses van koolstof (C) en stikstof (N). Tijdens de fotosynthese leggen primaire producenten zoals planten en algen zowel de ^{12}C en ^{13}C als ^{14}N en ^{15}N stabiele isotopen in een bepaalde verhouding vast in hun weefsel. Deze stabiele isotopen worden doorgaans op redelijk voorspelbare wijze doorgegeven in het natuurlijke voedselweb. Doorgaans wordt aangenomen dat de ratio $^{12}\text{C}/^{13}\text{C}$ ongeveer 0-1 ‰ toeneemt en de ratio $^{14}\text{N}/^{15}\text{N}$ met 2-4 ‰ per niveau hoger in het voedselweb. Daardoor kan aan de hand van $\delta^{13}\text{C}$ en $\delta^{15}\text{N}$ bepalingen inzicht worden verkregen in de relatieve positie van een organisme in het voedselweb. Ook kunnen $\delta^{13}\text{C}$ en $\delta^{15}\text{N}$ bepalingen laten zien of organismen trofisch van elkaar verschillen.

In totaal heb ik 1401 krabben verzameld op de 16 locaties die onderdeel uitmaakten van mijn habitat inventarisaties. *Platythelphusa praelongata* en *P. polita* werden niet gevonden tijdens deze inventarisaties en daarom kan ik geen verdere uitspraken doen over de ecologie van deze twee soorten. *Platythelphusa*



Figuur 4. *Platythelphusa maculata* in een lege schelp van de endemische slakkensoort *Neothauma tanganyicensis*. Schaal geeft 1 centimeter aan.

denticulata werd slechts in hele lage aantallen aangetroffen en het is daardoor moeilijk om duidelijke uitspraken te doen over dit taxon. De resultaten van mijn onderzoek ondersteunen de aanname dat er inderdaad sprake is van ecologische niche-scheiding tussen een aantal van de overige endemische krabbensoorten, maar tegelijkertijd is er ook overlap te zien. Tijdens mijn inventarisaties van verschillende habitats op dieptes van 0-30 meter trof ik geen enkel exemplaar van *P. tuberculata* aan.

Wel kreeg ik deze soort regelmatig aangeboden door vissers die hun netten uit hadden gezet in de modderige delta van de Luichi rivier op dieptes variërend van 50 tot meer dan 100 meter. Dit klopt met de aanname dat deze soort vooral op diepgelegen, modderige bodems voorkomt. *Platythelphusa maculata* werd tijdens mijn inventarisaties alleen aangetroffen in *Neothauma tanganyicensis* schelpenbedden, wat ook in overeenstemming is met eerdere aannames. De meeste overlap tussen de ecologische niches van de krabben is te zien in rotsachtige habitats, waar zowel *P. conculcata*, *P. echinata* en *P. immaculata* regelmatig worden aangetroffen, alsook *P. armata* en *Po. platynotus*. Toch lijkt het erop dat ook hier enige scheiding plaats vindt, met name op basis van substraat grootte en diepte. De invloed van variabelen zoals chlorofyl *a* gehalte, organisch of anorganisch materiaal en de hoeveelheid schelpdieren op de verspreiding van krabbensoorten is echter minder duidelijk.

Analyses van de maaginhoud konden voor 6 van de 10 soorten worden uitgevoerd. In totaal werden 574 krabben ontleed, waarvan er 386 gebruikt konden worden voor verdere analyses. Alhoewel de maaginhoud data niet goed geschikt zijn voor statistische toetsing, kan er op basis van de in grafieken zichtbare patronen worden vastgesteld dat de maaginhoud van *P. armata* vaker overblijfselen van schelpdieren bevat dan de maaginhoud van de andere krabbensoorten. Alle onderzochte soorten hadden regelmatig detritus in hun maag. Bij *P. echinata* en *P. maculata* was dit voor respectievelijk 80% en 100% van de individuen het geval. Verder waren er geen duidelijke patronen te ontdekken op basis van de maaginhoud analyses. Ook *P. armata*, *P. concilcata*, *P. immaculata* en *Po. platynotus* hadden regelmatig detritus in hun maag. Daarnaast werd bij alle onderzochte soorten plantaardig materiaal in de magen aangetroffen, alsmede fragmenten van schelpdieren, aquatische insectenlarven en ostracoden.

Het nadeel van maaginhoud-analyses is dat ze slechts een momentopname leveren, tenzij ze consequent gedurende lange periodes worden uitgevoerd. Stabiel isotopen onderzoek daarentegen heeft als voordeel dat het een geïntegreerd beeld oplevert van wat een organisme gedurende een langere periode consumeert. Mijn analyses tonen aan dat de gemiddelde $\delta^{13}\text{C}$ en $\delta^{15}\text{N}$ waarden van *P. armata* en *P. maculata* statistisch niet van elkaar verschillen. De gemiddelde $\delta^{13}\text{C}$ en/of $\delta^{15}\text{N}$ waarden van de overige krabbensoorten vertonen echter wél statistisch significante verschillen. Toch is het te simpel om te concluderen dat deze krabbensoorten complete trofische segregatie vertonen. Alhoewel de gemiddelde waarden significante verschillen laten zien, liggen de $\delta^{13}\text{C}$ en/of $\delta^{15}\text{N}$ waarden van de individuele krabben binnen de soorten vrij ver uit elkaar en vertonen in een aantal gevallen overlap met andere soorten. Dit duidt er ten eerste op dat de individuen binnen een soort vrij flexibel kunnen zijn in hun eetgedrag en ten tweede dat de trofische scheiding tussen deze soorten incompleet is.

De vraag of de verschillende endemische krabbensoorten verschillende ecologische niches bezetten in het Tanganyikameer, kan derhalve niet eenduidig worden beantwoord. Hierbij moet in aanmerking worden genomen dat volgens theoretische modellen ecologische soortsvorming niet persé uitsluit dat soorten zich flexibel gedragen. Dit bemoeilijkt het vinden van een antwoord op de vraag of ecologische selectiedruk een belangrijke rol heeft gespeeld bij het ontstaan van diversiteit van deze krabben. De theorie van ecologische soortsvorming kan uitgebreider worden getest door combinatie van meer veldobservaties en experimenten. Onderzoek aan sympatrische soortsvorming benadrukt dat ecologische- en seksuele selectie regelmatig met elkaar verweven zijn. De mogelijkheid dat seksuele selectie heeft bijgedragen aan het ontstaan van de diversiteit van de endemische krabben uit het Tanganyikameer moet zeker niet terzijde gelegd worden. Daarnaast ben ik van mening dat de wetenschap ook

open moet staan voor de mogelijkheid dat hybridisatie een rol heeft gespeeld in de evolutionaire geschiedenis van deze krabben. Mijn onderzoek heeft laten zien dat de endemische krabben uit het Tanganyikameer een waardevolle modelgroep vormen. Verdere studies aan deze groep kunnen bijdragen aan een beter begrip van hoe de biodiversiteit in dit unieke systeem tot stand is gekomen en hoe het ecosysteem zich in stand houdt.

BEHOUD VAN BIODIVERSITEIT

De biodiversiteit van het Tanganyikameer staat onder steeds grotere druk door vervuiling, overexploitatie en wijdverspreide ontbossing van de omringende gebieden. Behoud van de biodiversiteit in het meer is niet alleen van enorm belang omdat het een hotspot van endemisme en soortenrijkdom is, maar ook omdat het meer voorziet in maar liefst 17% van de wereld oppervlaktewater voorraad en een belangrijke bron van drinkwater, voedsel en inkomsten vormt voor de ongeveer tien miljoen bewoners van het omringende bekken. In het algemeen geldt dat bescherming van tropische zoetwater-biodiversiteit wordt bemoeilijkt door een gebrek aan ecologische kennis. Onderzoek aan deze systemen is meestal voornamelijk gericht op vissen, terwijl andere ecologisch belangrijke groepen vaak over het hoofd worden gezien. Dit geldt ook voor zoetwaterkrabben. Van krabben is bekend dat ze een belangrijke rol kunnen spelen in zowel aquatische als terrestrische ecosystemen. Krabben kunnen een groot deel uitmaken van de totale hoeveelheid bentische biomassa van een ecosysteem en ze kunnen grote invloed uitoefenen op de verspreiding en dichthesen van hun prooidieren. Het is dus van belang om ook krabben in oogschouw te nemen bij aquatische ecosysteem- en natuurbehoudstudies. Helaas hebben projecten gericht op de bescherming van biodiversiteit in het Tanganyikameer de krabben tot nu toe genegeerd.

Door middel van het onderzoek dat wordt beschreven in HOOFDSTUK 6 probeer ik hier verandering in te brengen. Het doel van dit onderzoek was om meer inzicht te krijgen in de verspreiding en dichthesen van de krabben en hun functionele rol in het aquatische ecosysteem, alsmede het bepalen van hun kwetsbaarheid ten opzichte van door menselijk handelen veroorzaakte habitat verstoringen. Daarnaast bespreek ik aan het eind van dit hoofdstuk enige algemene implicaties voor het behoud van biodiversiteit in het Tanganyikameer.

Om de verspreiding en dichthesen van de verschillende krabbensoorten te onderzoeken heb ik op drie dieptes (5, 10 en 20 meter) willekeurig 20 kwadranten van 50x50 centimeter uitgezet. Alle krabben die zich binnen een kwadrant bevonden werden geteld. Ik heb deze procedure herhaald op 12 verschillende locaties. Hiervan bevonden zich er 3 in de delta van de Luichi rivier, 5 in rotsachtige gebieden waar de kustlijn volledig ontbost was en 4 in rotsachtige gebieden waar nog een redelijk natuurlijke vegetatie groeide. Met

behelp van een formule kon ik een schatting maken van de biomassa in ieder kwadrant. Daarnaast heb ik zowel van de krabben als van hun mogelijke voedselbronnen (waaronder algen, detritus, verschillende soorten schelpdieren en aquatische insectenlarven) materiaal verzameld voor stabiele isotopen analyses van koolstof (C) en stikstof (N).

De resultaten van dit onderzoek tonen aan dat de krabben een belangrijk onderdeel vormen van benthische ecosystemen in het Tanganyikameer. Hoewel hun verspreiding zeer onregelmatige patronen vertoont, kunnen de dichtheden van de krabben lokaal hoog zijn. Ook laten mijn schattingen zien dat de krabben een belangrijke bijdrage leveren aan de benthische biomassa. De gemiddelde $\delta^{13}\text{C}$ waarden van de verschillende krabbensoorten en hun mogelijke voedselbronnen lopen vrij ver uit elkaar, waardoor het niet mogelijk is om deze direct met elkaar te verbinden. Zoals de maaginhoud-analyses eerder ook al aangaven lijkt het erop dat de krabben hun energie uit niet één, maar verschillende voedselbronnen halen. De gemiddelde $\delta^{15}\text{N}$ waarden van de krabben liggen hoger dan die van andere ongewervelde benthische organismen zoals schelpdieren en aquatische insectenlarven. Dit toont aan dat de krabben een hogere positie in het benthische voedselweb bezetten. Daarnaast is het bekend dat krabben een onderdeel vormen van het dieet van een aantal endemische vissoorten, waaronder de stekelaal *Mastacembelus plagiostomus*, de meervallen *Chrysichthys brachynema* en *C. stappersi* en de cichliden *Boulengerochromis microlepsis* en *Lamprologus lemarii*. Het wordt daardoor duidelijk dat de krabben een relatief centrale positie bezetten in het benthische voedselweb.

Ondanks het feit dat ik tijdens mijn inventarisaties zowel locaties heb bekeken in gebieden waar de kustlijn volledig ontbost was als in gebieden waar nog een redelijk natuurlijke vegetatie groeide, kon ik geen duidelijke verschillen vinden in de samenstelling of dichtheden van de krabbensoorten. Dat is opmerkelijk, want eerder onderzoek aan ostracoden, slakken en vissen in het Tanganyikameer duidde erop dat ontbossing en de daarvan gerelateerde sedimentatie in aquatische habitats aantoonbaar negatieve effecten heeft op de samenstelling en dichtheden van benthische soorten. Ik postuleer de hypothese dat krabben dankzij hun relatieve ecologische flexibiliteit waarschijnlijk minder gevoelig zijn voor de gevolgen van sedimentatie dan sommige andere endemische taxa. Toch kan worden voorspeld dat de krabben indirect wel zullen reageren, vanwege het feit dat ze door hun eetgedrag verbonden zijn met organismen die aantoonbaar gevoelig zijn voor sedimentatie.

In het kader van een inventarisatie voor de IUCN werd ik drie jaar geleden benaderd om te helpen bij het inschatten van de kwetsbaarheid van de verschillende krabbensoorten uit het Tanganyikameer. Aan de hand van aantallen krabben uit verschillende museumcollecties en het relatieve aantal

krabben dat per soort was aangetroffen tijdens recent veldwerk werd een schatting gemaakt. Momenteel staan er hierdoor 7 endemische krabbensoorten als niet kwetsbaar, 2 als kwetsbaar en 1 als bijna bedreigd op de IUCN Rode Lijst van Bedreigde Soorten (zie www.iucnredlist.org). Mijn onderzoek geeft echter aan dat het belangrijk is om deze schattingen op grotere schaal te testen voordat er harde conclusies worden getrokken.

Er is momenteel geen overeenstemming over hoe de biodiversiteit in het Tanganyikameer het beste beschermd zou kunnen worden. Een aantal wetenschappers is enthousiast over het idee om onderwaterparken in te richten. Die zouden volgens hen moeten liggen aan de voet van bestaande beschermde gebieden zoals Gombe Stream en Mahale National Park in Tanzania of Nsumbu National Park in Zambia. Er is echter nog te weinig kennis over de verspreiding van functioneel ecologische en evolutionaire diversiteit in het meer om beslissingen te kunnen nemen over welke locatie het meest waardevol zou zijn voor een onderwaterpark. Het is sowieso nog maar de vraag of het oprichten van lokale onderwaterparken kan leiden tot algemene bescherming van de biodiversiteit in het Tanganyikameer. De bedreigingen voor de aquatische flora en fauna worden niet zozeer gevormd door processen in het meer zelf, als wel door activiteiten in het omringende gebied.

In de toekomst zou wetenschappelijk onderzoek in het Tanganyikameer zich moeten gaan richten op het verkrijgen van een duidelijker beeld over hoe menselijk handelen in het aangrenzende bekken de diversiteit van organismen in het meer kan beïnvloeden. Meer kennis over de manier waarop het aquatische ecosysteem op lokale en regionale schaal reageert op verstoring is onontbeerlijk voor het maken van beslissingen over natuurbehoud. Het is waarschijnlijk het meest zinvol om natuurbehoudactiviteiten te richten op zowel het meer, alsook het omringende gebied. Hierbij moeten vooral ook initiatieven worden genomen om de sociaal-economische situatie van de lokale bevolking te verbeteren. Alleen dan kan de unieke biodiversiteit van dit waardevolle aquatische ecosysteem in de toekomst worden gewaarborgd.



VERKLARENDE WOORDENLIJST

Allopatrisch	Met betrekking tot populaties die geografisch van elkaar gescheiden zijn.
Bentisch	Nabij, op, of in de bodem levend.
Carapax	Bij schaaldieren is door een vergroeiing van de kop- en het borststuk exoskelet één beschermend pantser ontstaan, wat de carapax (schild) wordt genoemd.
Carcinoloog	Iemand die kreeftachtigen bestudeert.
Cichliden	De familie van de Cichlidae behoort tot de orde van de baarsachtigen. De cichliden familie is bijzonder succesvol. Het verspreidingsgebied van deze vissen omvat Midden- en Zuid Amerika, Afrika, Madagaskar en Zuid-India. Cichliden behoren tot de meest geliefde aquarium vissen ter wereld.
Chlorofyl <i>a</i>	Een groengekleurde stof die in planten en algen voorkomt. Ook wel bladgroen genoemd. Chlorofyl <i>a</i> gehalte kan gebruikt worden als een maat voor primaire productiviteit.
Convergente evolutie	Het verschijnsel waar zich bij verschillende taxonomische groepen zeer sterke (uiterlijke) overeenkomsten hebben ontwikkeld.
Ecologische niche	De plaats die een populatie of soort binnen een ecosysteem inneemt. Dat kan bijvoorbeeld een specifieke habitat zijn, maar ook een bepaalde positie binnen de voedselketen.
Endemisch	Geografisch tot slecht één gebied beperkt. Synoniem: inheems.
Fylogenetisch	Met betrekking tot de evolutionaire geschiedenis van een organisme.
Isotoop	Het aantal neutronen in de kern van chemische elementen zoals koolstof en stikstof kan variëren. Wanneer dit het geval is, zoals bijvoorbeeld bij ¹² C en ¹³ C dan spreekt men van verschillende isotopen.
Monofyletisch	Een groep organismen is monofyletisch als het de meest recente voorouder omvat én alle nakomelingen van die voorouder
Ostracoden	De orde van de Ostracoden behoort tot de klasse van de Kreeftachtigen. Ostracoden zijn zeer kleine kreeftachtige diertjes die worden omhult door twee 'schelpjes'. De Nederlandse naam is mosselkreeftje.
Reproductieve isolatie	Wanneer twee soorten niet met elkaar kunnen voortplanten doordat ze (a) elkaar niet herkennen, of (b) geen vruchtbare nakomelingen kunnen krijgen, is er sprake van reproductive isolatie.
Seksuele selectie	Een proces van natuurlijke selectie, waarbij partnerkeuze plaatsvindt op basis van voorkeur voor bepaalde (uiterlijke) kenmerken. Dit proces kan leiden tot soortsvorming.
Soortenzwerm	De Engelse term 'species flock' wordt in de wetenschappelijke literatuur gebruikt om een monofyletische groep van nauw verwante organismen aan te duiden. Meestal gaat het om een groep die snelle soortsvorming heeft ondergaan binnen een geografisch beperkt gebied.
Sympatrisch	Met betrekking tot populaties die in hetzelfde leefgebied voorkomen.
Taxon	Een taxonomische eenheid, bijvoorbeeld een soort of een familie. Het woord taxon kan ook gebruikt worden als de taxonomische status van een organisme niet geheel duidelijk is.
Taxa	Meervoud van taxon.
Trofisch	Met betrekking tot de positie van een organisme in het voedselweb.

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*I should have been a pair of ragged claws
Scuttling across the floors of silent seas*

*We have lingered in the chambers of the deep
By sea-girls wreathed in seaweeds red and brown
Till human voices wake us and we drown*

T.S. Elliot, 1917

From: The love song of J. Alfred Prufrock

