

Ecology and conservation status of endemic freshwater crabs in Lake Tanganyika, Africa

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Abstract Sedimentation resulting from riparian deforestation has a wide range of detrimental effects on aquatic biodiversity, but predicting the full consequences of such disturbances requires an understanding of the ecosystem's key functional components. We investigated the ecology and response to sedimentation of the diverse, endemic freshwater crabs of Lake Tanganyika, which may occupy important positions in littoral foodwebs. Our surveys revealed crab distribution patterns to be patchy, and that crabs can be locally abundant (0–28 individuals m^{-2}). Crab densities decreased with depth and the dry mass of crab assemblages ranged from 0.0 to 117.7 $g\ m^{-2}$. Comparisons among sites revealed significant effects of sedimentation on crab assemblage evenness, but provided no evidence that sedimentation has altered densities, incidence or species richness. The resilience of crabs to sedimentation might be related to their intraspecific dietary breadth. Stable isotope data ($\delta^{13}C$ and $\delta^{15}N$) from crabs and their potential food resources indicated differences in trophic roles among endemic crab species. Overall, crabs occupy higher trophic positions than most other invertebrates, and they draw upon both benthic and planktonic energy pathways. The high biomass and top-predator status of some crab species suggests the potential for cascading effects on organisms lower in the food web.

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Introduction

Freshwater habitats and the species they support are among the most threatened ecosystems worldwide (Dudgeon et al. 2005; Revenga et al. 2005). The conservation of tropical freshwater ecosystems in particular is hampered by a dearth of baseline ecological data (Dudgeon 2000, 2003; Abell 2001). Moreover, the available data are heavily skewed towards fish (Abell 2001; Strayer 2006), reflecting the economic and cultural importance of fisheries. Advancing the conservation of freshwater biodiversity and ecosystem functioning requires data on key functional groups in addition to fish. The lack of such information is especially problematic in the African Rift Valley region, where human population growth is causing widespread degradation of freshwater habitats while at the same time increasing demands for reliable water and fishery resources (Odada et al. 2003).

Lake Tanganyika, the largest of the African Rift lakes, exemplifies the challenge of simultaneously trying to conserve biodiversity and provide essential resources for human populations. The lake is a globally significant hotspot of freshwater biodiversity and endemism (Groombridge and Jenkins 1998), harbouring at least 1,500 species (Coulter 1991). Approximately 600 species are considered endemic, 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; Martens, personal communication), >90 gastropod species (West et al. 2003; Michel and Todd, unpublished data), 13 shrimp species (Fryer 2006), and 10 crab species (Marijnissen et al. 2004; Reed and Cumberlidge 2006). Lake Tanganyika also contains ~17% of the world's surface freshwater, and serves as an irreplaceable source of clean water, transportation, and economic opportunities for ~10 million people in four riparian countries (Mölsä et al. 2005). Its commercial and artisanal fish harvests employ ~45,000 people and provide 25–40% of the protein needs of local communities (Jorgensen et al. 2005). Maintaining the ecological integrity of Lake Tanganyika is crucial for both biodiversity conservation and human needs.

The Lake Tanganyika ecosystem is increasingly threatened by environmental problems including eutrophication (Bootsma and Hecky 1993), over-fishing (McIntyre et al. 2007), and climate change (O'Reilly et al. 2003; Verburg et al. 2003). One of the most pervasive environmental problems is sedimentation on Lake Tanganyika's littoral habitats caused by watershed deforestation, resulting in a decline in diversity of lacustrine species (Alin et al. 1999; Cohen et al. 2005). Accumulation of sediment on the substrate can adversely affect benthic organisms by reducing habitat quality and heterogeneity, compromising foraging and respiration efficiency, decreasing reproductive success, and altering predator–prey and host–parasite interactions (McIntyre et al. 2005, and references therein).

Here, we investigate the ecology and conservation status of the endemic crabs of Lake Tanganyika. In tropical freshwater ecosystems, crabs often play key ecological roles because of their relatively high abundance and biomass (Turnbull-Kemp 1960; Hill and O'Keefe 1992; Somers and Nel 1998; Dobson et al. 2007a, b), their ability to utilize both terrestrial and aquatic energy pathways (Gherardi and Vannini 1989; Gherardi et al. 1989; Dobson et al. 2002; Moss 2005), and their central position in foodwebs as primary and secondary consumers (Williams 1961, 1962; Gherardi et al. 1987). Crabs can also be effective indicators of pollution and general aquatic ecosystem health (Schuwerack et al. 2001; Bowen and Depledge 2006, and references therein). Based on their benthic habitat

use (Marijnissen et al. 2008), we expect that the endemic crabs of Lake Tanganyika are highly sensitive to sedimentation. Shifts in crab abundance or diversity could have wide-ranging consequences through their effects on prey populations. For instance, marine crabs are important predators involved in trophic cascades (e.g. Silliman and Bertness 2002; Trussell et al. 2002) and freshwater crabs may play similar roles.

Assessments of the status and distribution of freshwater biodiversity in Eastern Africa (Darwall et al. 2005) indicate that Lake Tanganyika is a regionally important area for freshwater crab diversity (Cumberlidge, personal communication). An evaluation based on museum collection data and pilot surveys (Cumberlidge and Marijnissen 2004) tentatively listed two out of ten endemic crab species (*Platythelphusa denticulata* Capart 1952, and *P. praelongata* Marijnissen et al. 2004) from Lake Tanganyika as vulnerable (VU D2), and one (*P. immaculata* Marijnissen et al. 2004) as near threatened (NT B1ab(i); D1) under version 3.1 (2001) of the IUCN Red List of Threatened Species. Although these evaluations were based on occurrence data from a number of locations around the lake, no quantitative data are available on crab densities or functional roles in the ecosystem. Such information is critical for predicting the impact of environmental disturbances on littoral biodiversity and ecosystem functioning.

This paper presents the results of ecological surveys of the endemic crabs that can serve as baseline data for conservation initiatives in Lake Tanganyika. Specifically, we (1) examine patterns of crab species distributions and abundance across sites; (2) assess the functional role of crabs in littoral foodwebs; and (3) evaluate the vulnerability of the crab fauna to human-induced sedimentation. We conclude with a discussion of general implications for the conservation of crab species diversity and ecosystem functioning 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 (Fig. 1). It is the oldest (~9–12 my) and deepest (maximum depth 1,470 m) lake in Africa (Cohen et al. 1997). Only the upper 100–250 m of the water column is oxygenated, and a large majority of the species in the lake are restricted to the near-shore zone (Coulter 1991). Different substrate types are interspersed along the shoreline on scales of 10–1,000 m, but these can be highly patchy even on smaller scales (Michel et al. 2004). Much of the lake's shoreline is rocky and steeply sloped, and the littoral zone consists of a narrow fringe that rapidly drops to >50 m depth over distances of <500 m (J. Corman et al., unpublished data). Where major rivers enter the lake, gently sloping deltas consisting predominantly of sand, mud or shell beds have developed.

We surveyed littoral crab assemblages at 12 sites along ~50 km of the lake shoreline near Kigoma, Tanzania during the dry seasons between 2002 and 2004 (Fig. 1). Nine sites were situated in rocky areas where the substrate is composed of boulders, cobbles, and/or pebbles interspersed with sand patches, and occasionally with aggregations of shells from the large bivalve *Pleidodon spekii* (Woodward 1859). We conducted qualitative evaluations of the sedimentation status of each rocky site at the beginning of the study. Sites were considered sediment-impacted when rocks were covered in a layer of loose silt (generally >1 mm thick). Rocky sites without such a sediment layer were considered reference sites. Results of this qualitative evaluation agreed with quantitative analyses of sedimentation at many of the same

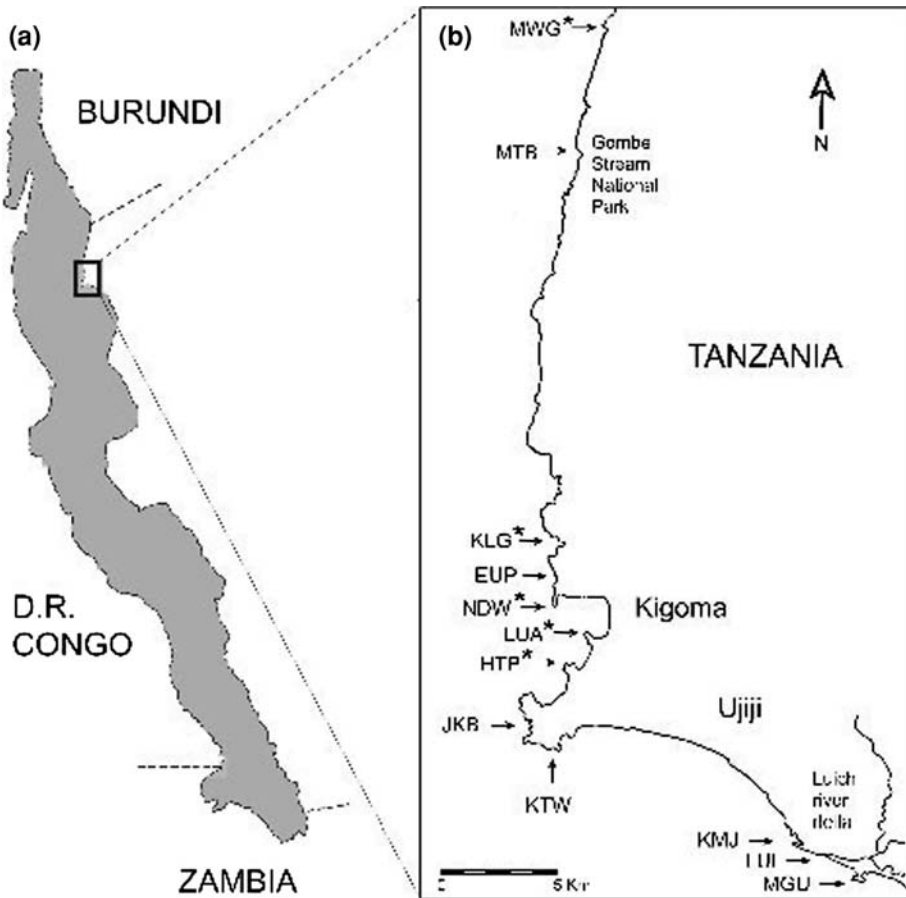


Fig. 1 Map of Lake Tanganyika (a) and study sites (b). *MWG* Mwamgongo (4°36.597'S, 29°38.329'E); *MTB* Mitumba (4°38.153'S, 29°37.811'E); *KLG* Kalalangabo (4°49.701'S, 29°36.202'E); *EUP* Euphorbia (4°51.003'S, 29°36.537'S); *NDW* Nondwa (4°51.787'S, 29°36.492'E); *LUA* Luansa (4°52.521'S, 29°37.168'S); *HTP* Hilltop (4°53.455'S, 29°35.804'E); *JKB* Jakobsen's Beach (4°54.875'S, 29°35.856'E); *KTW* Kitwe (4°55.375'S, 29°36.777'S); *KMJ* Kangamoja (4°57.925'S, 29°41.205'E); *LUI* Luichi River northernmost outlet (4°58.003'S, 29°41.825'E); *MGU* Mgumile (4°58.759'S, 29°43.278'S). Sites adjacent to deforested areas are denoted with an *asterisk*. All sites are situated in rocky areas, except *KMJ*, *LUI* and *MGU*, which are situated on muddy substrates in the Luichi River delta

sites (Alin et al. 1999; McIntyre et al. 2005). Five of the rocky sites (*MWG*, *KLG*, *NDW*, *LUA*, *HTP*) were categorised as sediment-impacted sites, and the other four rocky sites (*MTB*, *EUP*, *JKB*, *KTW*) categorised as reference sites. The remaining three study sites (*KMJ*, *LUI*, *MGU*) were situated in the Luichi River delta, where the substrate consists of mud alternated with extensive shell beds of the gastropod *Neothauma tanganyicense* (Smith 1880), and shell hash of the bivalve *Coelatura burtoni* (Woodward 1859).

Abundance and species distributions

Preliminary sampling between 5 and 30 m depth at two sites (*HTP* and *JKB*) indicated that crabs were absent from sandy substrates that lacked any rocks or shells, and that crab

densities were very low (≤ 0.7 individuals m^{-2}) at 30 m depth. Based on these results, we used a stratified random sampling strategy focusing on 5, 10, and 20 m depths at rocky sites. At each depth, SCUBA divers established 20 replicate $0.25 m^2$ quadrats ($0.5 \times 0.5 m^2$), spaced $>5 m$ apart. Within each quadrat, all rocks and shells were turned over to expose crabs. At the three river delta sites (KMJ, LUI, MGU), we focused on *Neothauma* shell beds. Logistical constraints allowed sampling only at 10 m depth at the delta sites. All shells within each quadrat were transported to the surface and checked for crabs. Each crab was identified, sexed and measured. Because very small crabs were difficult to sample reliably, only crabs with a carapace width (CW) ≥ 10 mm were used in our analyses.

Assemblage evenness (Pielou's J) and species incidence were calculated following Krebs (1999). Standard errors for species richness were calculated using the Vegan package in R (Oksanen 2008). To obtain more robust comparisons of species richness, we used rarefaction to a minimum sample size (19 individuals). Rarefied species richness and assemblage evenness were compared among depths, sediment impacted and reference sites using a two-way PERMANOVA in PRIMER v6 (Primer-E Ltd, UK). The density and incidence of each species (defined as the number of quadrats occupied per site) were compared among sediment impacted and reference sites, species and depth using a three-way PERMANOVA (Anderson 2001).

To compare species distributions, we used principal component analysis (PCA) of species abundances at each site and depth. Abundance data were converted into Hellinger distances (Rao 1995; Legendre and Gallagher 2001) using the Vegan CRAN package in R to avoid the problems of Euclidean-based distance metrics in PCA (Legendre and Gallagher 2001; Oksanen 2008). PCA was performed using the ADE4 package in R (Thioulouse et al. 1997). Variation in species composition was compared among depths, sediment impacted, and reference sites using a two-way PERMANOVA in PRIMER v6. We tested all interaction terms in each PERMANOVA, but only significant or marginally-significant interactions are reported.

To estimate crab biomass, we used a scaling function derived from potamonautid crabs in Kenyan rivers (Dobson et al. 2007a): $\log(DM) = -3.75 + 2.89\log(CW)$, where dry mass (DM) is in grams and CW is in millimetres.

Stable isotope analyses

Stable isotope analyses were used to evaluate the position of crabs in the littoral food web. Nitrogen isotope ratios provide an index of relative trophic position, while carbon isotope ratios reflect the flow of energy through the food web (Fry 2006). Crabs and potential food resource types identified from gut content analyses (Marijnissen 2007) were sampled between August and November 2002 from three sites (HTP, JKB and KMJ; Fig. 1), at depths between 5 and 15 m. In addition to this, the deep-water crab *Platythelphusa tuberculata* was obtained from fishermen in the region. In total, muscle tissue was analyzed from 83 adult crabs, including a minimum of six individuals (half males, half females) of each species from each site. Food resources included algae, coarse terrestrial plant matter, fine detritus, aquatic insect larvae (chironomids, trichoptera, baetids), shrimp (carids, limnocarids), gastropods (*Lavigeria coronata* Bourguignat 1888, *L. grandis* (Smith 1881), *L. new sp. J*, *L. new sp. M*, *L. nassa* (Woodward 1895), *Paramelania damoni* Smith 1881, *Reymondia horei* (Smith 1880), *Spekia zonata* (Woodward 1859), and *Vinundu guillemei* (Martel and Dautzenberg 1899); taxonomy following West et al. 2003), and bivalves (*Coelatura burtoni* and *Pleiodon spekii* (Woodward 1859)). At least four individuals were collected for each invertebrate taxon, with the exception of the snail *L. new sp. M* ($n = 1$).

To obtain algal samples free of detritus and microinvertebrates, we scrubbed periphyton from the top of cobbles and separated the filamentous algae ($<1.2 \text{ g ml}^{-1}$) using a colloidal silica density gradient following Hamilton et al. (2005). Terrestrial plant matter (wood, leaves) was collected from the lake floor, and homogenized into a single sample. Fine, loose detritus was collected from the lake floor, rinsed with 1 M HCl to remove carbonates, and rinsed with distilled water. Insect larvae of each taxonomic group were homogenised into a single sample. Mollusc foot muscle was dissected from shell material, and each individual was analyzed separately.

Samples for isotope analyses were dried on ethanol-cleaned aluminium foil to constant weight (60°C , $\geq 48 \text{ h}$). Subsamples of dried, homogenized material were analysed using a Europa Scientific 20/20 Isotope Ratio Mass Spectrometer (Iso-Analytical Ltd, Cheshire, UK). Isotope ratios are expressed using delta notation (δ) relative to PDB carbonate for C and atmospheric N_2 for N (see Fry 2006). Duplicate measurements of crab samples indicated good analytical precision (SD 0.02–0.18‰ $\delta^{15}\text{N}$, 0.02–0.22‰ $\delta^{13}\text{C}$; $n = 17$).

Results

Abundance and species distributions

A summary of the data collected during our surveys is presented in “Appendix” Tables 1 and 2. A total of 892 individual crabs with a CW $\geq 10 \text{ mm}$ (range 10.0–56.8 mm, average $17.8 \text{ mm} \pm 8.9 \text{ SD}$) were collected from 600 quadrats. *Platyhelphusa conculcata*, *P. denticulata*, *P. immaculata* and *Potamonautes platynotus* were found in rocky habitats. *Platyhelphusa armata* and *P. echinata* were found both in rocky habitats as well as at the three river delta sites. *Platyhelphusa maculata* was only found at the river delta sites. We did not find *P. polita*, *P. praelongata*, or *P. tuberculata* at any of our sampling sites between 0 and 20 m depth. However, *P. tuberculata* was regularly caught by fishermen who reported setting their nets at 50 to 100+ m depths.

Distribution patterns were patchy, and median densities per quadrat were generally low. Estimated densities at the nine rocky sites ranged from 0 to 28 crabs m^{-2} . Densities at the three soft-substrate sites near the Luichi River delta ranged from 0 to 8 crabs m^{-2} . In general, crab densities decreased with depth (Fig. 2). Estimated crab biomass per quadrat ranged from 0.0 to 117.7 g m^{-2} , and averages from each depth ranged from 0.9 to 21.0 g m^{-2} (Fig. 2). Large crabs contributed disproportionately to assemblage biomass: *Platyhelphusa armata* and *Po. platynotus* with CW $> 40 \text{ mm}$ constituted only 5.3% of individuals but accounted for 42.5% of assemblage biomass.

Rarefied species richness varied from 1.8 species at EUP to 5.0 species at JKB (Fig. 2). There was considerable variation among sites with respect to trends in species richness with depth. For example, richness decreased with depth at JKB but increased at KLG. Evenness ranged from 0.3 at EUP to 1.0 at LUA (Fig. 2). Overall, incidence of *P. conculcata* and *P. echinata* was significantly higher than that of *P. denticulata*, *P. immaculata* and *P. maculata*. Incidence of *P. armata* was also significantly higher than that of *P. denticulata* and *P. maculata* (Fig. 3).

The first two axes of the PCA explained 32.9 and 26.4% of the variance and revealed marked spatial segregation among species (Fig. 4), which can be explained by interspecific differences in combinations of site and depth distributions. *Platyhelphusa armata* and *Po. platynotus* were similar in exhibiting a wide distribution across sites and depths. *Platyhelphusa maculata* segregated from other species by being absent from all rocky sites and only

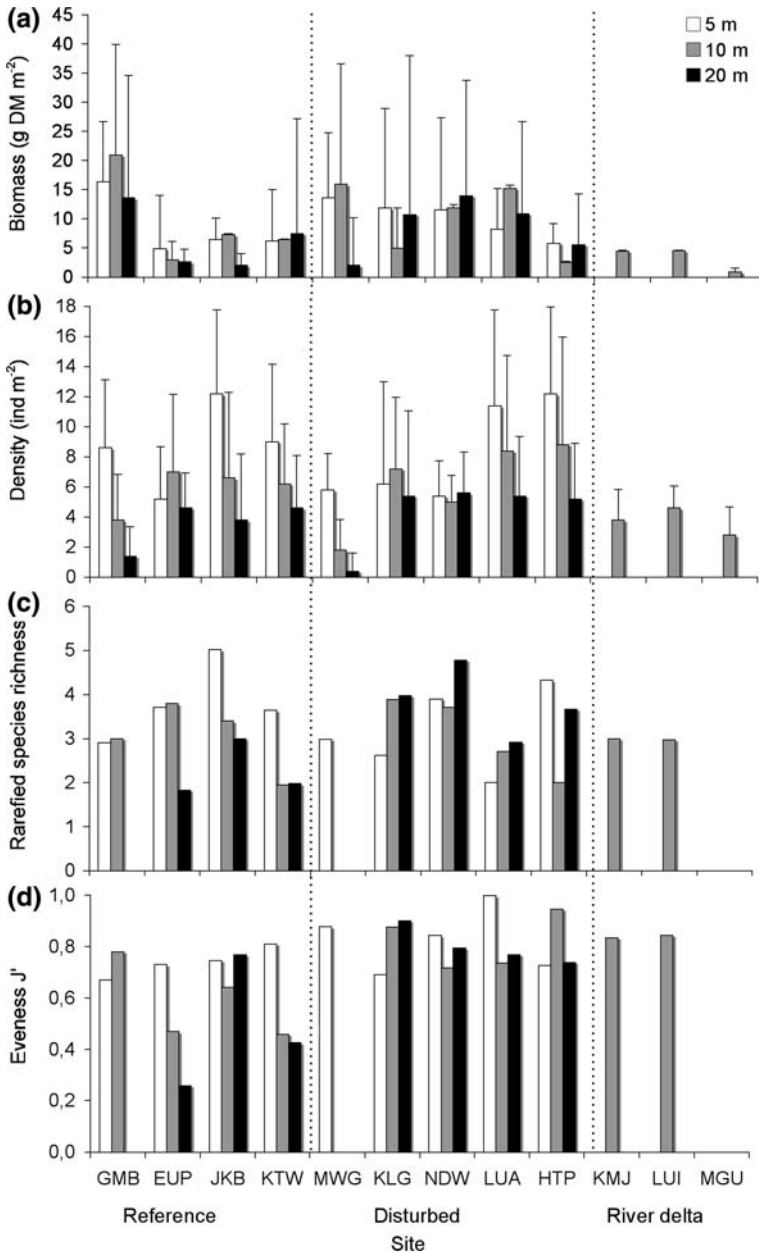


Fig. 2 Spatial variation in crab assemblage biomass (a), density (b), rarefied species richness (c), and evenness (d). Bars indicate means (\pm SD) from 20 quadrats at each site–depth combination. DM dry mass

present at the river delta sites. *Platythelphusa echinata* was present at all sites, and segregated from other species by exhibiting the greatest abundance at 20 m depth. *Platythelphusa immaculata* was distributed across the entire depth range, but was found only at EUP, JKB, KLG, NDW, and HTP, whereas *P. denticulata* was only found at JKB at

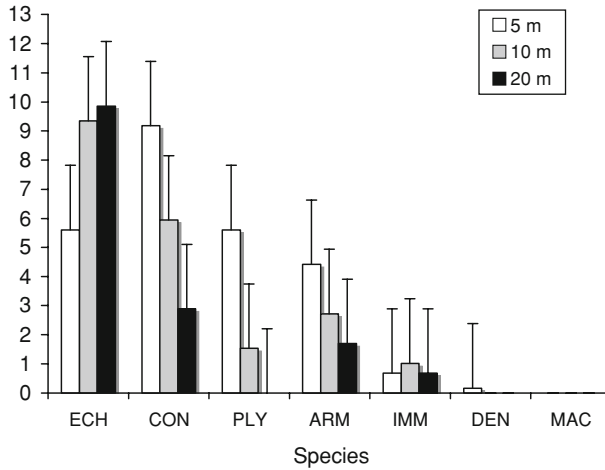


Fig. 3 Crab species incidence (% of sites occupied) across depths. ARM, *Platythelphusa armata*; CON, *P. conculcata*; ECH, *P. echinata*; IMM, *P. immaculata*; DEN, *P. denticulata*; MAC, *P. maculata*; PLY, *Potamonautes platynotus*. Site acronyms are explained in Fig. 1

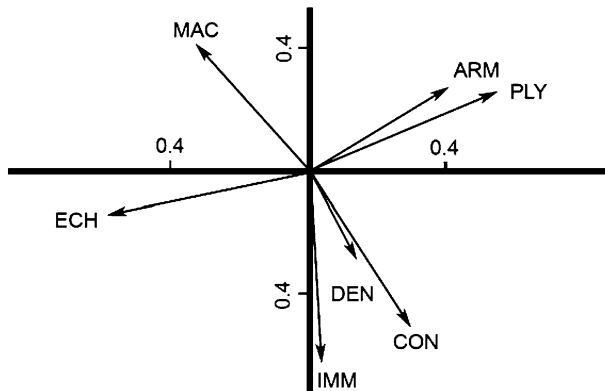


Fig. 4 Results of principal component analyses on crab species distribution, showing the first two axes. PLY, *Potamonautes platynotus*; ARM, *Platythelphusa armata*; CON, *P. conculcata*; ECH, *P. echinata*; IMM, *P. immaculata*; DEN, *P. denticulata*; MAC, *P. maculata*

5 m depth. *Platythelphusa conculcata* was present at all sites except the river delta sites, and exhibit was most abundant at 5 m depth.

Crab densities varied significantly among depths (PERMANOVA: Pseudo- $F = 4.029$, $P = 0.019$) and species (PERMANOVA: Pseudo- $F = 16.020$, $P < 0.001$), and there was a significant interaction between depth and species (PERMANOVA: Pseudo- $F = 2.132$, $P = 0.018$). There was no significant difference in crab densities between sediment-impacted and reference sites (PERMANOVA: Pseudo- $F = 0.023$, $P = 0.879$). Rarified species richness did not vary significantly with depth (PERMANOVA: Pseudo- $F = 0.754$, $P = 0.484$) or sedimentation (PERMANOVA: Pseudo- $F = 0.836$, $P = 0.373$), but there was a marginally non-significant interaction between depth and sedimentation (PERMANOVA: Pseudo- $F = 3.450$, $P = 0.053$). Crab assemblage evenness was significantly higher in sediment-impacted sites than reference

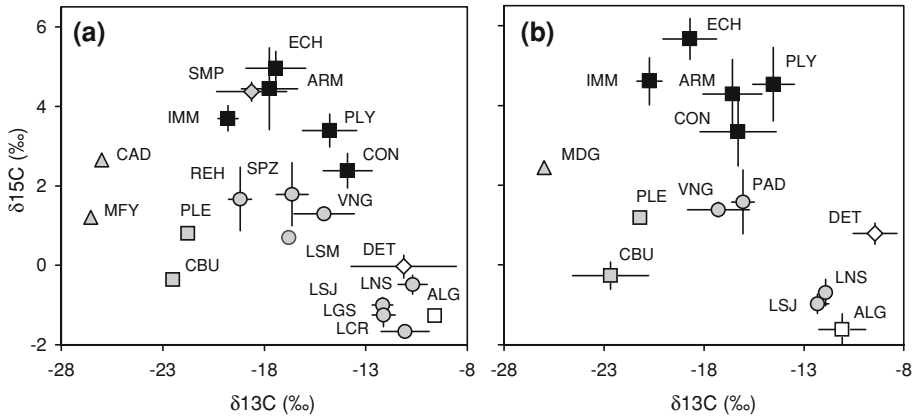


Fig. 5 Stable carbon and nitrogen isotope signatures of crabs and potential food resources in Lake Tanganyika littoral habitats at Jakobsen's Beach (a) and Hilltop (b). Markers indicate mean (\pm SD) isotope values of crabs (black square), shrimp (grey diamond), insects (grey triangle), snails (grey circle), mussels (grey square), algae (open square), and detritus (open diamond). ARM, *Platythelphusa armata*; CON, *P. conculcata*; ECH, *P. echinata*; IMM, *P. immaculata*; DEN, *P. denticulata*; MAC, *P. maculata*; PLY, *Potamonautes platnotus*; SMP, shrimp; CAD, caddisfly; MFY, mayfly; MDG, midge; PLE, *Pleiodon spekii*; CBU, *Coelatura burtoni*; PAD, *Paramelania damoni*; REH, *Reymondia horei*; SPZ, *Spekia zonata*; VNG, *Vinundu guillemei*; LCR, *Lavigeria coronata*; LGS, *L. grandis*; LSJ, *L. sp. J.*; LSM, *L. sp. M.*; LNS, *L. nassa*; DET, detritus; ALG, algae

sites (PERMANOVA, sedimentation: Pseudo- F = 14.502, P = 0.001), but did not vary significantly across depths (PERMANOVA: Pseudo- F = 2.158, P = 0.141). There was no difference in incidence between sediment-impacted and reference sites (PERMANOVA: Pseudo- F = 0.002, P = 0.990), but incidence differed significantly among depths (PERMANOVA: Pseudo- F = 3.237, P = 0.042) and species (PERMANOVA: Pseudo- F = 21.979, P < 0.001), and the depth-species interaction was significant as well (PERMANOVA: Pseudo- F = 2.691, P = 0.003). Crab species composition differed marginally between sediment-impacted and reference sites (PERMANOVA: Pseudo- F = 2.080, P = 0.079) and significantly among depths (PERMANOVA: Pseudo- F = 3.338, P = 0.006).

Stable isotope analyses

The variation among crab species and potential food resources was similar between the JKB and HTP sites (Fig. 5). Benthic resources (periphyton, fine detritus) showed high $\delta^{13}\text{C}$ relative to planktonic production pathways inferred from bivalve data. Caddisflies, mayflies, and midges were more depleted in ^{13}C than filter-feeding bivalves, and probably derive their energy from planktonic pathways or perhaps terrestrial plant detritus ($\delta^{13}\text{C}$ = -26.1‰ , $\delta^{15}\text{N}$ = 0.8‰ , n = 1 at HTP). These insects showed somewhat higher $\delta^{15}\text{N}$ than bivalves, suggesting occasional carnivory. Snails fell into two distinct groups: one with high $\delta^{13}\text{C}$ that matched algal and detrital values but $\delta^{15}\text{N}$ showing very little trophic enrichment (*L. coronata*, *L. grandis*, *L. sp. J.*, *L. nassa*), and another with $\delta^{13}\text{C}$ intermediate between benthic and planktonic signatures and $\delta^{15}\text{N}$ comparable to other primary consumers (*Paramelania damoni*, *Reymondia horei*, *Spekia zonata*, *Vinundu guillemei*, *L. sp. M.*). Shrimp at JKB appeared to rely on both benthic and planktonic energy pathways, and their high $\delta^{15}\text{N}$ suggested a largely carnivorous diet.

Crabs at JKB and HTP occupied higher trophic positions than all other invertebrates sampled during this study with the exception of shrimp, and showed intermediate $\delta^{13}\text{C}$

suggesting a mixing of benthic and planktonic energy pathways. We elected not to estimate trophic position or carbon source mixtures quantitatively due to the broad range of isotopic composition of potential food resources. However, the total range of variation in mean $\delta^{15}\text{N}$ (2.58‰ at JKB; 2.31‰ at HTP) indicates ~ 0.8 trophic levels of variation among crab species based on standard estimates of trophic fractionation per level ($\sim 3\text{‰}$; Vanderklift and Ponsard 2003). Additionally, differences among individual species were concordant among sites. *Platythelphusa echinata* ($5.66 \pm 0.30\text{‰}$ $\delta^{15}\text{N}$, -18.71 ± 0.83 $\delta^{13}\text{C}$) showed the highest $\delta^{15}\text{N}$ of the crabs that were collected in rocky habitats, whereas *P. conculcata* ($3.35 \pm 0.94\text{‰}$ $\delta^{15}\text{N}$, -16.29 ± 1.77 $\delta^{13}\text{C}$) showed the lowest $\delta^{15}\text{N}$. Among the two large species, *Po. platynotus* ($4.53 \pm 1.08\text{‰}$ $\delta^{15}\text{N}$, -14.51 ± 0.33 $\delta^{13}\text{C}$) showed a more benthic $\delta^{13}\text{C}$ than *P. armata* ($4.29 \pm 0.47\text{‰}$ $\delta^{15}\text{N}$, -16.57 ± 1.46 $\delta^{13}\text{C}$). *Platythelphusa immaculata* ($4.61 \pm 0.45\text{‰}$ $\delta^{15}\text{N}$, -20.73 ± 0.29 $\delta^{13}\text{C}$) had the lowest $\delta^{13}\text{C}$. Of the two crab species sampled at the river delta, *P. maculata* ($4.12 \pm 0.36\text{‰}$ $\delta^{15}\text{N}$, -16.41 ± 0.85 $\delta^{13}\text{C}$) was similar to the average of the crab species from JKB and HTP. *Platythelphusa tuberculata* ($6.12 \pm 0.31\text{‰}$ $\delta^{15}\text{N}$, -20.15 ± 0.82 $\delta^{13}\text{C}$) was enriched in ^{15}N relative to all other species.

Discussion

Our results indicate that crabs are important components of benthic communities in Lake Tanganyika. Although their distribution within and between littoral sites is patchy, crabs can be locally abundant (Fig. 2). Patchy local distribution patterns are typical for marine crabs (e.g. Deudero et al. 2005; Flores et al. 2005; Ribeiro et al. 2005), and may reflect a combination of predator avoidance, reproductive aggregation, and the distribution of suitable habitats or food resources. Marked spatial variability in densities has also been observed for potamonautid crabs in other African freshwaters (King 1983; Somers and Nel 1998; Abdallah et al. 2004), with local abundance peaks of up to 48 individuals m^{-2} (Abdallah et al. 2004). Studies in East African forest streams have demonstrated that crabs can represent from 58 to 94% of total benthic invertebrate biomass (Abdallah et al. 2004; Dobson et al. 2007a). Our estimates of crab DM up to 118 g m^{-2} (Fig. 2) suggest that crabs represent a substantial portion of benthic invertebrate biomass in Lake Tanganyika. However, the diverse and abundant gastropod assemblage is also important. Mean gastropod densities on rocky littoral substrates in Lake Tanganyika range from 0.1 to 64.1 individuals m^{-2} (Donohue et al. 2003; McIntyre et al. 2005), and dry biomass (including shell) estimates range from ~ 3 to 42 g m^{-2} (Donohue et al. 2003). In contrast, wet biomass of other invertebrates (ostracods, copepods, insects, shrimp) in Lake Tanganyika has been estimated as <1 g m^2 (Yuma and Kondo 1997). Thus, it appears that crabs and gastropods dominate benthic invertebrate biomass in Lake Tanganyika. Interestingly, evidence derived from functional morphological analyses, laboratory experiments, and gut content analyses suggests that the two largest species of crabs (*Platythelphusa armata* and *Potamonautes platynotus*), which account for roughly half of assemblage biomass, are molluscivorous (West et al. 1991; Marijnissen 2007; Michel, unpublished data). As such, an inverse relationship between the biomass of these crabs and their snail prey might be expected across sites.

Our quadrat surveys probably underestimated the true density and biomass of the largest species of crabs. We have previously demonstrated a significant relationship between crab body size (CW) and substrate size in rocky areas (Marijnissen 2007). Densities in the substrates (boulders, rocks) that typically harbour the largest crabs are difficult to assess adequately because these substrates often cannot be moved or sampled underneath by

divers. Similarly, we were unable to obtain data for the deep lake dwelling species *P. tuberculata* and *P. praelongata*, which occur at depths > 40 m (Marijnissen et al. 2004, 2007). Trapping or mark recapture techniques will be required to determine the abundance and biomass of these species.

Our survey results indicate that several generalizations can be made regarding the distribution of crabs in Lake Tanganyika. Firstly, crabs are found predominantly in rocky habitats. Though river deltas with abundant *Neothauma* shells (KMG, LUI, MGU) harboured three out of the eight endemic Lake Tanganyika crab species that were found during this study, densities were much lower than at rocky sites. Secondly, densities of crabs in rocky areas are highest at shallow depths (5–10 m), and typically decrease sharply by 20 m depth. Similar patterns have been observed in many trophic guilds of fishes in Lake Tanganyika (Alin et al. 1999). Higher densities of crabs in rocky habitats at shallow depths may be attributable to a higher abundance of food resources compared to greater depths. Finally, the distribution of individual species varied widely and we did not find consistent patterns in species richness or evenness among sites or depths (Fig. 2). Nevertheless, there is evidence of habitat segregation among species as demonstrated by the results of the PCA (Fig. 4). This suggests that in spite of the overall wide distribution of crab species across sites and depths, some species prefer or avoid certain habitats. This is most clearly the case for *P. maculata*, which was only found in *Neothauma* shells on river delta sites. Interestingly, of the two most widespread crab species in the rocky littoral zone, *P. echinata* and *P. conculcata*, the former had a higher incidence in deep (20 m) habitats than other species, whereas the latter had the highest incidence at shallow (5 m) depths (Fig. 3). This inverse density relationship between the most common species could be driven by current competition or evolutionary niche displacement.

Functional role of Lake Tanganyika's endemic crabs

The endemic faunas of African rift lakes are renowned for their high functional diversity as well as species richness. Functional differences among related species have important implications for speciation (Schluter 2000), ecological coexistence (Bootsma et al. 1996; Bouton et al. 1997), and ecosystem conservation (McIntyre et al. 2007). So far, analyses of species richness and functional diversity have focused almost entirely on fishes. Recent comparisons of habitat use and functional morphology of the endemic crabs of Lake Tanganyika indicate ecological divergence, but gut contents suggest substantial dietary overlap among species (Marijnissen 2007). Stable isotope analyses offer an ideal method of assessing long-term patterns in trophic niche width and interspecific differentiation (Genner et al. 1999; Bearhop et al. 2004), and also for evaluating the roles played by crabs in the littoral food web.

Previous analyses of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ indicated wide dietary breadth of most crab species as well as significant differences among species (Marijnissen 2007). These analyses lacked the trophic web context provided by sampling of stable isotopes from potential food resources. The present analyses fill this gap, and show that crabs play different roles within the littoral food web, including primary consumers as well as top predators among benthic invertebrates (Fig. 5). The high $\delta^{15}\text{N}$ of *P. echinata* compared to that of the other crab species that were sampled in rocky habitats suggests a carnivorous diet. *Platythelphusa armata* and *Po. platynotus*, the two largest crab species in the lake, are known to be molluscivores (West et al. 1991; Marijnissen 2007; Michel, unpublished data), but showed intermediate $\delta^{15}\text{N}$ signatures relative to other crabs. Gut content analyses suggested that these species consume algae, detritus, and aquatic insects as well as molluscs (Marijnissen 2007).

Platythelphusa immaculata showed the lowest $\delta^{13}\text{C}$ of all crab species, suggesting a greater reliance on planktonic or terrestrial energy pathways. The low $\delta^{15}\text{N}$ of *P. conculcata* indicates that this species is primarily herbivorous or detritivorous. Of the two crab species sampled at the river delta, *P. maculata* was similar to the average of the crab species that were sampled in rocky habitats. Detritus could be the primary food for *P. maculata*, but further site-specific sampling of potential resources is needed. The low $\delta^{13}\text{C}$ of the deep-water species *P. tuberculata* suggests that it depends primarily on plankton-derived energy. Its high $\delta^{15}\text{N}$ relative to other crab species is most likely a reflection of depth-related differences in ambient $\delta^{15}\text{N}$. Deep-water dissolved N is enriched in ^{15}N compared to surface waters (O'Reilly et al. 2002), and this difference is likely transferred into the food web near the thermocline.

In terms of energy flow, their intermediate $\delta^{13}\text{C}$ values indicate that crabs draw upon both planktonic and benthic pathways. Since consumption of phytoplankton by crabs is unlikely but most species readily eat filamentous algae from rock surfaces, the balance between planktonic and benthic contributions to crab diets probably reflects the relative consumption of benthic insects with low $\delta^{13}\text{C}$ and either periphyton or snails with high $\delta^{13}\text{C}$. This interpretation is also supported by the overall diagonal-downward patterns of both interspecific (Fig. 5) and intraspecific (Marijnissen 2007) variation in crab isotopic composition. However, the wide variation among insects and snail taxa in our results precludes the confident use of quantitative mixing models to estimate the relative importance of insects, periphyton, and snails in crab diets.

The high biomass and top-predator status of crabs among littoral invertebrates suggests the potential for strong cascading effects on organisms lower in the food web. The influence of molluscivorous crabs on the ecology and evolution of snails in Lake Tanganyika is well-documented (West et al. 1991; McIntyre et al. 2005; Michel, unpublished data), and smaller crab species may have similarly strong effects on soft-bodied invertebrate prey. Grazing controls benthic algal biomass and productivity (McIntyre et al. 2006), therefore crabs could influence primary production through both direct effects of algivory and indirect effects of preying upon grazers. In addition, crabs serve as prey for many endemic fish species, including spiny eels (*Mastacembelus plagiostomus* Matthes, 1962), catfish (*Synodontis dhonti* Boulenger 1917, *Chrysichthys brachynema* Boulenger 1900, *C. stappersi* Boulenger 1917), and cichlids (*Boulengerochromis microlepis* Boulenger 1899, and *Lamprolus lemairii* Boulenger 1899) (Coulter 1991; Hori 1983; Hori et al. 1993). The numerous pathways by which crabs are involved in the food web indicate that they play varied and important functional roles in the littoral ecosystem.

Threats to endemic crabs

Previous studies have demonstrated large differences in sediment loads among many of the same sites that we surveyed (Alin et al. 1999; McIntyre et al. 2005). Although evaluating the effects of sedimentation in Lake Tanganyika is complicated by naturally high spatial variability in littoral communities (McIntyre et al. 2005; Michel et al. 2004) and potential spatiotemporal variation in response thresholds (Donohue and Irvine 2004a), several studies have revealed significant reductions in density or diversity of benthic organisms (Cohen et al. 1997; Alin et al. 1999; Donohue et al. 2003). Our surveys revealed significant effects of sedimentation on assemblage evenness. The impact of sedimentation on crab species composition and the interactive effects of sedimentation and depth on species richness were nearly statistically significant. However, our surveys revealed no effects of sedimentation on crab densities or incidence.

One explanation for the apparently low impact of sedimentation on crab assemblages is that their dietary breadth allows crabs to adapt to local changes in the biomass of algal, detrital, and invertebrate food resources. McIntyre et al. (2005) found lower frequencies of snail shell scarring from crabs at sediment-disturbed sites, possibly suggesting shifts in crab foraging patterns. Given that all major taxa consumed by crabs in Lake Tanganyika (algae, insects, ostracods, gastropods; Marijnissen 2007) are sensitive to sedimentation (Cohen et al. 1997; Alin et al. 1999; Donohue et al. 2003; Donohue and Irvine 2004a, b), it is likely that crab diets are affected by sediment-related shifts in prey densities and foraging efficiency. However, these impacts could be sub-lethal, yielding effects that are difficult to detect (McIntyre et al. 2005).

The endemic crabs of Lake Tanganyika may also be profoundly affected by the predicted invasion of Louisiana crayfish *Procambarus clarkii* (Girard, 1852). This species was introduced in Lake Naivasha, Kenya, in 1970 (Parker 1974), and has subsequently spread throughout East Africa. Expanding populations presently exist in Uganda, Kenya and Zambia (Arrignon et al. 1990), and in parts of the Nile River basin as far north as Egypt (Howard, IUCN, personal communication). It is possible that Louisiana crayfish will reach the upper Kagera River system in Rwanda and/or Burundi and subsequently move into the Lake Tanganyika catchment (Howard, IUCN, personal communication). Due to their broad environmental tolerances, high dispersal capacity, and opportunistic diet, these crayfish can cause a dramatic loss of native biodiversity after they invade (Smart et al. 2002; Snyder and Evans 2006; Cruz and Rebelo 2007).

A conservation assessment of Lake Tanganyika crabs based on surveys conducted between 1993 and 2004 considered *Po. platynotus*, *P. armata*, *P. conculcata*, *P. echinata*, and *P. tuberculata* to be of least concern (LC) under version 3.1 (2001) of the IUCN Red List of Threatened Species (Cumberlidge and Marijnissen 2004). *Platyhelphusa maculata* and *P. polita* were also assessed to be of least concern (LC) based on historical records suggesting that these species have a lake-wide distribution and occur in more than 10 locations (Cumberlidge and Marijnissen 2004). However, recent collection efforts yielded only very small numbers of individuals from these two species (Cumberlidge et al. 1999; Marijnissen, personal observation). The present study suggests that *P. maculata* has narrow habitat preferences and occurs in relatively low densities. Moreover, *P. polita* was absent from sites that we surveyed in Tanzania and Zambia between 2002 and 2004 (Marijnissen, personal observation). 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 and Marijnissen 2004). The more comprehensive surveys reported here indicate a need to critically re-examine lake-wide and local distribution patterns to improve conservation assessments of Lake Tanganyika endemic crab species.

There are increasing calls to conserve not only species diversity but also ecosystem functioning and services (Karieva et al. 2007). Several authors have advocated plans to conserve biodiversity in Lake Tanganyika (Coulter and Mubamba 1993; Allison et al. 2000), but there is no consensus on how this can best be achieved (e.g. Pendleton and van Breda 1994; Allison 2002; Coulter et al. 2004) and there is a need for more research to enable sound management decisions. Our results indicate that the endemic crabs of Lake Tanganyika merit further attention with regard to protecting both biodiversity and ecosystem processes. In particular, the central roles played by crabs and other invertebrates need to be taken into account when predicting the impact of environmental perturbations on littoral species diversity and food web dynamics.

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Appendix

Tables 1 and 2.

Table 1 Number of individual crabs of seven endemic species collected during surveys at 12 sites along the shoreline of Lake Tanganyika near Kigoma, Tanzania

Site	Category	Depth (m)	<i>Platythel-phusa armata</i>	<i>P. concul-cata</i>	<i>P. dentic-ulata</i>	<i>P. echi-nata</i>	<i>P. immac-ulata</i>	<i>P. macu-lata</i>	<i>Potamo-nautes platynotus</i>
EUP	RE	5	3	1	0	16	0	0	6
EUP	RE	10	1	1	0	28	3	0	2
EUP	RE	20	0	0	0	22	1	0	0
MTB	RE	5	7	4	0	0	0	0	32
MTB	RE	10	8	1	0	0	0	0	10
MTB	RE	20	5	1	0	0	0	0	1
MWG	SI	5	9	4	0	0	0	0	16
MWG	SI	10	3	1	0	0	0	0	5
MWG	SI	20	1	1	0	0	0	0	0
HTP	SI	5	6	37	0	10	6	0	2
HTP	SI	10	0	28	0	16	0	0	0
HTP	SI	20	2	9	0	14	1	0	0
JKB	RE	5	5	34	2	11	5	0	4
JKB	RE	10	1	22	0	8	2	0	0
JKB	RE	20	0	3	0	13	3	0	0
KLG	SI	5	0	10	0	0	1	0	20
KLG	SI	10	5	15	0	13	3	0	0
KLG	SI	20	4	12	0	8	3	0	0
KTW	RE	5	15	22	0	6	0	0	2
KTW	RE	10	3	0	0	28	0	0	0
KTW	RE	20	2	0	0	21	0	0	0
LUA	SI	5	0	27	0	30	0	0	0
LUA	SI	10	2	14	0	26	0	0	0
LUA	SI	20	2	8	0	17	0	0	0
NDW	SI	5	2	11	0	11	0	0	3
NDW	SI	10	2	7	0	15	1	0	0
NDW	SI	20	3	6	0	15	2	0	2
KMJ	RD	10	2	0	0	11	0	6	0
LUI	RD	10	2	0	0	11	0	10	0
MGU	RD	10	0	0	0	7	0	7	0

Total counts are shown for an area of 5 m², representing 20 replicated quadrats (each 0.25 m²). Site acronyms are explained in Fig. 1

SI sediment impacted; RE reference; RD river delta

Table 2 Crab assemblage statistics for 12 sites along the shoreline of Lake Tanganyika near Kigoma, Tanzania

Site	Category	Depth (m)	<i>N</i>	<i>S</i> (SE)	Evenness
EUP	RE	5	26	3.72 (0.46)	0.73
EUP	RE	10	35	3.80 (0.82)	0.47
EUP	RE	20	23	1.83 (0.38)	0.26
MTB	RE	5	43	2.90 (0.30)	0.67
MTB	RE	10	19	3.00 (0.00)	0.78
MTB	RE	20	7	3.00 (0.00)	0.72
MWG	SI	5	29	2.99 (0.09)	0.88
MWG	SI	10	9	3.00 (0.00)	0.85
MWG	SI	20	2	2.00 (0.00)	1.00
HTP	SI	5	61	4.32 (0.64)	0.73
HTP	SI	10	44	2.00 (0.00)	0.95
HTP	SI	20	26	3.67 (0.50)	0.74
JKB	RE	5	61	5.02 (0.78)	0.75
JKB	RE	10	33	3.40 (0.61)	0.64
JKB	RE	20	19	3.00 (0.00)	0.77
KLK	SI	5	31	2.61 (0.49)	0.69
KLK	SI	10	36	3.89 (0.32)	0.88
KLK	SI	20	27	3.98 (0.15)	0.90
KTW	RE	5	45	3.64 (0.49)	0.81
KTW	RE	10	31	1.95 (0.22)	0.46
KTW	RE	20	23	1.98 (0.15)	0.43
LUA	SI	5	57	2.00 (0.00)	1.00
LUA	SI	10	42	2.71 (0.46)	0.74
LUA	SI	20	27	2.92 (0.27)	0.77
NDW	SI	5	27	3.90 (0.30)	0.84
NDW	SI	10	25	3.71 (0.47)	0.72
NDW	SI	20	28	4.78 (0.43)	0.80
KMJ	RD	10	19	3.00 (0.00)	0.84
LUI	RD	10	23	2.98 (0.15)	0.84
MGU	RD	10	14	2.00 (0.00)	1.00

Crabs were collected from an area of 5 m², representing 20 replicate quadrats (each 0.25 m²). Site acronyms are explained in Fig. 1

N total number of individual crabs sampled; *S* mean rarefied species richness ($n = 19$); *SE* standard error; *Evenness* Pielou's *J*; *SI* sediment impacted; *RE* reference; *RD* river delta

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