Species in the spotlight

A unique species flock of freshwater crabs in Lake Tanganyika: a model for studies in evolution and extinction

Marijnissen, S.A.E.

Lake Tanganyika is unique among the African Great Lakes in harbouring 10 endemic species of freshwater crabs, including Potamonautes platynotus and nine species in the genus Platythelphusa which form the only known lacustrine species flock of freshwater crabs in Africa. Platythelphusid crabs have a striking variety of morphological and ecological features making them ideal subjects for studies in adaptive evolution (Cumberlidge et al. 1999, Marijnissen et al. 2004). For instance, both males and females of Platythelphusa armata are armed with one significantly enlarged claw that they use to crush snail shells. Platythelphusa conculcata has evolved an extremely flat body that enables it to hide inside narrow crevices underneath rocks and stones. Platythelphusa maculata, on the other hand, is a tiny round-bodied species, which is often found taking refuge within empty shells of the large endemic snail Neothauma tanganyicensis.

As Africa’s oldest (estimated 9-12 million years) and most species diverse lake, Lake Tanganyika is a famed natural laboratory for studying processes of adaptive evolution (e.g. Glor 2010, and references therein). Initially, it was thought that the platythelphusids were a relict group of marine crabs that got trapped in the lake after a recession of the sea and remained unchanged over millions of years (Moore 1903). However, genetic evidence indicates that all Lake Tanganyika crabs are derived from freshwater ancestors.

The evolutionary divergence of the platythelphusids coincides with a period of climate change and drought, when the lake levels dropped substantially and Lake Tanganyika was split into separate basins (Cane and Molnar 2001; Marijnissen et al. 2006). Other taxa, including several cichlid groups (Duftner et al. 2005; Koblümüller et al. 2004, 2005, 2007), as well as the Synodontis catfish species flock (Day and Wilkinson 2006), diverged during the same period, about 3.3-2.5 million years ago.

The morphological differences between the platythelphusid crabs seem to have evolved within a relatively short period of time. A longstanding hypothesis is that the high levels of species diversity in the African Great Lakes are the result of competition and ecological niche diversification (Schluter 2000). Research on the crabs shows morphological differentiation that could indeed be linked to ecological niche divergence (Marijnissen 2007). However, there is also evidence of considerable ecological versatility among platythelphusid species that coexist in rocky shore areas (Marijnissen et al. 2008).

Lake Tanganyika offers a wide diversity of habitats, ranging from cobble beaches, rocky outcrops, and stromatolite reefs, to extensive beds of empty Neothauma tanganyicensis shells, sandy beaches and deep layers of mud. Crabs can be found in all these habitats, but the majority of the species are found in the rocky areas. The crabs are important components of the food-web as prey as well as predators. They are included in the diet of numerous endemic fish, such as spiny eels (Mastacembelus plagiostomus), bagrid catfish (Chrysichthys brachynema and C. stappersi), and catfish.
(Synodontis dhonti), as well as cichlids (Boulengerichromis microlepsis and Lamprolus lemarii). The crabs themselves are top invertebrate predators, and their relative abundance can have important implications for organisms lower in the food web, including algae, insect larvae, ostracods, and snails (Marijnissen et al. 2008, 2009).

Lake Tanganyika is increasingly under pressure from environmental problems generated by human populations (reviewed in Lowe-McConnell 2003). The majority of species diversity is found in rocky near-shore areas, which are severely impacted by sedimentation resulting from ongoing deforestation in the lake catchment (Cohen et al. 2005). Sedimentation can negatively affect aquatic organisms through a range of factors including deterioration of habitat quality and heterogeneity, reduction of food intake, alteration of competitive relationships, decrease of reproductive success, and breakdown of mate recognition systems as water visibility is reduced (Donohue and Molinos 2009). Research in Lake Tanganyika has demonstrated negative impacts of sedimentation on algal productivity as well as on species diversity and densities of ostracods, snails, and fishes (McIntyre et al. 2004, and references therein). As crabs are closely linked, either as predators or prey, to many other organisms that are vulnerable to the impacts of increased sedimentation, it is likely that they will respond by shifting their foraging patterns (e.g. McIntyre et al. 2004). However, demonstrating and predicting the effects that habitat disruptions will have on the endemic crabs requires taking into account the complexity of the ecosystem. Changes in the species flock may be delayed relative to those of other species as crabs occupy multiple positions within the food web, and a considerable amount of overlap exists among the ecological niches of the different Lake Tanganyika crab species (Marijnissen et al. 2008).

Lake Tanganyika’s crabs are also threatened by invasion of the non-native Louisiana Crayfish (Procambarus clarkii) and the Red Claw Crayfish (Cherax quadricarinatus). Both of these crayfish have been introduced to Africa for aquaculture purposes and are spreading rapidly throughout the continent (e.g. Arribong et al. 1990; G. Howard, IUCN, pers. comm.). Considering their current presence in catchments adjacent to Lake Tanganyika, it is likely that these crayfish will move into the lake basin in the near future. Due to their resilience to different environmental circumstances, high dispersal capacity and opportunistic diet, crayfish are capable of causing dramatic biodiversity shifts (e.g. Smart et al. 2002; Snyder and Evans 2006; Cruz and Rebelo 2007), and could cause an ecological disaster if they establish themselves in Lake Tanganyika.

Without conservation effort to address environmental threats in the Lake Tanganyika basin, this could lead to the loss of a dynamic endemic species flock that provides unique insight into the evolution and ecological functioning of this unusually diverse lake system.
Species in the spotlight

The East African tree hole crab – spectacular adaptation

Potamonautes raybouldi, the East African tree hole crab, is a bizarre example of crab evolution. It is exceptionally rare for a crab to live in a tree (an arboreal species), and most of those that do depend on an external water supply – for example, several species of mangrove crab reside in trees for protection but lay their eggs in the sea.

There are over 1,200 species of freshwater crab, out of which only a handful exhibit some kind of arboreal association. The East African tree hole crab is unique in this case. It lives solely in the water filled tree holes formed where a tree branches. When branching occurs it often creates a small hole, or bole, which fills with water. The East African tree hole crab has evolved to occupy this niche, adapting its behaviour and morphology accordingly.

What is remarkable about this species is its natural history. This species has an apparent lack of dependence on any water body, except that collected in tree holes as water run-off from the host tree. What is yet more remarkable is the way in which it obtains the calcium in order to build its exoskeleton (Bayliss 2002). It forages at night or in heavy rain, when it leaves its hole to search for leaf-litter snails. When it finds these snails it takes pieces of the snail shell back to its water-filled tree hole and masticates them, which releases the calcium ions into solution. It then ingests the calcium in order to obtain sufficient quantities to build its own exoskeleton. It also eats its old exoskeleton when it moults. As crabs have a hard exoskeleton they need to moult in order to be able to grow and mature. Below the hard exoskeleton is soft tissue that expands over time. Eventually the hard exoskeleton will prevent any further expansion, at which stage the process of moulting (or ecdysis) occurs.

It was first observed and collected by Professor John Raybould in 1966, but it was not until 2004 when it was eventually described under the patronym Potamonautes raybouldi (Cumberlidge and Vannini 2004). It is a forest species found in just a few sites in east Africa, such as the East Usambara Mountains in northern Tanzania, and several sites in southern Kenya (e.g. the Shimba Hills).

It has primitive lungs that enable it to spend time outside water, and elongated legs that allow it to climb up and down the tree trunks. The males have one claw that is larger than the other, which is presumably used for display and eventual mating. The females have been found protecting their young (parental care), living in the same tree holes with a brood of juvenile crabs that is presumably their own. These tree holes need cleaning on a regular basis as leaves...
and other debris accumulate. The juvenile crabs are often too small to cope with moving larger leaves and debris, and would be unable to clean the tree-hole without assistance from the adult female crab. They also need protection from predators, possibly including other crabs.

The local people in the East Usambara Mountains use the water that *Potamonautes raybouldi* lives in as a medicinal potion. They often collect the water, which they call 'Mazi yangodi' (the water from holes with crabs), to give to pregnant women. The water contains calcium, which is required by pregnant women to reduce the risk of pregnancy-induced hypertension (PIH), high blood pressure (pre-eclampsia), and kidney failure, all of which can result in miscarriage. Exactly how and when the connection between the 'crab water' and calcium deficiency in pregnant woman was arrived at is a mystery.

The East African tree hole crab is a spectacular example of adaptation, essentially of an aquatic species not only to a terrestrial environment but also to an arboreal existence. It has lost its dependency on larger water bodies such as streams and rivers, and via the process of natural selection, through trial and error (otherwise known as evolution), it has managed to exploit a niche that crabs have rarely occupied. The further connection between the local population of the East Usambara Mountains and their use of the Mazi Yangodi further highlights this species scenario as an amazing example of natural history and a connection with a human society. However, this story of natural history is not finished. Exactly how the males and females find each other in order to mate in closed canopy, dark forest, when each crab resides in a different tree and they are relatively short-sighted, remains an exciting mystery yet to be solved.