

Functions of macrobenthos in mangrove forests: >20 years of research lessons

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Abstract

Mangroves forests can truly be considered as evolutionary hotspots where terrestrial species have re-adapted to marine life, and marine species have undergone the transition to terrestrial species. In fact, mangroves are salt tolerant trees which evolved from rainforest trees over 50 million years ago (Duke 1995; Ellison et al. 1999), unique in their adaptation to the distinct environmental requirements of the intertidal habitat (Tomlinson 1986). These intertidal forests harvest a diverse and distinctive macro-faunal assemblage mainly consisting of marine taxa which developed evolutionary trends from marine to semi-terrestrial and terrestrial life-styles, such as snails, crabs and even fish (Giomi et al. 2012; Ngo-Massou et al. 2012; Ravichandran and Wilson 2012; Vannini and Fratini 2012). As pointed out in recent reviews (Cannicci et al. 2008; Lee 2008), the relevance to mangrove functioning of these faunal assemblages has been totally reconsidered in the last 20 years. A number of recent studies indeed clarified how faunal components of both marine, brachyurans, gastropods and oligochaetes, and terrestrial origin, insects and arachnid, exert a strong influence on ecosystem functions as well as on vegetation structure of mangrove forests (Smith 1987; Smith et al. 1991; Lee 1998; Lee 1999; Kristensen and Alongi 2006; Cannicci et al. 2008; Kristensen 2008; Lee 2008).

Indeed, the evolutionary sea-land bridge represented by mangroves was mostly covered by brachyuran crabs, which evolved intertidal, supratidal and even arboreal habits (Hartnoll 1975; Jones 1984; Dahdouh-Guebas et al. 2002; Fratini et al. 2005; Vermeiren and Sheaves 2012). They literally invaded a wide range of terrestrial mangrove micro-habitats, reaching a very high number of evolutionary units, such as species complexes and cryptic species whose taxonomy and phylogenetic relationships are updated monthly and are still largely unknown (Ragionieri et al. 2009; Ragionieri et al. 2010; Silva et al. 2010; Ragionieri et al. 2012; Fratini et al. 2012). Such an astonishing diversity resulted in the occupation of several ecological niches, fundamental for mangrove ecosystem functioning (Duke et al. 2007; Mukherjee et al. 2012). The role of sesamid crabs in mangrove structuring processes have been studied since the late 1970s and early 1980s, and the huge number of studies performed ever since on their feeding and burrowing ecology leave no doubts about the great importance of these mainly litter-feeding and burrowing crabs in structuring and functioning Old world ecosystems (Lee 1997; Lee 1998; Dahdouh-Guebas et al. 2011; Van Nederveelde et al. 2012). However, their trophic role is still a matter of debate (Skov and Hartnoll 2002; Meziane et al. 2006) and, as a consequence, their real roles in mangrove food web, litter processing and exportation and,

ultimately, on organic matter dynamics in mangroves are still controversial (Lee 2008, 2012). As an example of their importance, the difference in the standing crop biomass of mangrove forests between the Indo-west-Pacific and Atlantic-east-Pacific systems is thought to be related not only to the different richness in tree species, but also to differences in macrobenthos diversity. Although less diverse, the crab fauna of New World mangroves showed to maintain a critical role in the retention of forest products and organic matter processing, since the crabs of the genus *Ucides* have been shown to have the similar role to the Old World Sesarmidae (Nordhaus et al. 2006).

Since propagule recruitment supports natural regeneration of mangrove forests, determining in the long term the structure and functioning of mangrove ecosystems, seed, seedling and propagule predation has been considered an important factor determining seedling distribution patterns in many mangrove stands (Cannicci et al. 2008; Dahdouh-Guebas et al. 2011; Van der Stocken et al. 2012; Van Nederveelde et al. 2012; Nayar et al. 2012). Crabs are the main actors in this process, but our understanding of the strong impact of gastropods, by means of high and differential consumption of propagules, has greatly developed recently (Fratini et al. 2001; Fratini et al. 2008). At least three models have been proposed to quantify and explain the impact of crabs' propagule predation on vegetation structure of mangrove forests. The 'dominance-predation model' suggests an inverse relationship between the rate of predation of a certain species and its dominance in the forest canopy (Smith 1987), while the 'canopy-gap mediated model' hypothesizes that predation could be more intense under closed canopies than in adjacent relatively large gaps (Osborne and Smith 1990; Clarke and Kerrigan 2002). A third model, the so called 'flooding regime model' (Osborne and Smith 1990; Clarke and Myerscough 1993) considers the time available for semi-terrestrial crabs to forage due to differential aerial exposure of different inundation belts, suggesting that propagule predation may be lower in the lower intertidal than in upper belts. At present, a number of experiments trying to corroborate and/or challenge these three hypotheses are depicting a controversial scenario, whereas many studies offered new and alternative explanations (e.g. McKee 1995; McGuinness 1997; Dahdouh-Guebas et al. 1998; Sousa and Mitchell 1999; Clarke and Kerrigan 2002). Recently some authors suggested a possible 'mutual relationship' between sesarmid crabs and mangroves. Under this model, mangroves provide food and a suitable habitat for the crabs, which in turn reduce competition through propagule predation (Bosire et al. 2005; Cannicci et al. 2008). For mangroves with almost no tidal influence and a subsequent mosaic vegetation, DahdouhGuebas (2001) and Dahdouh-Guebas et al. (2011) proposed a spatio-temporal biocomplexity hypothesis that can explain the role of propagule predators in the shaping of vegetation structure, and how local hydrography and anthropogenic effects may influence the apparently natural process of propagule predation. In fact, Dahdouh-Guebas et al. (2011) illustrated how hydrography changes alter the behaviour of propagule predators and play a role in the shaping of vegetation structure by reconstructing the lagoon water level of a Sri Lankan mangrove site on the base of rainfall data over a period of 50 years. In this way, they could show the importance of spatial and temporal microhabitat variations in opening multiple successional pathways in vegetation dynamics, confirming that a chain of events, rather than the influence of localized biotic and abiotic factors, seems to lead to a particular mangrove vegetation structure or zonation.

In both New and Old world mangroves, Sesarmidae and Ocypodidae process, retain, macerate and ingest large amounts of litter and microalgal mats, contributing consistently to retention of mangrove organic matter and, according to Kristensen (2008), acting as ecosystem engineers. In fact, most species belonging to these two families actively dig and

maintain burrows as a refuge from predation and environmental extremes, as well as for reproductive purposes. As shown since the classical work by Smith et al. (1991), crab burrowing activities significantly decrease ammonium and sulphide concentrations in mangrove soil, thus positively benefiting mangrove productivity (Ferreira et al. 2007). Recent studies, however, conducted in both natural and semi-natural conditions, shifted the accent on the ecosystem engineering effects of both feeding and burrowing activities of fiddler crabs (bioturbation). Kristensen and Alongi (2006) were the first to adopt the mesocosm approach to investigate the effects of *Uca vocans* activities on redox sensitive elements such as Fe and S in mangrove sediments. They proved that the continuous mixing and oxidation of surface sediment due to burrowing, feeding and walking activities of crabs caused a higher content of oxidized compounds in the upper 2 cm of soil. This resulted in an enhanced growth rate of *Avicennia marina* saplings when associated with fiddler crabs (Kristensen and Alongi 2006; Kristensen 2008). More recently, however, other mesocosm experiments carried out in East Africa, showed that the beneficial effect of *Uca* spp. activities on mangrove soil biogeochemistry can be strongly impaired by organic waste discharge. In fact, a large set of experiments aimed at understanding the effect of sewage loadings on the biology of macrofauna is now clearly showing that fiddler crabs cannot take advantage of the surplus of organic content present in sewage-polluted mangroves. On the contrary, loadings of organic waste proved to strongly affect survival, feeding behaviour and burrow morphology of fiddler crabs species, resulting in an overall reduced bioturbation action of impacted populations with respect to those of pristine areas (Bartolini et al. 2009; Cannicci et al. 2009; Penha-Lopes et al. 2009a; Penha-Lopes et al. 2009b; Penha-Lopes et al. 2010a; Penha-Lopes et al. 2010b; Bartolini et al. 2011). Crabs inhabiting at pristine conditions, in fact, achieved higher survival than those living in sewage-exposed mesocosms (Penha-Lopes et al. 2009a). Moreover, during their activity period, crabs inside contaminated mesocosms satisfied their feeding demand faster than those of the control cells and such a reduced foraging activity depressed their sediment bioturbation activity (Bartolini et al. 2009). In addition, a study aimed at investigating possible alterations in the ecosystem engineering activities of fiddler crab communities dominating the landward belts of Kenyan mangrove forests, showed how a peri-urban site hosted a higher biomass of crabs, which produced a significantly lower amount of processed sediment compared with pristine sites (Bartolini et al. 2011).

Gastropods are not doing better than crabs in sewage contaminated mesocosms, and *Terebralia palustris* ecosystem engineering activity was depressed as well. In fact, a significant decrease in mobility due to anoxic condition generated by sewage contamination leads to a 3–4 fold decrease in the amount of sediment disturbed (Penha-Lopes et al. 2010a). Furthermore, the growth rate of treated mud whelks decreased significantly with increasing sewage concentrations.

In summary, the described overall depression of macrobenthic ecological engineering activities due to domestic sewage contamination could probably cause long-term ecological implications such as eutrophication caused by benthic microalgae overgrowth and accumulation of toxic compounds (H₂S) due to scarce sediment aeration.

Growing pressures of urban developments along coastlines are strongly increasing the levels of pollution in mangroves forests and the ecological degradation due to several kinds of contaminants can be subtle and difficult to ascertain at certain levels of concentration (Cannicci et al. 2009; Fusi et al. 2012). Thus, an actual risk is to become aware too late of the degradation of mangrove systems and the crucial functions and services they provide to coastal communities.

Decapod crustaceans, gastropods and other infaunal macro-invertebrates proved to be reliable bio-indicators not only for habitat recovery assessment (e.g. Dahdouh-Guebas et al. 2012), and also for cryptic changes (Bartolini et al. 2011) acting as early-warning signals of ecological degradation. The infaunal community structure of contaminated peri-urban mangrove swamps from Kenya and Mozambique proved to differ significantly from nearby pristine mangroves of similar ecological traits. Although some differences at local scales were detected, a trend of decrease in densities of oligochaetes, molluscs and polychaetes was determined, ultimately result in a lower biodiversity in peri-urban sites than in pristine areas (Penha-Lopes et al. 2010c). Differences between peri-urban mangroves and sites not affected by sewage disposal were also investigated in terms of crabs and molluscs abundance and diversity. The results manifested a consistent decrease, especially in Kenya, in gastropod biomass, mainly due to the disappearance of the mud whelk *Terebralia palustris*, while the total biomass of crabs increased significantly at peri-urban sites both in Kenya and Mozambique (Cannicci et al. 2009). Moreover, the peri-urban mangrove systems were richer than the non-urban ones, both in terms of fiddler crabs (*Uca* spp.) which feed on benthic microalgae and bacteria, and sesarmids, such as *Perisesarma guttatum* and *Neosarmatium africanum* (= *meinerti*), which feed on both substratum and leaf litter (Cannicci et al. 2009).

Another important early bio-indicator of heavy organic loads showed to be the shrimp *Palaemon concinnus*, a very abundant inhabitant of East African mangrove creeks, as demonstrated by Penha-Lopes et al. (2011) working in Mozambique. *P. concinnus* populations from peri-urban and pristine mangrove creeks were compared in Mozambique. Surprisingly, the shrimps at the peri-urban location were larger, experienced longer reproductive periods, presented a higher proportion of ovigerous females and a better embryo quality when compared to shrimps inhabiting non-impacted locations. Physiological indices (RNA/ DNA ratio) were similar between shrimps at pristine and peri-urban mangroves. However, a higher level of parasitism by *Pseudione elongata* (Isopoda; Bopyridae) indicated some degree of stress on the host at the peri-urban mangroves, with potential effects on the host population dynamics (Penha-Lopes et al. 2011).

Taken all round, these results indicate that, in East African mangrove systems, domestic wastewater has detectable effects on crabs, molluscs and other macrobenthic taxa, suggesting their usefulness as bioindicators of its effects on the whole system. The presence of 'cryptic ecological degradation' (*sensu* Dahdouh-Guebas et al. 2005) in benthic assemblages and biogeochemical processes at the peri-urban sites indicated the need for further studies concerning the actual potential of natural mangrove forests in excess nutrients metabolization and contaminants retention (Cannicci et al. 2009).

In summary, there is no doubt about the role of macrobenthos in ecosystem functioning of mangrove forests, but macrobenthic species themselves seem to be more strongly, and earlier, impacted than trees by anthropogenic pressure. Moreover, on the stressed populations of crabs and molluscs inhabiting mangroves all over the world, a new pressure is acting, exerted by rapid climate change, through warming, acidification, hypoxia and salinisation of sea water (Rockstrom et al. 2009; Hoegh-Guldberg and Bruno 2010; Diele et al. 2012; Kochey et al. 2012). In particular, marine ectotherms are mostly affected by changes in temperature through the oxygen limitation of thermal tolerance (Pörtner and Farrell 2008) and this can generate potential cascading effects on their overall fitness. At present there are only a few information on the thermal response of mangrove ecosystem engineers (Babbini et al. 2012), and it is nearly impossible is to forecast the effects of climate warming on ecosystem functionality. Preliminary experiments on thermal tolerance of two mangrove ecosystem

engineer crabs inhabiting the eulittoral fringe of East and South African mangrove forests, *Perisesarma guttatum* and *Uca urvillei*, suggest that these subtropical mangrove populations are vulnerable to long-term increases in temperature, particularly because of reduced oxygen content in water (Fusi et al. 2012). This thermal vulnerability, merged with the ongoing pressure from direct anthropogenic stress, is likely to lead to a loss of individual fitness with serious consequences for overall mangrove ecosystem functioning.

Keywords

evolutionary hotspot, macrobenthos, propagule predation, urban development, pollution, bioindicator species

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