Benthic Animals in Mangrove Swamp: A Review

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Abstract

This paper reviews the current knowledge of macrobenthic animals in mangrove swamps, focusing on their spatial organization and ecological functions. Spatial patterns are described separately for arboreal animals and animals living on the bottom, in dead wood, and in rivulets. Some sesarmid crabs and snails graze on higher proportions of mangrove litter in various parts of the world. Positive influences of macrobenthic animals on mangrove plants have been identified: sesarmid crabs and fiddler crabs are beneficial to the growth of mangrove trees, and some fouling and boring animals enhance the growth of mangrove prop roots.

Key words: macrobenthic animals, mangrove swamp, positive interaction, spatial organization

1. Introduction

Mangrove swamps contain diverse marine and terrestrial fauna. Mangrove-associated animals depend on the environment created by mangrove plants and they, in turn, affect mangrove plants. The faunal composition of mangrove swamps and their spatial organization have been described in various tropical areas (e.g., Berry, 1963; Macnae, 1966; Day, 1974; Sasekumar, 1974; Frith et al., 1976; Shokita et al., 1989). The intimate interrelationships between animals and mangrove plants have recently been unraveled (e.g., Perry, 1988; Ellison et al., 1996; Lee, 1998; Cannicci et al., 2008; Kristensen, 2008; Smith et al., 2009; Chen & Ye, 2010). Knowledge about the faunal composition of mangrove swamps and relationships among mangrove plants and associated fauna are important for understanding the ecological structure of mangrove ecosystems.

This paper reviews two aspects of benthic animals that occur in mangrove swamps: faunal composition and their spatial organization, and the ecological roles of benthic animals.

2. Benthic Animals and Spatial Organization

The spatial organization of benthic animals can be described according to distinct habitat types. Arboreal animals are found on leaves, stems and aerial roots of mangrove trees. Littorinid snails live on leaves or stems in the supratidal to uppermost intertidal zones. Their vertical zonation in Japan and Indonesia has been described as Littoraria pallescens on leaves in the uppermost zone (Fig. 1), L. scabra on stems in the middle level, and L. intermedia on stems in the lower level (Ohgaki, 1992; Boneka, 1994). The bark of lower stems and aerial roots is inhabited by several gastropod species, such as Nerita spp. and the pulmonates Cassidula mustelina and Melampus coffeus (Berry, 1963; Proffitt & Devin, 2005).

Typical arboreal crabs include the sesarmids Aratus pisonii, Armases elegans, and Parasesarma leptosoma, all of which spend their entire adult life on trees. Aratus pisonii, a Caribbean species, moves up to six meters above the ground to feed on mangrove leaves and buds (Hagen, 1977; Beever III et al., 1979). Parasesarma leptosoma occurs in East African mangrove forests and shows vertical migrations from the lower part of the mangrove aerial root to the canopy of the tree (ca 12-13 m height) to forage on leaves (Vannini & Ruwa, 1994). This species has recently been found to forage on mangrove flowers on Iriomote Island, Japan (Takaso, unpublished). Parasesarma leptosoma also shows conspicuous tree fidelity: crabs that were moved to trees seven meters away returned to the original tree within a few days (Cannicci et al., 1996).
Mangrove roots, trunks, branches, and leaves bear rich sessile animals, including sponges, hydroids, anemones, polychaetes, bivalves, barnacles and ascidians. The most conspicuous are barnacles (*Balanus* spp.), which foul trunks, aerial roots, and leaves (Fig. 2). Zonation in sessile animals on red mangrove prop roots was described by Rützler (1995); the mangrove oyster *Isognomon alatus* occupied the uppermost part, followed by the sponges *Haliclona implexiformis* and *Lissodendoryx isodictyalis*, and the lower area was occupied by the sponge *Scopolina ruetzleri*.

Macrofauna that live underground in mangrove forests show vertical zonation. The dominant animals are crustaceans, mollusks and polychaetes. Shaded areas under the mangrove canopy are inhabited by various decapod crustaceans. The most conspicuous is the mud shrimp *Thalassina anomala* (Fig. 3), which constructs large mounds and burrows that are 2.5 m deep (Sankolli, 1963). The mounds created by this species harbor many other benthic animals, such as sesarmid crabs. Sesarmid crabs are generally decomposers of mangrove litter and are most common in forested areas. Benthic animals in forested areas are difficult to sample quantitatively because of the underground root systems. However, Wada et al. (1987) investigated the depth distributions of burrowing animals to a depth of one meter in a natural mangrove forest (tree height: ca. 30 m) in southern Thailand. Most species, including polychaetes (*Leonnantes* sp., *Glycera* sp. and *Dasybranchus* sp.) and sesarmid crabs (*Chiromantes haswelli*, *Sarmatium germani*, *Neosarmatium smithi* (Fig. 4) and *Clistocoeloma merguiense*), occurred above 60 cm depth and only two crustaceans, *Alpheus euphrosyne* (Fig. 5) and *Callianassa ranongensis*, were found from the shallow layer to the bottom layer (1 m depth).

Nakasone (1977) described the vertical zonation of brachyuran crabs in a mangrove swamp in Okinawa, Japan. The uppermost supratidal area was occupied by land crabs such as *Cardisoma carnifex* and was termed the cardisomine zone. This was followed by the upper intertidal area under mangrove stands, which was occupied by sesarmid crabs (the sesarmine zone). The middle intertidal area of open flats was occupied by fiddler crabs such as *Uca perplexa* (Fig. 6; the ocypodine zone). This was followed by the lower intertidal area, which was occupied by macrophthalmid crabs such as *Macrophthalmus convexus* (Fig. 7; the macrophthalmine zone); a mixed zone; and the lowermost subtidal area, where the portunid crab of *Scylla* spp. occurred (the *Scylla* zone).

The zonation of mollusks in mangrove forests has a *Littorina* zone, represented by *Littorina scabra* and *L. melanostoma*, on the upper parts of trees; a *Nerita* zone, represented by *Nerita birmanica* and *N. planospira*, on the lower parts of trees and on the mud surface; and a
bivalve zone, represented by *Enigmonia rosea* and *Trapezium sublaevigatum*, on the mud surface of the seaward fringe of forested areas (Berry, 1963).

Dead wood (Fig. 8) has characteristic fauna that live on the wood surface, such as gastropods and barnacles, and inside the wood, including boring animals such as the bivalve *Teredo* and sphaeromatid isopods. Interstices in rotten wood are inhabited by the gastropod *Ellobium* (Fig. 9), grapsoid crabs, sea anemones, and sipunculids. However, dead wood fauna in mangrove swamps have not yet been studied quantitatively.

Rivulets bear fauna that differ from other habitats in mangrove swamps. They include both a variety of fish larvae and mudskippers. In mangrove swamps in the Ryukyu Islands, rivulet bottoms are inhabited by brachyuran crabs of *Scylla* and *Deiratonotus cristatus* (Fig. 10), and shrimps of *Palaemon* and *Penaeus*. Benthic animals in mangrove channel areas have not yet been surveyed quantitatively.

### 3. Mangrove Litter Decomposers

Stable isotope analysis suggests that fiddler crabs and bivalves consume algae, and grapsoid crabs and gastropods eat a variety of food items, from algae to mangrove plants (Rodelli *et al*., 1984). Grapsoid crabs and some gastropod species function as decomposers of mangrove litter. The most well-known are sesarmid crabs, which graze on litter or bury litter in their burrows for later feeding. These species include *Sesarma plicata* in China (Chen & Ye, 2008); *Perisesarma eumolpe* and *P. onychophorum* in Peninsular Malaysia (Malley, 1978; Ashton, 2002); *Sesarma messa*, *Sesarma erythrodactyla*, and *Neosarmatium smithi* in Australia (Giddins *et al*., 1986; Robertson, 1986; Camilleri, 1989; Micheli, 1993); and *Sesarma guttatum*, *Sesarma ortmanni*, and *Neosarmatium meineriti* in East Africa (Emmerson & McGwynne, 1992; Dahdouh-Guebas *et al*., 1999). In Brazil, litter consumption is led by the ocypodoid crab *Ucides cordatus* (Nordhaus *et al*., 2006; Nordhaus & Wolff, 2007). It is estimated that this species eats...
approximately 81% of total litter fall from mangroves (Nordhaus et al., 2006). In Australia, the sesarmid crab *Sesarma messa* can remove 28% of the annual litter fall of *Rhizophora stylosa* (Robertson, 1986). In southern Africa, *Sesarma meinerti* is estimated to consume 44% of leaf litter from *Avicennia marina* (Emmerson & McGwynne, 1992).

Some gastropod species are also responsible for the degradation of mangrove litter. The potamidid snail *Terebralia palustris* (Fig. 11) is a grazer of mangrove leaf litter in Japan (Nishihira, 1983) and Kenya (Slim et al., 1997; Fratini et al., 2004). Mangrove leaves on the substrate surface are grazed on by aggregations of large snails of this species (Nishihira, 1983), but juvenile snails do not graze on leaves (Slim et al., 1997). In African mangroves, it is estimated that 11.2% and 18.6% of litter is processed by macrobenthic animals, including *Terebralia palustris*, in *Ceriops tagal* and *Rhizophora mucronata* vegetation, respectively (Slim et al., 1997). In Florida, USA, the pulmonate gastropod *Melampus coffeus* consumes 40.5% of the litter from *Rhizophora mangle* and *Avicennia germinans* (Proffitt & Devlin, 2005). Recently, cellulase activity has been found in the potamid snail *Terebralia palustris* (Niiyama & Toyohara, 2011) as well as some sesarmid crabs (Adachi et al., 2012), which indicates that the ability to digest cellulose using enzymes is responsible for the breakdown of mangrove litter by these animals.

### 4. Positive Influences of Macrofauna on Mangroves

Fiddler crabs in salt marshes have beneficial effects on marsh plants (Bertness, 1985); similarly, sesarmid crabs have a positive influence on mangroves. Smith III et al. (1991) was the first to demonstrate such positive effects of burrowing crabs (mainly *Sesarma messa* and *S. temperi*) through field manipulation experiments in *Rhizophora*-dominated forests in Australia. They found that when crabs were removed by pitfall traps over a twelve-month period, there was a significant reduction in cumulative forest growth (measured as the stipule fall rate) and increased soil sulfide and ammonium concentrations. Similar experiments were conducted in a Florida mangrove swamp by Wada and Hines (unpublished), in which the removal of fiddler crabs (*Uca pugilator* and *U. rapax*) via pit traps caused a significant decrease in mangrove (*Avicennia germinans*) survivorship after two years. Smith et al. (2009) also examined the effect of fiddler crab presence on the mangrove *Laguncularia racemosa* in a Florida mangrove swamp. They found that the removal of fiddler crabs over a one-year period caused significant decreases in mangrove growth and leaf production, together with increases in interstitial water salinity and the oxidation-reduction potential of low-organic sediments. Predation on mangrove propagules can cause damage that hinders mangrove regeneration. In Australia, seed predation by grapsoid crabs affects ca. 75% of the seeds on the bottom surface (Smith III, 1987). However, some propagules are found inserted into crab burrows, with some parts grazed (Fig. 12). On Amami-Oshima Island, a similar phenomenon has been observed in burrows of the grapsoid crab *Pseudohelice subquadrata* (Fig. 13). It is likely that by carrying propagules into burrows, these crabs enhance the regeneration of mangrove plants.

The boring isopod *Sphaeroma peruvianum* and the encrusting barnacle *Balanus* spp., which are closely associated with prop roots of the mangrove *Rhizophora mangle*, cause 50% and 30% reductions in the root growth rate, respectively (Perry, 1988). However, these effects are indirectly mediated by predation by the snails *Thais kiosquiformis* and *Morula lugubris* and the hermit
crab *Clibanarius panamensis* (Perry, 1988). On the other hand, the boring isopod can be beneficial to mangroves. Damage to prop roots by this boring animal causes branching, so that the number of roots that actually reach the soil surface increases, helping to stabilize the mangrove tree (Simberloff et al., 1978).

Mangrove roots host a range of epibionts, such as macroalgae, barnacles, mollusks, sponges, tunicates, serpulid annelid worms, hydroids, and bryozoans. Encrustations of these organisms can reduce root growth. For example, encrustation by the barnacle *Balanus* can decrease root production by 52% by blocking lenticels and reducing gas exchange and respiration (Perry, 1988). In contrast, epibionts can benefit mangrove roots in some cases. Ellison and Farnsworth (1990, 1992) found that epifaunal sponges and ascidians reduced damage to the roots of *Rhizophora mangle* by wood-boring isopods. Foraging by some ocypodoid crabs on prop roots (Fig. 14) can be beneficial for mangroves because the activity removes algae and mud covering the root surfaces (Wada & Wowor, 1989).

Symbiotic nutrient exchange occurs between mangrove roots (*Rhizophora mangle*) and fouling sponges (*Tedania ignis* and *Halichona implexiformis*) (Ellison et al., 1996). A transplant experiment that moved sponges to bare roots found significant increases in root growth. Furthermore, the transplanted sponges grew 1.4 to 10 times faster than control sponges that were attached to PVC pipes in the same habitat. That study also provided evidence that mangrove roots obtain inorganic nitrogen from sponges and that sponges obtain carbon from mangrove roots.

**5. Concluding Remarks**

Due to the diversified environmental conditions created by mangrove plants, the diversity and spatial organization of macrobenthos are yet to be fully described. For example, few quantitative studies have described the zonation of macrobenthos because it is difficult to dig into substrates containing mangrove root systems. The spatial organization of organisms living in unique habitats, such as dead wood and rivulets, has not yet been studied. The faunal diversity and spatial organization of such habitats represent significant gaps in our understanding of the structure of mangrove ecosystems.

Macrobenthos are important functional components in mangrove swamps through their feeding or burrowing activities. Litter grazing by grapsoid crabs and snails can enhance nutrient processing and contribute to ecosystem function. Burrowing activities by crabs can also be beneficial for mangrove plants. Such positive interactions demonstrate the importance of these animals for maintaining mangrove ecosystems. This knowledge is of prime importance for the conservation and restoration of mangrove ecosystems, which are being degraded and lost worldwide.

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**References**


