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Review

The habitat function of mangroves for terrestrial and marine fauna: A review

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Abstract

Mangroves are defined by the presence of trees that mainly occur in the intertidal zone, between land and sea, in the (sub) tropics. The intertidal zone is characterised by highly variable environmental factors, such as temperature, sedimentation and tidal currents. The aerial roots of mangroves partly stabilise this environment and provide a substratum on which many species of plants and animals live. Above the water, the mangrove trees and canopy provide important habitat for a wide range of species. These include birds, insects, mammals and reptiles. Below the water, the mangrove roots are overgrown by epibionts such as tunicates, sponges, algae, and bivalves. The soft substratum in the mangroves forms habitat for various infaunal and epifaunal species, while the space between roots provides shelter and food for motile fauna such as prawns, crabs and fishes. Mangrove litter is transformed into detritus, which partly supports the mangrove food web. Plankton, epiphytic algae and microphytobenthos also form an important basis for the mangrove food web. Due to the high abundance of food and shelter, and low predation pressure, mangroves form an ideal habitat for a variety of animal species, during part or all of their life cycles. As such, mangroves may function as nursery habitats for (commercially important) crab, prawn and fish species, and support offshore fish populations and fisheries. Evidence for linkages between mangroves and offshore habitats by animal migrations is still scarce, but highly needed for management and conservation purposes. Here, we firstly reviewed the habitat function of mangroves by common taxa of terrestrial and marine animals. Secondly, we reviewed the literature with regard to the degree of interlinkage between mangroves and adjacent habitats, a research area which has received increasing attention in the last decade. Finally, we reviewed current insights into the degree to which mangrove litter fuels the mangrove food web, since this has been the subject of long-standing debate.

Keywords: Mangrove; Habitat use; Fauna; Ecosystem interaction; Ecology; Biodiversity; Food web

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1. Introduction

Mangroves are predominantly intertidal habitats that occur worldwide in the (sub) tropics along sheltered and shallow-water coastlines. The prop-roots and pneumatophores of mangrove trees extend into the intertidal and subtidal where they become a rare feature: hard substrata in an otherwise soft sediment environment (Ellison and Farnsworth, 1992). As such, mangrove roots become home to terrestrial as well as marine plants, algae, invertebrates and vertebrates. Mangroves form a habitat for a wide variety of species, some occurring in high densities. They are productive habitats and may support coastal fisheries for prawns and fishes (Manson et al., 2005). Mangroves are also important to humans for a variety of reasons, including aquaculture, agriculture, forestry, protection against shoreline erosion, as a source of fire-wood and building material, and other local subsistence use (Hogarth, 1999; Walters et al., 2008). Worldwide, loss of mangroves has been significant in recent decades, although in some regions of the world mangroves still occur as very extensive forests (Spalding, 1998; Alongi, 2002). They suffer from direct impacts such as cutting and pollution, as well as from hidden impacts such as changes in inland freshwater management (Dahdouh-Guebas et al., 2005), and are often regarded as unpleasant environments with little intrinsic value.

Animals found within mangrove environments include a variety of taxa, many of which are vulnerable or threatened as a result of human activities in the coastal zone. Determining the value of mangroves and other estuarine habitats for these animals requires knowledge of their life history, physiology and ecology as they interact across the dynamic mosaic of available habitats. Evidence suggests that mangroves are important to these species, but a lack of research is a major impediment to an evaluation of their mangrove dependency. A challenge for future research is separating the roles of mangroves from those of estuaries and other shallow-water habitats, to help determine the appropriate temporal and spatial scales for habitat protection (see Manson et al., 2005). Estuarine habitats have been recognised as important drivers of nearshore fish productivity. Worldwide, about 30% of all commercial fish species are mangrove-dependent (Naylor et al., 2000), producing an annual catch of almost 30 million tonnes in 2002 (FAO, 2004). Of all ecosystems, estuaries have the highest value per hectare (Costanza et al., 1997), making it significant for subsistence in many coastal communities. In Bragança (N-Brazil), for example, 68% of the cash income is primarily derived from mangrove crabs and fish (Glaser, 2003).

Recent and extensive reviews on mangroves as habitats for terrestrial and marine fauna include Hogarth (1999), Kathiresan and Bingham (2001), and Qasim and Kathiresan (2005). Studies related to the linkages between mangroves and coastal fish populations and fisheries, and new insights relating to the debate on the degree to which mangrove litter fuels the mangrove food web, form an important body of work published since these reviews; hence there is the need for a more up-to-date review. The current review summarises the available data on mangroves as a habitat for terrestrial and marine fauna, with special reference to the interlinkages with adjacent habitats and the importance of litter in the mangrove food web. We focus on the main groups of animals found in the mangrove habitat: sponges, various groups of meiofauna and macrofauna (epifauna and infauna), prawns, insects, fishes (bony fishes and elasmobranchs), amphibians, reptiles, and birds, accepting that a review of the complete fauna would be too far-reaching for this special issue, and that some mangrove fauna are not discussed here. These include less-well studied taxa like zooplankton (e.g., Mohan and Sreenivas, 1998; Ferrari et al., 2003; Krumme and Liang, 2004), tunicates (e.g., Carballo, 2000; Goodbody, 2003; Rocha et al., 2005), and mammals such as bats (Bordignon, 2006), buffalo (Dahdouh-Guebas et al., 2006), deer (Barrett and Stiling, 2006), dolphins (Smith et al., 2006), flying foxes (Moore, 2002), manatees (Spiegelberger and Ganslosser, 2005), marsupials (Fernandes et al., 2006), otters (Angelici et al., 2005), primates (Nijman, 2000), rabbits (Forys and Humphrey, 1996), raccoons (Cuaron et al., 2004), and tigers (Gopal and Chauhan, 2006).

2. Mangroves as habitats for sponges

2.1. Diversity and distribution of sponges

Sponges occurring on mangrove roots are conspicuous because they often have large sizes (±50 cm in diameter or more) and brilliant colours (e.g., Rützler and Feller, 1996; Diaz et al., 2004). Although some encrusting mangrove sponges can survive above the water line for many hours during a tidal cycle (Barnes, 1999), the aquiferous system of larger sponges will collapse when emerged for periods longer than 4 h (Rützler, 1995). Considering the typical zonation of mangrove habitats (Nybakken, 1997), the mangrove area available to sponge communities is very small, especially when compared to the much larger adjacent subtidal habitats afforded by seagrass beds, hard-bottom areas, and coral reefs. In addition, while only prop-roots that extend below lowest low water (LLW) will support most sponge growth (Ellison and Farnsworth, 1992; Rützler, 1995), the vast majority of these roots are in water that is either too shallow or too stagnant. Most mangrove sponge assemblages are restricted to prop-roots that hang over tidal channels that cut through soft sediment habitats (e.g., Engel and Pawlik, 2005) or raised rock, rubble or peat banks that drop off abruptly to depths greater than LLW (e.g., Farnsworth and Ellison, 1996). These two types of shoreline are also accessible by boat and snorkelling, while the vastness of the remaining intertidal mangrove is not. Therefore, to infer that sponge-covered prop-roots are a common feature of mangrove habitats as a whole would be false. Nevertheless, where they occur, mangrove sponges form distinctive, high-biomass communities with associated fish and invertebrate faunas (Kathiresan and Bingham, 2001). For example, at Punta del Este, Cuba, Alcolado (1991) estimated 50–80 individual sponges per meter of shoreline, while at study sites in the Florida Keys, U.S.A., Engel and Pawlik (2005) counted 1195 sponges comprising ten species that occupied 73.5% of available mangrove root space.

The great majority of published information on mangrove sponge communities comes from the Caribbean rather than the Indo-Pacific (Barnes and Bell, 2002). There are probably several reasons for this disparity, related both to differences in the mangrove habitats and the sponge assemblages of the two regions. In the lower intertidal zone, Caribbean mangroves are dominated by *Rhizophora mangle*, which has long prop-roots that extend into deeper water and support a great diversity of epibiotic algae and invertebrates below the LLW line (Farnsworth and Ellison, 1996), while in most Indo-Pacific mangroves the equivalent zone is dominated by *Avicennia* and *Sonneratia* spp. which lack prop-roots (Nybakken, 1997). Unlike the large sponges found in Caribbean mangroves, Barnes (1999) found 91.9% of mangrove sponges from Mozambique were encrusting and the remainder were buried. The taxonomy of Caribbean sponges is much better described than sponges of the Indo-Pacific, and this has limited ecological studies of the latter. Caribbean sponge communities are remarkably similar over the breadth of the biogeographic region (see below), while those in the Indo-Pacific are more diverse and variable from location to location (van Soest, 1994).

There tends to be lower species diversity of sponges in mangroves than adjacent subtidal habitats (seagrass beds, coral reefs, hard-bottom, etc.) in both the Caribbean and Indo-Pacific (Barnes, 1999; Barnes and Bell, 2002). Numbers of sponge species can be high, ranging from 3 to 147 for Caribbean mangroves (Diaz et al., 2004), although these communities are usually made up of less than ten dominant species on the basis of biomass, and generally the same dominant species are found throughout the biogeographic area. Among the most common Caribbean species are *Tedania ignis*, *Lissodendoryx isodictyalis*, *Chondrilla nucula*, *Geodia gibberosa*, *Halichondria melanodocia*, *Haliclona manglaris*, *Dysidea etheria*, *Hyrtios proteus*, *Mycale microsigmatosa* and *Spongia tubulifera* (cf. Sutherland, 1980; Alcolado, 1991; Engel and Pawlik, 2005; Diaz et al., 2004). Too few studies exist to generate a similar list for Indo-Pacific mangrove sponges, but it is interesting that some of the same genera were represented in a survey of the Quirimba Archipelago of Mozambique (Barnes, 1999), where *Tedania digitata*, *Haliclona* sp. and *Biemna* sp. were found in mangrove habitats.

2.2. Influence of abiotic factors on sponge communities

As primarily nearshore, estuarine habitats, mangroves are strongly influenced by abiotic factors such as freshwater runoff, sedimentation, and rapid temperature fluctuations from the influence of sun and wind on tidally driven shallow water. After many years of studying communities around Kingston Harbour, Jamaica, Goodbody (1961) concluded that mangrove root communities seldom reach a climax condition because of mortality after intense rain events. Studies of mangrove sponge communities in the Florida Keys, U.S.A., have also documented yearly cycles of mortality associated with physical disturbance, temperature extremes and rain events (Bingham and Young, 1995; Pawlik et al., 2007). Quite the opposite was found for mangrove sponge communities at Bahía de Buche, Venezuela, which, despite having the same community structure as other Caribbean sites, was remarkably stable over time (Sutherland, 1980). This unusual situation can be attributed to a combination of little or no rainfall runoff or storm events at this site as well as constant annual temperatures (Sutherland, 1980).

The cline in abiotic effects as a function of proximity to the shore has best been demonstrated by Ellison and Farnsworth (1992), who documented the prop-root faunal assemblages at six sites in Belize, ranging from nearshore to offshore sites. Species richness of all epibionts increased with distance offshore, with only two sponge species present in the most nearshore site increasing to nine in the most offshore site. In a subsequent study of four mangrove islands in Belize, Farnsworth and Ellison (1996) found that sponge diversity and abundance was greatest on the leeward rather than the windward side of islands, which they attributed to a combination of abiotic (physical disturbance) and biotic (larval supply) factors acting at different spatial and temporal scales. Compared with sponges growing in other tropical subtidal habitats (i.e., seagrass beds and coral reefs), species that comprise the typical Caribbean mangrove sponge community are specifically adapted to survive extremes in salinity, temperature and sedimentation, either through tolerance or rapid recovery after catastrophic loss (Engel and Pawlik, 2005; Pawlik et al., 2007). Adaptations to abiotic extremes do not preclude mangrove sponges from living in habitats where physical conditions are better, such as reef habitats, but biotic factors, particularly predation, limit their distribution in those habitats (Pawlik, 1997; and see below).

2.3. Influence of biotic factors on sponge communities

While abiotic factors control the large-scale distribution of sponge assemblages in mangrove habitats, biotic factors may have important effects at smaller scales. Seastars of the genus *Echinaster* may be locally abundant in some Caribbean mangrove habitats, where they consume sponges on prop-roots that become accessible to them when they grow into the subtidal sediment (Waddell and Pawlik, 2000). Parrotfishes and angelfishes make excursions from reef habitats to some mangrove sites to feed on sponges (Dunlap and Pawlik, 1998). When the most common mangrove sponge species were transplanted to reef sites, they were quickly consumed by angelfishes, yet many of these same mangrove species can be found in interstices in the reef framework where predatory fishes cannot eat them (Dunlap and Pawlik, 1996; Pawlik, 1998). Therefore, mangrove habitats serve as a refuge from fish predation for sponges that are able to survive the abiotic conditions found there.

Competition for available stilt-root space within Caribbean mangrove sponge communities appears to be intense, with a clear dominance-hierarchy based on growth rate and the production of putative allelochemical agents (Engel and Pawlik, 2005). Interestingly, some mangrove sponges appear to use chemical cues to foster the growth of other sponge species on their surfaces, with the overgrowing species providing an anti-predatory chemical defence to the undefended species under them (Engel and Pawlik, 2000, 2005; Wilcox et al., 2002). While allelochemicals may be important in sponge–sponge interactions, Bingham and Young (1991) could find no allelochemical effect of existing mangrove sponges on other epifaunal invertebrate species in settlement experiments. Wulff (2005) recently suggested that the competitive superiority of mangrove sponges prevented the colonisation of mangrove sponge habitats by sponge species usually found in reef habitats. This conclusion, that biotic factors may be more important than abiotic factors in affecting mangrove sponge ecology, was based on transplantation experiments conducted in offshore mangrove habitats in Belize (Wulff, 2005), where Ellison and Farnsworth (1992) had previously found abiotic conditions were least stressful, and species richness was highest. In subsequent experiments at three coastal mangrove sites in the Florida Keys, U.S.A., and one offshore site on Grand Bahama island, Bahamas, Pawlik et al. (2007) observed that reef sponges declined in health and died within 60 days of being transplanted to mangrove sites, a result that was attributed to abiotic conditions of high temperature, rainfall events and sedimentation in mangrove habitats. While some mangrove sponge communities have been documented to be less influenced by abiotic factors, particularly freshwater runoff (Sutherland, 1980; Wulff, 2005), these are the exception rather than the rule (Goodbody, 1961; Ellison and Farnsworth, 1992; Bingham and Young, 1995; Farnsworth and

Ellison, 1996; Kathiresan and Bingham, 2001; Pawlik et al., 2007).

In addition to mutualisms between sponge species in mangrove habitats (Wilcox et al., 2002), sponges also form mutualisms with the mangrove plants themselves. Ellison and Farnsworth (1990, 1992) reported that epifaunal sponges and ascidians reduce damage to prop-roots of *R. mangle* by wood-boring isopods: roots without epifaunal cover exhibited damage and 55% lower growth relative to roots with epibiont cover. In addition, Ellison et al. (1996) discovered that transplantation of sponges onto prop-roots induced, within 4 weeks, the formation of fine rootlets that pervade sponge tissue.

Aside from the hard substratum provided by prop-roots, mangroves may also offer an enhanced food source for sponges. In general, sponges feed primarily on particles the size of bacteria. The rich microbial community that results from the productivity and nutrient cycling in mangroves (Kathiresan and Bingham, 2001) may promote faster sponge growth than in adjacent oligotrophic habitats, such as coral reefs.

3. Mangroves as habitats for meiofauna

3.1. Diversity and distribution of meiofauna

In mangroves a distinct ‘phytal’ meiofauna (generally defined as animals passing through a 1.0 or 0.5 mm sieve but retained on a 63 μm mesh), often dominated by acari, inhabits hard substrata such as prop-roots and pneumatophores (Proches et al., 2001; Bartsch, 2003). The focus of the majority of studies of meiofauna in mangroves, however, is on communities living in sediment or on decomposing leaves. Within mangrove sediments, as in most estuarine habitats, meiofauna are the numerically dominant metazoans. For practical purposes meiofauna may be split into hard-bodied and soft-bodied components (Somerfield et al., 2005). The former are organisms that preserve well in formalin and so can be identified in preserved samples. They are easier to study than the soft-bodied forms for which specialised preservation and examination techniques are required. Nematodes and harpacticoid copepods usually constitute over 90% of the hard-bodied component of the meiofauna and are the subject of most studies. Soft-bodied forms, such as Turbellaria, are generally ignored although they may be equally abundant (Alongi, 1987b).

Although a number of studies of meiofauna in mangrove habitats document the abundances of organisms identified to high taxonomic levels, such as phyla or classes, there are relatively few studies which provide information on the species composition and structure of meiofaunal communities. Species-level information for copepods is available from a geographically widespread set of mangrove systems with very different environmental characteristics, including a lagoonal system in Brazil (Gerlach, 1958; Por, 1984; Por et al., 1984), fringe mangrove forests in Florida (Hopper et al., 1973; Fell et al., 1975), hard-bottom mangroves in Sinai (Por, 1977; Reice et al., 1984), and soft-sediment tropical mangroves in India (Kondalarao, 1984; Kondalarao and Raman-Murty, 1988) and southern Malaysia (Sasekumar, 1994; Gee and Somerfield, 1997; Somerfield et al., 1998). The heterogeneity of systems studied makes it difficult to draw general conclusions about benthic copepods in mangroves. For example, reports of the number of species found in mangroves vary widely. Por et al. (1984) recorded 14 species from the mangrove system of Cananeia in Brazil. Kondalarao (1984) and Kondalarao and Raman-Murty (1988) found 32 and 22 species of harpacticoid copepods, respectively, from 2 estuarine mangrove systems in India. Sasekumar (1994) found 25 species in mangrove systems in Selangor, Southwest Malaysia. Between 60 and 70 putative species of Copepoda were recorded from the Merbok estuary in Northwest Malaysia (Somerfield et al., 1998). One reason for the relatively high number of species recorded in the latter study was that, as well as documenting sediment-dwelling species, it examined leaf-litter assemblages in detail. Particularly, a high number of species of the family Darcythompsoniidae, especially species of *Leptocaris*, were recorded. This family of copepods were only found on leaf litter, and appear to be adapted to feeding directly on litter, or for grazing epiflora off flat surfaces (Somerfield et al., 1998). Although there is little general evidence for a specialised mangrove copepod fauna, Por (1984) speculated that amongst the Darcythompsoniidae some specialised species might have evolved. The findings of Somerfield et al. (1998) support that speculation.

Species-level information on nematodes also comes from a heterogeneous set of mangrove environments which fall into two main groups: (1) seasonally arid, subtropical or temperate mangroves in Australia (Decraemer and Coomans, 1978; Hodda and Nicholas, 1986; Nicholas et al., 1991; Gwyther, 2003) and Brazil (Netto and Gallucci, 2003), and (2) tropical mangroves in Australia (Alongi, 1987a,b, 1990), India (Krishnamurthy et al., 1984), Malaysia (Gee and Somerfield, 1997; Somerfield et al., 1998) and eastern Africa (Ólafsson, 1995; Ólafsson et al., 2000). Neither Ólafsson (1995) nor Somerfield et al. (1998) found any evidence for a specialised nematode assemblage in mangrove sediments, as most of the genera found by them are typical of intertidal sediments worldwide. Estimates of the number of species inhabiting mangrove sediments vary widely. The number of nematode taxa found in the Merbok mangrove forest in Malaysia (107 putative species: Somerfield et al., 1998) compares well with numbers of nematode taxa from mangroves in Zanzibar (94 genera: Ólafsson, 1995) and Brazil (94 putative species, 86 genera: Netto and Gallucci, 2003), but is more than three times as many as were recorded from *Rhizophora* mangrove forests in Selangor, Malaysia (29 species: Sasekumar, 1994) or southern Australia (21 putative species: Gwyther, 2003). There are no nematode taxa which have been found exclusively on mangrove litter, but species in the genera most abundant on litter, such as *Diplolaimelloides*, *Diplolaimella*, *Atrochromadora* and *Theristus*, have been recorded in association with mangrove detritus from as far afield as Australia (Alongi, 1990; Nicholas et al., 1991), Southeast Asia (Gee and Somerfield, 1997; Somerfield et al., 1998; Zhou, 2001), Africa (Ólafsson, 1995) and Florida (Hopper et al., 1973).

3.2. Influence of abiotic and biotic factors on meiofauna distribution

Studies of meiofaunal distributions within mangrove sediments tend to highlight the importance of generalised intertidal and estuarine environmental gradients known to influence meiofaunal distributions everywhere, such as tidal height, salinity, oxygen availability, and sediment properties such as organic content and granulometry (Somerfield et al., 1998; Coull, 1999). Meiofaunal distributions are patchy, and vary seasonally (Alongi and Christoffersen, 1992), leading to widely varying estimates of abundance. The majority of individuals are concentrated near to the sediment surface, especially in muds (Somerfield et al., 1998), although in relatively oxic sandier sediments more specimens are found below the sediment surface (Vanhove et al., 1992). Siphonolaimid nematodes from genera such as *Parastomonema*, which contain chemosynthetic symbionts and are typically found in anoxic environments rich in methane, are known to occur in mangrove sediments (Somerfield et al., 1998; Kito and Aryuthaka, 2006). Ansari et al. (1993), working on an Indian mangrove mudflat, showed that meiofauna depth distributions correlated with vertical gradients in redox potential, but also with interstitial water content, organic matter content, adenosine triphosphate concentrations, phytobenthic abundance and bacterial counts.

The fact that different mangrove plants have different environmental niches, and affect their surroundings differently, makes it difficult to assess the extent to which tree diversity influences meiofaunal diversity. Gee and Somerfield (1997) found no strong differences in meiofaunal communities between sediments underlying stands of *Rhizophora apiculata* and *Bruguiera parviflora* in otherwise similar areas of the Merbok mangrove forest, Malaysia. Such differences as were detected were attributed to differences in tree root structure, the degree of disturbance by macrofauna, and the physical and chemical nature of the leaves falling to the sediment surface. It appears that the presence or absence of mangrove vegetation is relatively unimportant in determining the composition of meiofaunal communities.

It has been suggested that high levels of sediment-associated tannins in mangrove sediments reduce the abundance of meiofauna (Alongi, 1987c) but mangrove leaves that fall onto the sediment are rapidly colonised, and there is a succession of species associated with their decomposition (Schrijvers et al., 1995; Gee and Somerfield, 1997; Somerfield et al., 1998; Zhou, 2001). Such observations support the view that meiofauna play an important role in litter degradation. Another important ecological role of meiofaunal organisms in mangroves is that they are an important component of the diet of commercially important fish (Coull et al., 1995) and crustaceans (Dittel et al., 1997). Despite their abundance and ubiquity, however, detailed knowledge of the taxonomy, biology and interactions of these animals, and their role in the functioning of mangrove ecosystems, is lacking.

4. Mangroves as habitats for macrofauna

Mangroves are inhabited by a variety of benthic invertebrates, such as brachyuran crabs, gastropods, bivalves, hermit crabs, barnacles, sponges, tunicates, polychaetes and sipunculids. Mangrove invertebrates often show marked zonation patterns, and colonise a variety of specific micro-environments. While some species dwell on the sediment surface or reside in burrows, others live on pneumatophores and lower tree trunks or prop-roots, burrow in decaying wood, or can even be found in the tree canopies (Sasekumar, 1974; Ashton, 1999). The burrowing activities of certain benthic invertebrates have a pronounced effect on sediment properties and biochemical processes, by enhancing the porosity and water flow through the sediment, assisting in flushing toxic substances. In addition, their feeding on the sediment surface (deposit feeding) and plant matter (detritivory) promotes nutrient recycling (see also Kristensen et al., 2008). In turn, benthic invertebrates are a source of food for vertebrate predators including shallow-water fishes that enter the mangroves at high tide (Sheaves and Molony, 2000).

Macrobenthos may be operationally separated in two groups, i.e., epifauna and infauna. Epifauna refers to those invertebrates that live on various substrates such as lower tree trunks and the sediment surface, but which do not burrow in it. A range of gastropods, crabs, and bivalve species are typical representatives of epifauna. Infauna refers to burrowing invertebrates which live within the sediment, and includes crabs, pistol prawns, polychaetes, and sipunculids. The distinction between infauna and epifauna is not always straightforward, however, and not always related to the organisms' functional role. For example, while many sesarmid crabs create extensive burrow systems, others appear to find refuge in crevices from decaying wood or root structures, or their burrowing status is unknown (see Gillikin and Kamanu, 2005).

4.1. Diversity and distribution of macrofauna

Macrofaunal communities in high and low intertidal mangroves are often distinctly different, and this relates in part to highly different environmental conditions. They appear to be influenced by hydroperiod, availability of organic matter and sediment characteristics (Lee, 2008). Lower intertidal mangrove sediments (typically silt- or clay-dominated) provide substratum for growth of benthic microalgae and macroalgae (Dor and Levy, 1984; King and Wheeler, 1985; Tanaka and Chihara, 1988; Aikanathan and Sasekumar, 1994; Sarpedonti and Sasekumar, 1996). In high intertidal mangroves, the substratum is often more sandy, and the reduced frequency of tidal inundation results in a drier, more saline environment where more leaf litter accumulates and which is less suitable for growth of micro- and macroalgae. Frequent inundation in the low intertidal zone also favours the presence of filter feeders and deposit feeders, whereas fauna in the high intertidal zone does not have frequent direct access to such food sources and other trophic groups therefore predominate there.

Gastropods are typically one of the dominant and most conspicuous macrofauna in mangrove systems, and occupy a wide range of ecological niches (Cantera et al., 1983; Plaziat, 1984). The distribution of gastropod species within a mangrove forest is influenced by a variety of factors such as light (as a major factor determining algal growth and as a factor influencing humidity), tidal exposure, salinity, and substrate type. The trophic position of gastropods is equally varied (see also Section 9): sediment dwellers feed – selectively or not – on sediment organic matter and/or microphytobenthos, *Littoraria* spp. feed on epibenthic crusts on stems and roots, and some species have been reported to feed on mangrove litter and/or propagules (such as *Melampus coffeus* and adult *Terebralia palustris*). Predatory and scavenging species such as *Thais* spp. and *Nassarius* spp. are much less abundant. Gastropods can attain very high species diversity in some mangrove ecosystems: Camilleri (1992) mentions 39 species of gastropods in an Australian mangrove, Jiang and Li (1995) found 28 species in a Chinese mangrove, and Wells (1990) reports 23 mollusc species from a mangrove forest in Hong Kong. On the other hand, species diversity differs strongly in different parts of the world, e.g., *M. coffeus* is the only gastropod present in the mangroves of Guadeloupe (Plaziat, 1984). The numerical abundance and biomass of molluscs can be equally impressive (e.g., Sasekumar, 1974), and they can even reach higher densities and biomass than brachyuran crabs in some cases (e.g., Wells, 1984), although the number of comparative studies is limited. A number of gastropod genera (e.g., *Ellobium*, *Enigmonia*) and species (e.g., *Littoraria scabra*, *T. palustris*) appear to occur exclusively in mangrove systems (Plaziat, 1984). The global pattern in species richness of mangrove gastropods closely follows that of mangrove trees (Ellison et al., 1999).

Bivalves are often considered to be confined to a narrow seaward zone, due to feeding and larval settlement restrictions (Plaziat, 1984). In Southeast Asia, however, *Polymesoda erosa* is adapted for a semi-terrestrial existence by living on the high shore where only occasional high tides inundate the habitat (Morton, 1976). A number of bivalves with chemo-symbiotic associations have also been reported from mangroves (e.g., Lebata and Primavera, 2001). Wood-boring bivalves are also common in the mangrove forest, and Singh and Sasekumar (1994), for example, reported 10 species of teredinids and 1 pholadid in several mangroves along the west coast of Peninsular Malaysia. These wood-boring bivalves are ecologically significant as they stimulate the decomposition of wood and live in symbiosis with nitrogen-fixing bacteria (Waterbury et al., 1983). It has been suggested that the latter process may represent a very significant yet overlooked source of nitrogen fixation in mangrove ecosystems in view of the abundance of dead wood and Teredinidae (Boto and Robertson, 1990). Although mangrove-associated bivalves are only rarely studied, their diversity can be surprisingly high: Alvarez-Leon (1983) reported 29 species of bivalves from the mangrove root systems on the Atlantic coast of Colombia, and Jiang and Li (1995) mention 24 bivalve species from a mangrove system in Hong Kong.

Together with molluscs, brachyuran crabs are the dominant macrofauna in most intertidal mangrove ecosystems. Early reports on the species diversity of mangrove-associated crabs in the Indo-Pacific (Jones, 1984) now appear to be outdated (see Lee, 1998), and as taxonomical difficulties are still a major restriction, the diversity and distribution of mangrove-associated crabs is likely to be far from understood. Ocypodid crabs (*Uca* spp. and *Macrophthalmus* spp., or *Ucides cordatus* in Central and South American mangroves) and grapsid crabs (Sesarminae, *Metopograpsus* spp., *Metaplax* spp.) usually dominate the crab fauna and species often exhibit marked horizontal and vertical zonation patterns (e.g., Frith et al., 1979; Jones, 1984; Frusher et al., 1994; Sivasothi, 2000). Whether these distribution patterns are related to physico-chemical characteristics of the environment (e.g., Frusher et al., 1994), or to the presence of specific tree species or tree diversity, remains to be determined (see Lee, 1997; Dahdouh-Guebas et al., 2002). Similar to what is observed for gastropods (Ellison et al., 1999), species richness of sesarmid crabs appears to follow global patterns in mangrove tree species richness (Lee, 1998), although the number of detailed surveys is relatively limited and taxonomical problems still exist. Sesarmids are most diverse in Southeast Asia and decrease to low numbers in Central America. Only five species of Grapsidae have been found in the mangroves of Florida and Central America (Abele, 1992). However, Alvarez-Leon (1983) recorded an impressive array of Grapsidae (16 species) on the Caribbean coast of Colombia.

Other relatively well represented groups of macrofauna such as polychaetes and hermit crabs have been much less frequently studied, and little is known on their overall diversity, abundance and functional role in mangroves. Worms can attain a high diversity in the soft, unconsolidated substrates on the seaward sides of mangroves, with polychaetes predominating in diversity as well as abundance (Metcalfe and Glasby, in press).

4.2. Functional role of macrobenthos

The mangrove macrobenthos is intimately associated with the bottom substratum. Crabs and gastropods ingest sediment and food such as bacteria, microalgae, meiofauna and detritus adhering to it, they burrow in it and move through it, and modify it in many physical and chemical ways (e.g., Warren and Underwood, 1986; Smith et al., 1991). Crab burrows provide an efficient mechanism for exchanging water between the anoxic substrate and the overlying tidal water (Ridd, 1996). This observation was confirmed by Stieglitz et al. (2000) who demonstrated that a burrow inhabited by a sesarmid crab and a pistol prawn was completely flushed within 1 h by the activities of the crustaceans during a single tidal event.

Crabs and gastropods are the two major seed predators in mangrove forests, and thus play an important role in determining plant community structure (Smith et al., 1989). An inverse relationship between the dominance of a given tree species in the canopy and the amount of seed predation was found for species of *Avicennia*, *Rhizophora* and *Bruguiera*. It is apparent there is a mutual relationship between sesarmid crabs and mangroves, whereby mangroves provide a suitable habitat for the crabs, and the crabs reduces competition between mangrove plant species through selective predation on seedlings (Bosire et al., 2005). The selective effects of seed predation are not limited to sesarmid crabs, but can include land crabs and hermit crabs (Lindquist and Carroll, 2004). High seed predation by crabs can sometimes have a negative influence on regeneration of mangrove stands (Dahdouh-Guebas et al., 1997, 1998). Grapsid crabs dominate in Australia, Malaysia and Panama, while the gastropods *Cerithidea scalariformis* and *Melampus coeffeus* are the most important seed predators in Florida mangroves.

Detritus-feeding invertebrates dominate the mangrove fauna. *Ucides cordatus*, a semi-terrestrial ocypodid crab in Brazilian mangroves, feeds almost exclusively on plant material. Large male crabs consumed 3.3 g dry weight daily corresponding to 6% of their dry body weight (Nordhaus, 2004). Deposit feeders like *Uca* spp. scoop the surface layers of the sediment and derive nutrition from microalgae, bacteria and detritus. Some large sesarmid crabs are tree climbing and feed on fresh leaves (Sivasothi, 2000). Competition for mangrove litter has been observed in East African mangroves where many *Terebralia palustris* (potamidid gastropod) feed on the same leaf to prevent crabs from removing the leaf (Fratini et al., 2001).

The dominant role of grapsid crabs in the mangrove community structure and function has been investigated in Australia, Asia and East Africa (Giddens et al., 1986; Robertson and Daniel, 1989; Micheli, 1993; Lee, 1997; Ashton, 2002; Cannicci et al., 2008). The role of grapsid crabs as an agent affecting mangrove litter turnover in the Indo-Pacific is indisputable, but the exact trophic link remains unknown (Lee, 1997; see Section 9).

Numerous studies in Australia and East Africa indicate that grapsid crabs are major consumers of mangrove leaf litter and as a consequence produce large quantities of faecal material rich in nutrients and energy (Leh and Sasekumar, 1985; Micheli et al., 1991; Emmerson and McGwynne, 1992; Lee, 1997). These crabs also spend considerable time grazing and picking organic material off the surface of the substrate (Skov and Hartnoll, 2002), suggesting that they are using microbial resources for their nitrogen needs.

Fish predation on mangrove invertebrates occurs at high tide when the mangroves are inundated (Sasekumar et al., 1984; Wilson, 1989; Sheaves and Molony, 2000). For example, the mangrove crabs *Chiromantes* spp. and *Metaplax* spp., and the sipuncula *Phascolosoma arcuatum* were found in the gut of fishes that were netted within the mangroves at high tide (Sasekumar et al., 1984). To what extent this form of feeding contributes to the food of shallow-water fish community and controls the structure of the mangrove benthic community awaits further studies.

In summary, benthic invertebrates in mangrove forests play an important ecological role by their activities of burrowing in the sediment where they assist in flushing toxic substances, and modifying the oxidation status of the surrounding sediment. Feeding on plant matter (detritivory) assists in recycling organic matter and produces animal biomass which is a source of food for vertebrate predators (e.g., reptiles, birds, and otters) and inshore fishes that come in with the high tide.

5. Mangroves as habitats for prawns

Dall et al. (1990) classified penaeid prawn life cycles into four different types according to the environments in which the adults spawned and the postlarvae settled. Adults of two of these types both spawn offshore, and their larvae move inshore where the postlarvae settle in their preferred nursery grounds, either estuarine or nearshore habitats. The postlarvae develop into juveniles which spend between 6 and 20 weeks in the nursery ground before emigrating offshore (Haywood and Staples, 1993). The nursery grounds are generally dominated by some form of vegetation: either seagrasses (Coles and Lee Long, 1985), algae, mangroves (Staples et al., 1985), or saltmarshes (Webb and Kneib, 2002; Minello et al., 2003).

In one of the few comprehensive studies on epibenthic communities of mangroves, Daniel and Robertson (1990) found that, along with small fish, penaeids dominated the epibenthos. While a range of juvenile prawn species have been caught either within, or (more often) in the river or creek channels adjacent to, mangroves, only a few species have been found to be almost exclusively associated with mangroves as juveniles, e.g., *Penaeus*[1] *merguiensis* (Staples et al., 1985), *P. indicus* (Rönnbäck et al., 2002; Kenyon et al., 2004) and *P. penicillatus* (Chong et al., 1990). Other species are less specific in their choice of nursery habitat, e.g., *Metapenaeus ensis* (Staples et al., 1985), *M. monoceros* (Rönnbäck et al., 2002), *M. brevicornis* and *M. affinis* (Chong et al., 1990). In addition to being associated with mangroves they are also found in other habitats such as mud flats and seagrass beds.

Prawns can only gain access to intertidal mangrove forests for 10–12 h each day, when they are inundated by the tide. When the tide recedes the prawns move out, and in the case of *Penaeus merguiensis* and *P. indicus*, aggregate close to the water's edge (Staples, 1980; Kenyon et al., 2004). Because of the difficulty of sampling amongst the mangrove trunks, prop-roots and pneumatophores, most sampling for juvenile prawns (and other epibenthos) in mangrove habitats has been done using small beam trawls (Staples and Vance, 1979) or seines (Robertson, 1988) in the creek or river channels adjacent to the mangroves after the water has receded, or by setting trap nets on an ebbing tide across the small channels which drain the mangroves (Robertson, 1988; Robertson and Duke, 1990b). It is only relatively recently that researchers have examined the distribution of prawns and fishes within the mangrove forest using either drop samplers (Sheridan, 1992) or some form of stake- or lift-net to enclose an area of mangrove at high tide and collect the fish and epibenthos once the water has receded (Vance et al., 1996, 2002; Rönnbäck et al., 1999, 2002; Meager

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[1] The subgenera of *Penaeus* were elevated to genera by Pérez-Farfante and Kensley (1997). However, as there is some controversy over this revision we have chosen to use the old names in this paper (Lavery et al., 2004; W. Dall, CSIRO Marine and Atmospheric Research, personal communication).

et al., 2003). Prawns seem to make extensive use of the mangrove forest during high tide; in northern Australia, Vance et al. (1996) sampled mangroves at the creek fringe and at sites up to 59 m inland from the creek banks. Juvenile *P. merguiensis* appeared to distribute themselves throughout the forest as the tide rose, sometimes moving as far as 200 m into the mangroves (Vance et al., 2002). Similarly, working in the Philippines, Rönnbäck et al. (1999) found *P. indicus* and *Metapenaeus ensis* moved between 55 and 93 m from the mangrove fringe into the forest. In contrast, other studies have indicated that while *P. merguiensis*, *P. indicus* and *M. bennettae* move into the forest as the tide rises, densities are higher closer to the creek-mangrove interface (Rönnbäck et al., 2002; Vance et al., 2002; Meager et al., 2003). It is possible that these differences are due to variation in local topography between the study sites.

5.1. Influence of abiotic factors on prawn distribution

Many mangrove systems are located in estuaries and so are characterised by being subjected to a wide range of salinities. Juvenile prawns are euryhaline and so are able to cope with these fluctuations. Large postlarvae and juveniles of many species of penaeids are more tolerant of low salinities than early-stage postlarvae or adults (Dall, 1981). In fact, some authors have suggested that the postlarvae of certain species may use low salinity as a means of locating potential nursery grounds (Williams and Deubler, 1968; Hughes, 1969; Young and Carpenter, 1977), although high levels of rainfall (and presumably very low salinity) may inhibit postlarval immigration (Vance et al., 1998). Salinity fluctuations do no appear to significantly affect abundance, growth or mortality of penaeids (Staples, 1980; Haywood and Staples, 1993; Ahmad Adnan et al., 2002; Meager et al., 2003).

One of the main factors attributed to eliciting emigration of penaeids from mangroves out to sea is rainfall (Staples, 1980; Staples and Vance, 1986). Presumably the penaeids are responding to some other factor resulting from the increased rainfall, such as decreased salinity, increased current velocity, or changes in the levels of nutrients or other chemicals (Staples, 1980). Rainfall alone explained 70% of the observed variation in numbers of *Penaeus merguiensis* emigrating from the Norman River in northern Queensland, Australia (Staples and Vance, 1986). The amount of rainfall also determined the size at which the prawns emigrated; in very wet years a wide size range of prawns emigrated, whereas in relatively dry years only the larger prawns emigrated (Staples, 1980; Staples and Vance, 1986). In contrast to these results, studies on the closely related species *P. indicus* in South Africa indicated that emigration was related to temperature, although only temperature and salinity were recorded in this study and not rainfall (Benfield et al., 1990). Garcia and Le Reste (1981) noted that the relative importance of rainfall and temperature in determining emigration varies geographically. They postulated that in areas with a small temperature range, but seasonal rainfall, rain is the most important stimulus, whereas in areas that have rainfall that is extended throughout the year, change in temperature is more important.

Temperature has been shown to be positively related to the growth rate and negatively related to the mortality rate of juvenile *Penaeus merguiensis* in a tropical mangrove system in northern Australia (Haywood and Staples, 1993). Temperature has also been shown to influence penaeid catches in a temperate mangrove forest in Southeast Queensland, Australia. Meager et al. (2003) found that temperature was positively correlated there with catches of postlarval and juvenile *P. merguiensis*, although a long-term (6 years) study in tropical Queensland indicated that temperature explained very little of the variation in numbers of postlarval or juvenile *P. merguiensis* (Vance et al., 1998). Southeast Queensland is close to the southern limit of the distribution of *P. merguiensis*, and it is likely that the relationship with temperature found in the Meager et al. (2003) was because temperatures here ranged from 14 to 30 °C compared to 23.5 to 31.9 °C in the study by Vance et al. (1998).

Several studies have found higher densities of juvenile prawns, other crustaceans, and fishes in mangroves compared to adjacent nearshore habitats, and the hypotheses offered to explain this can be grouped into three general categories (Robertson and Duke, 1987; Robertson and Blaber, 1992; Chong, 1995; Manson et al., 2005): (1) that mangrove forests are more productive than alternative inshore habitats and so provide more food, (2) that the structural complexity provided by mangrove trunks, roots and debris, high turbidity and soft sediment afford greater protection from predators (Robertson and Duke, 1987), and (3) that the mangrove forest acts as a larval-retention mechanism, preventing planktonic prawn larvae from being distributed further by local currents (Chong et al., 1996). The remainder of this section will discuss the existing evidence for these hypotheses.

5.2. Feeding

There appears to be little doubt that juvenile prawns are foraging while they are inside the mangrove forests. Wassenberg and Hill (1993) collected samples of juvenile *Penaeus merguiensis* at various intervals during the tidal cycle and found that prawns had full guts as they left the mangrove forest on a receding tide, and inferred that the prawns had been feeding amongst the mangroves. An hour before low water, their guts were almost empty, indicating they had not been feeding after leaving the mangrove forest. Dietary studies have suggested that prawns eat a wide variety of food items including crustaceans, bivalves, gastropods, polychaetes, mangrove detritus, fish, insects, foraminiferans and diatoms (Chong and Sasekumar, 1981; Moriarty and Barclay, 1981; Leh and Sasekumar, 1984; Robertson, 1988; Wassenberg and Hill, 1993).

Because mangroves produce large amounts of detritus (Odum and Heald, 1975) it has been assumed that juvenile prawns and other mangrove-associated epibenthos have been able to utilise this production. However, although mangrove detritus has been identified in prawn guts (Chong and Sasekumar, 1981; Leh and Sasekumar, 1984; Robertson, 1988), cellulose is not digestible by penaeids (Omondi and Stark, 1996; Gonzalez-Pena et al., 2002) and so detritus, although ingested by penaeids, may not be assimilated (see Section 9).

5.3. Protection from predation

Predation is generally considered to be one of the key causes of mortality in prawns (Minello and Zimmerman, 1983; Robertson, 1988; Salini et al., 1998) and several studies have indicated that predatory fish consume significant numbers of juvenile prawns (Davis, 1985; Robertson and Duke, 1990b; Salini et al., 1990). Mangrove systems provide shallow water, structural complexity and in many cases high turbidity and fine sediment, suitable for burrowing prawns. These factors, in combination with the behaviour of prawns, acts to protect prawns by reducing their visibility to, and lowering their encounter rate with potential predators (Minello and Zimmerman, 1983; Laprise and Blaber, 1992; Kenyon et al., 1995).

Large predatory fish tend not to move far into the mangroves at high tide, whereas juvenile *Penaeus merguiensis* move long distances from the mangrove margin, making them less vulnerable to fish predation (Vance et al., 1996). The structural complexity provided by mangrove roots, trunks, detritus and fallen timber is thought to provide protection to juvenile prawns and other prey from fish predation (Robertson, 1988; Robertson and Blaber, 1992; Primavera, 1997; Meager et al., 2005). Protection from predation by mangrove structures is not as simple as might be expected; instead, it appears to be a complex interaction between predator species, prey behaviour and habitat complexity (Primavera, 1997; Meager et al., 2005). Primavera (1997) examined predation rates on two species of prawns, *P. merguiensis* and *P. monodon*, in laboratory experiments conducted on bare sand, coconut leaf bracts (to simulate mangrove detritus) and a range of different densities of pneumatophores. Two different species of predator (the barramundi *Lates calcarifer* and the mangrove jack *Lutjanus argentimaculatus*) were tested. Overall, significantly more prawns were eaten on the bare sand (48%) and leaf bracts (44%) than among the pneumatophores (30%). The presence of the structure (leaf bracts and pneumatophores) did not appear to affect the hunting abilities of the barramundi which chased prawns underneath the leaf bracts and between the pneumatophores, whereas the mangrove jack restricted themselves primarily to the clear water, away from the structure. Predation rates on *P. monodon* were lower on medium density pneumatophores compared to those on bare sand whereas there was no significant difference between predation rates on *P. merguiensis* on bare, medium or high-density pneumatophores. Primavera (1997) speculated that this may be due to behavioural differences between the two prawn species. The behaviour of prawns in relation to shelter may be modified by the presence of particular predators. Meager et al. (2005) noted that while juvenile *P. merguiensis* selected habitats providing vertical structure (pneumatophores or mangrove debris) over those with no vertical structure (bare substrate or leaf litter), once *L. calcarifer* was introduced to the tank, the prawns selected the mangrove debris over the pneumatophores. However, the prawns did not react to the presence of an alternative predator, the blue catfish *Arius graeffei*. Previous experiments had demonstrated that *L. calcarifer* was a more effective predator of juvenile *P. merguiensis* than *A. graeffei* (Meager, 2003).

High turbidity is a characteristic of many, but not all mangrove forests and turbidity within the mangrove forests may change dramatically depending upon the strength of tidal currents. While high turbidity may decrease the effectiveness of some prawn predators, others, particularly those using chemosensory mechanisms for prey detection, may be more successful in capturing prawns in turbid water (Minello et al., 1987; Macia et al., 2003).

5.4. Larval retention mechanism

The mouths of many mangrove-lined creeks are shallow and are characterised by extensive intertidal mud flats. The resulting high friction between the water and the mudflats means that, rather than forming tidal jets, the ebbing water spreads out in a fan-like manner at the mouths of the creeks (Wolanski et al., 1992). During periods of little or no longshore current most of the water from the swamp is returned during the following flood tide. In this way, mangrove swamps trap the lateral movement of coastal water for periods of between 2 and 8 weeks (Wolanski and Ridd, 1986; Wolanski et al., 1990) and so planktonic prawn and other larvae may be retained within the mangrove forest rather than being dispersed by currents (Chong, 1995). Even during the wet season water can be retained for weeks in the mangroves and side creeks (Robertson and Blaber, 1992). Lateral trapping is more effective in the upper reaches of a mangrove estuary than at the mouth (Wolanski and Ridd, 1986). This phenomenon may be responsible for influencing the along-river distribution of postlarval and juvenile *Penaeus merguiensis* observed by Vance et al. (1990). They found densities were almost five times higher in the upstream reaches of a small creek compared to those in the main river channel, near the mouth of the creek.

In summary, the fact that some species of juvenile prawns are found in relatively high densities within mangrove forests has been well documented, although the precise nature of the prawn–mangrove relationship is still unclear. There is a possibility that mangroves may be acting as a physical trap for water bodies containing the prawn larvae. While this seems plausible it does not explain why other species of prawns which have different habitat preferences (e.g., for seagrass) are not retained within mangroves as well. Based on the evidence available, mangroves seem to provide both food and protection from predation. Juvenile penaeids appear to be gaining their nutrients from mangrove-associated bacteria, epi- and infauna rather than directly from mangrove leaves or detritus.

6. Mangroves as habitats for insects

The global distribution of mangroves has been divided into two biogeographical hemispheres, the Indo-West Pacific and the Atlantic-East Pacific (Duke, 1992). The former ranges from the east coast of Africa to Asia, Australia and the western

Pacific islands, while the latter includes the eastern Pacific islands, the coasts of the American continent and the African west coast. Insect diversity in the mangroves of the Indo-West Pacific is thought to be higher than in the Atlantic-East Pacific as a result of higher plant diversity in the former although, to some extent, the dearth of insect species in the latter reflects gaps in our knowledge rather than low species diversity (Macintosh and Ashton, 2002). In general, the mangrove insect fauna of the Indo West Pacific has been better studied.

Mangroves provide a habitat that supports a large number of insects at different trophic levels. The primary trophic groups are (1) herbivorous insects that feed on leaves and other plant parts, (2) saproxylic and saprophagous insects that feed on dead and decaying organic matter, and (3) parasitic and predatory insects that feed or prey on other animals.

6.1. Herbivorous insects

Although the herbivorous insects of mangrove trees have sometimes been portrayed as being poor in diversity and lacking in specialists, more recent studies have shown that there is greater host specialisation and herbivory levels than previously thought (Burrows, 2003). In a study on herbivorous insects of mangroves in Singapore, Murphy (1990) found 102 herbivore species feeding on 21 species of mangrove plants from nine principle taxa. A wide range of mangrove plant parts were fed on, including leaves, shoots, flowers, fruits and stems. Stenophagy (feeding on narrow host range) appeared to be more developed among insects in *Avicennia* and *Sonneratia*, and was thought to be reflective of the relative taxonomic isolation of these plant taxa. In Queensland, Australia, little overlap was found between the insect herbivore fauna of *A. marina* and *Rhizophora stylosa*, and the diversity of herbivores on these tree species was similar to the diversity of nearby non-mangrove trees, and to the diversity levels reported for other tree species elsewhere in the tropics (Burrows, 2003). Mangrove habitat specificity has also been noted in a study on moths of the superfamily Geometroidea in Peninsular Malaysia, although species diversity in the mangrove habitat was low in comparison to that in other lowland forest types (Intachat et al., 2005). At the habitat level, however, mangroves can be expected to have lower herbivore diversity than other lowland forest types as a result of their lower plant diversity.

In butterflies, for which habitat and host associations are better known, few species are entirely restricted to mangroves (Corbet and Pendlebury, 1992). However, some butterfly species such as *Junonia* spp. (Nymphalidae) that occur in landward edge zones of mangroves and upper reaches of estuaries have host plants that are primary colonisers. These plants may be rare or absent under the closed multi-storey canopies of inland forests, but are able to persist in more open coastal habitats. The significance of these populations in natural coastal habitats is rarely recognised because many of the species are also able to colonise disturbed and man-made habitats such as parks and gardens. The few mangrove-inhabiting butterflies that occur across a range of natural habitats are oligophagous or polyphagous species such as *Hypolycaena erylus* (Lycaenidae) and *Polyura schreiber* (Nymphalidae) that have been recorded feeding on one or more mangrove plant species (Murphy, 1990), but feed on other non-mangrove host plants as well (Corbet and Pendlebury, 1992). A notable example of a monophagous mangrove specialist butterfly is *Danaus affinis* (Nymphalidae). The larvae feed on the vine *Ischnostemma selangorica* (Asclepiadaceae) that grows in the landward edge zones of mangroves, and the adults feed on nectar only from the flowers of the coastal shrub *Wedelia biflora* (Kirton and Azmi, 1996, 2000, 2004).

Special adaptations to the mangrove environment occur in a number of taxa of herbivorous moths. Moths of the pyralid subfamily Nymphulinae have aquatic larvae that feed selectively on the algae *Dictyota* (Dictyotaceae) and *Murayella* (Rhodomelaceae) in the intertidal zones of the mangrove floor (Yoshiyasu, 1984; Murphy, 1989). *Eristena mangalis*, a moth of the family Pyralidae, has aquatic larvae that feed on brown algae. The larvae have breathing filaments on the body, and build tube-like shelters in drainage channels under rotting leaves (Ng and Sivasothi, 2002). Other moths, such as *Cleora injectaria* (Geometridae), *Aucha velans* and *A. velliana* (Noctuidae), feed on the leaves of mangrove trees but pupate in the intertidal zone under rotting vegetation or algal mats at the base of their host plants (Murphy, 1990). A leaf-tying caterpillar of the moth genus *Argyroploce* (Tortricidae) has also been reported feeding on the tidally inundated leaves of young *Sonneratia griffithii* in Peninsular Malaysia, and was able to survive submersion in seawater for 4.5 h (Lever, 1952).

6.2. Saproxylic and saprophagous insects

Insects that feed on dead trees or wood (saproxylic insects) or decaying organic material (saprophagous insects) play an important role in nutrient cycling in forests. Termites and wood-borers (usually the larvae of beetles or moths) form the majority of saproxylic insects, and a relatively characteristic assemblage occurs in mangroves. The relative abundance of a limited number of tree species provides an abundant and stable food source for this group of insects.

In the intertidal zone, periodic or continuous flooding makes mangroves uninhabitable for many termite species that forage from the ground. However, species that nest above the ground thrive in this habitat in the absence of competing fauna and in the presence of abundant food resources. Among these are drywood termites such as *Glyptotermes*, *Neotermes* and *Cryptotermes*, which feed on dead branches that die in the canopy, or on dead standing trees (e.g., Miller and Paton, 1983; Salick and Tho, 1984). Their ability to feed on relatively dry wood is thought to be a result of an ability to obtain metabolic water through physiological processes in their bodies, as well as a result of structural adaptations that enable them to conserve water (Collins, 1969). The uniform, single-tiered canopy of mangrove forests results in a relatively low humidity in the canopy. Trees that die or branches that die in the canopy dry faster than in the multi-storied canopies of inland forests. Other termite groups that readily colonise the mangrove habitat are *Prorhinotermes* (Tho, 1992) and some species of *Coptotermes*

(Kirton, 1995), which are able to nest in moist wood with no ground contact, and species that build arboreal carton nests on tree trunks and branches, such as *Microcerotermes* spp. and some members of the subfamily Nasutitermitinae (L.G. Kirton, personal observations).

Scolytids and platypodids are the primary wood-boring beetles in mangroves. The majority feed on dead branches that have yet to dry completely. They burrow under the bark or into the wood and culture fungi on which their brood feeds. However, some are seed or prop-root feeders (Ng and Sivasothi, 2002), and others may cause the death of branches and trees through girdling and hollowing of stems and twigs. Their effects on some mangrove communities are known to exceed that of herbivores (Feller and Mathis, 1997; Feller, 2002).

A large number of ground-dwelling saprophagous insects can also be found in the mangrove habitat, and many have specialised adaptations for survival in the intertidal zone. Collembola (springtails) are diverse among the roots of mangrove plants and in the leaf litter that accumulates on the ground (Murphy, 1965; Roque, 2007), where they feed on a range of organic material including detritus and fungi. *Pseudanurida billitonensis* (Neanuridae) is a springtail in the mangroves of Singapore that feeds at low tide and returns to underwater shelters during high tide (Ng and Sivasothi, 2002). A pyralid moth, *Hymenoptychis sordida*, is known to feed on fallen fruit of *Avicennia*, dead leaves, roots and rotting timber on the mangrove floor in Singapore (Ng and Sivasothi, 2002). The larvae shelter in silken tunnels when the tide rises.

6.3. Parasitic and predatory insects

A wide range of predatory and parasitic insects with a great diversity of host and habit occur in mangrove habitats. These include predatory larvae and adult insects that prey on other organisms, parasitoids that feed within a single host and eventually kill it, hyperparasitoids that parasitize parasitoids, and blood-sucking parasites of vertebrates. They occur throughout the mangroves, from the soil to the water surface and on mangrove plants, where they exert a restraining influence on populations of herbivorous and saprophagous organisms.

Ants (Formicidae) are important predators in mangroves. One species of weaver ant, *Oecophylla smaragdina*, that is common in mangroves in Australasia, nests by drawing the leaves of mangrove plants together with silk threads spun by their larvae. The ant has been shown to significantly reduce herbivory levels on the mangrove tree *Rhizophora mucronata* in Thailand (Offenberg et al., 2004a), and the presence of this ant's pheromones on leaves of *R. mucronata* have been shown to deter feeding by the leaf beetle, *Rhyparida wallacei* (Chrysomelidae) (Offenberg et al., 2004b).

The best-known predatory insects that characterise the mangrove habitat are, arguably, fireflies (Coleoptera: Lampyridae). Although fireflies occur in a range of habitats, some are associated with mangroves and mangrove estuaries, where their larvae prey on snails in the intertidal zones. These include species of *Pteroptyx*, which range from South and Southeast Asia to New Guinea (Ballantyne and McLean, 1970; Ballantyne, 1987), and are well known for their impressive group displays on certain trees (Buck and Buck, 1976; Nallakumar, 1999; Zaidi and Yong, 2004). In Southeast Asia, members of groups of *Pteroptyx tener* or *P. malaccae* flash in close synchrony (Buck and Buck, 1976; Hanson, 1978). The synchronous flashes have made sites with large congregations of fireflies ecotourism destinations in some countries such as Malaysia (Nallakumar, 1999). *Pteroptyx tener* is the species for which the biology and ecology has been better studied (e.g., Kumar, 1979; Motuyang, 1994; Rahmat, 1996; Nallakumar, 2002; Nada and Kirton, 2004), particularly in Kuala Selangor, Malaysia, where the adults display and mate on riverside trees, especially the mangrove tree *Sonneratia caseolaris*. The larvae prey primarily on the snail *Cyclotropis carinata* (Assimineidae) in tidally inundated areas of the riverbanks. They are able to enter the shells of the snails and inject a paralysing toxin and enzyme into the soft body tissues of the snails to aid in feeding.

Many other predatory insects live and feed on the ground, sheltering under plant debris during high tides and emerging to feed on springtails, copepods, protozoa and nematodes when the tides recede (Ng and Sivasothi, 2002). Among the more common are heimpterans and pselaphid beetles. On the water surface of mangrove tidal pools, water skaters (*Xenobates* sp., Veliidae) prey on smaller insects that fall or land on the water (Ng and Sivasothi, 2002).

Female mosquitoes (Culicidae) and other small biting flies (Ceratopogonidae, Simuliidae and Phlebotominae) that inhabit mangroves take a blood meal from vertebrate hosts prior to reproduction. Biting midges breed in the mud in mangroves and mosquitoes breed in stagnant pools as well as rot holes in trees. One species of mosquito in East Africa, *Aedes pembaensis*, is known to lay its eggs on the claws of the crab *Neosarmatium meinerti*, and the larvae develop in the burrow of the crab (see Hogarth, 1999).

7. Mangroves as habitats for elasmobranchs

The number of elasmobranch species recorded from fresh or estuarine waters is at least 171 species, representing 68 genera and 34 families, with the greatest diversity occurring along the rapidly developing tropical coastlines of South America, West Africa, and Southeast Asia. Of the 171 elasmobranch species, more than 50% occur in estuaries (Martin, 2005).

Estuaries are used by various species of euryhaline and obligate freshwater elasmobranchs, but their life history and ecology, including dependency on various habitats such as mangroves, is virtually unknown (Martin, 2005). Similarly, no information exists that compares the species diversity of rays versus sharks in mangrove habitats. Habitat selection by elasmobranchs is influenced by a multitude of interacting variables such as temperature, salinity, depth, substrate type, benthic vegetation, prey distribution and variability, predator distribution, social organisation, and reproductive activity (Simpfendorfer and Heupel, 2004). It is well known that many species of elasmobranchs rely on nearshore habitats as nursery grounds (Montoya and Thorson, 1982; Simpfendorfer and

Milward, 1993; White and Potter, 2004), with several species such as the nervous shark *Carcharhinus cautus* spending its entire life cycle in the estuaries of northern Australia (Lyle, 1987). However, separating the contribution of mangroves from that of the non-mangrove estuaries can be problematic as the functional roles of mangroves may be the same as those provided more generically by 'estuarine' and 'nearshore' environments (Loneragan et al., 2005). For example, estuaries without any mangroves can function as productive nursery habitats and thus the respective roles of estuary and mangroves may not be clear (Ruiz et al., 1993).

An acoustic telemetry study to determine habitat selection of juvenile lemon sharks (*Negaprion brevirostris*) at Bimini in the Bahamas, found that *Rhizophora* mangrove thickets were routinely selected according to their availability. The main abiotic factors influencing habitat selection were temperature, substrate type and depth (Morrissey and Gruber, 1993). It is well known that mangroves support large populations of prey on which elasmobranchs feed and also provide a complex habitat structure as a means of avoidance from large sharks and other marine predators (Robertson and Duke, 1987; Simpfendorfer and Milward, 1993). These biotic factors were considered to be the most likely to explain the use of mangrove habitat by *N. brevirostris* at Bimini (Morrissey and Gruber, 1993). In the large subtropical marine embayment of Shark Bay, Western Australia, mangrove tree density was found to influence the number of species and catch rates of elasmobranchs and their prey (White and Potter, 2004).

Within the shallow, nearshore waters of Shark Bay, the arid zone mangroves are considered particularly important feeding habitats for juvenile giant shovelnose rays (*Rhinobatos typus*) at high tide (White and Potter, 2004). In a comparable environmental setting in the remote, arid Exmouth Gulf of Western Australia, juvenile and neonate *R. typus* occur at a density of 3 m^{-2} within the fringing mangroves and salt flat habitats (H.M. Penrose, unpublished data). Due to fishing-related pressures, *R. typus* is listed on the IUCN Red List as 'vulnerable' to extinction on a global scale (IUCN, 2006). As with many other species of elasmobranch, clarification of the value of mangrove as habitat during this critical life history stage is fundamental for their conservation and management.

8. Mangroves as habitats for bony fishes

8.1. Diversity and distribution of fishes

The Indo-West Pacific region, stretching from the east coast of Africa through South and Southeast Asia to Australia and the Central Pacific, has the highest diversity of fishes in the world (at least 600 species in mangrove systems) (Blaber, 2000). The high diversity decreases latitudinally away from the equatorial *core area* (sensu Blaber, 2000) in Southeast Asia, but larger subtropical mangrove systems still contain at least 100 species. Many species occur throughout this region, while others are restricted to particular regions. Examples of species that occur in most mangrove areas of this region include the sly bream *Acanthopagrus berda*, the glassfish *Ambassis gymnocephalus*, the trevally *Caranx sexfasciatus*, the wolf herring *Chirocentrus dorab*, the tenpounder *Elops machnata*, the pursemouth *Gerres filamentosus*, the ponyfish *Leiognathus equulus*, the mangrove jack *Lutjanus argentimaculatus*, the flathead *Platycephalus indicus*, the flounder *Pseudorhombus arsius*, the whiting *Sillago sihama* and the thornfish *Terapon jarbua*. A special group of fish species found in mangroves are the mudskippers (family Periophthalmidae) which occupy a specialised niche in the intertidal zone. They are physiologically and morphologically adapted to an amphibious existence in this zone with highly variable environmental conditions (Clayton, 1993), and they are able to dwell on exposed mudflats when other fish species are forced to retreat to deeper waters with outgoing tides (Kruitwagen et al., 2007).

Mangroves occur in four tropical zoogeographic regions of the world (Indo-West Pacific, East Pacific, West Atlantic and East Atlantic) and the fish communities of all have many common characteristics. In almost all cases they are dominated by fishes of marine origin, with more than half the number of species as well as the number of individuals being contributed by either fully estuarine species or marine migrants. The mangroves of the tropical East Atlantic region along the west-African coast have somewhat fewer species than the Indo-West Pacific, but are still relatively rich, with larger estuaries such as the Senegal having more than 130 species, and smaller systems such as the Fatala in Guinea about 100 species. The tropical West Atlantic region from the Gulf of Mexico to northern South America has similar numbers of species, with most systems in the equatorial region containing at least 100 species.

The dominant taxa in each region are broadly similar, but there are some interesting contrasts. In all regions, except the Indo-West Pacific, Sciaenidae are one of the dominant families. In the Indo-West Pacific, sciaenids are important in the equatorial regions of Southeast Asia, but much less so elsewhere. This pattern may be connected with the amount of rainfall and the degree to which coastal waters approach estuarine conditions.

There are important differences in the relative proportions of freshwater species, both between and within regions. Freshwater species make up more of the fish fauna in tropical Atlantic mangrove systems than in the Indo-West Pacific or East Pacific, particularly in South America where many of the very diverse fauna of siluriid catfishes are common in estuaries (Barletta et al., 2005). Similarly, in West Africa various silurids and cichlids make a significant contribution to mangrove fish communities (Baran et al., 1999). In East Africa and Australia, however, freshwater species are usually insignificant components of the mangrove fish fauna (Blaber, 2000). The equatorial regions of Southeast Asia have somewhat more freshwater species than other areas of the Indo-West Pacific, but despite the diversity of the freshwater fish faunas of Borneo and Sumatra relatively few live in estuaries. Throughout the islands of the Caribbean most mangroves are non-estuarine and small in size (fringing), and typically contain marine species dominated by the families Gerreidae, Haemulidae, Lutjanidae and Scaridae (Rooker and Dennis, 1991; Acosta, 1997; Nagelkerken et al., 2000b).

One of the key influences of mangroves on fishes is the physical structure they provide. Their pneumatophores, prop-roots, trunks, fallen branches and leaves make a complex habitat for a host of potential prey organisms, and the rich epiflora of algae and diatoms found on the mangroves and associated substrata are an important food source for many fish species (Blaber, 2000; Verweij et al., 2006a). Because mangroves usually occur in shallow intertidal areas of deposition, with quiet waters, muddy substrata, variable turbidities and a rich fauna and flora, their effects on fish are inextricably linked with these factors. The whole suite of mangrove-associated biotic and abiotic conditions makes them one of the core fish habitats of tropical estuaries and lagoons (Blaber, 2007).

8.2. *Influence of abiotic factors on fish communities*

Almost all fishes living in subtropical and tropical mangroves are euryhaline and able to cope with salinities from almost freshwater (<1 ppt) to at least 35 ppt, but their ability to do so varies from species to species and hence may influence their distribution. Salinities down to about 25 ppt apparently pose few osmoregulatory problems for most tropical marine fishes. Salinities over vast areas of mangrove-fringed coastal waters in the tropics may decline in the wet season to as little as 20–25 ppt. In some areas, such as the Bay of Bengal and parts of the South China Sea, salinities seldom rise above 30 ppt and the fish communities of such areas are highly diverse (Pauly, 1985). Salinity is not only relevant to the distribution patterns and survival of fishes in estuaries, but may also affect metabolic processes. Peterson et al. (1999) have demonstrated that there is the potential for fluctuations and spatial variability in salinity to cause significant variability in the short-term growth rates of at least one species in nursery areas. Long-term salinity variations may also affect the distribution and occurrence of fish species in estuaries. In various studies, catch rates of the most abundant species were most strongly correlated with long-term (months and years) salinity patterns (Sheaves, 1998; Barletta et al., 2005; Lugendo et al., 2007a). In the coastal lake Nhlange, part of the Kosi system of northern KwaZulu-Natal, South Africa, the changes in the fish fauna in response to gradual changes in salinity were a reduction in the diversity of marine species and an increase in numbers of individuals of a few freshwater species (Blaber and Cyrus, 1981). Nevertheless, even at salinities of 1 ppt or less the system still contained 23 estuarine or marine species.

Turbidity is one of the major factors influencing the distribution of juvenile fishes in subtropical and tropical mangrove systems. In a study of the fishes of Moreton Bay, a large estuarine embayment on the Queensland coast, Blaber and Blaber (1980) showed that variations in turbidity correlated with different distribution patterns of fish which could be divided into three categories: those tolerant of turbidity, those indifferent to turbidity (comparatively few), and those intolerant of turbidity. Most fishes in mangroves are tolerant of high turbidities.

8.3. *Factors determining the attractiveness of mangroves for fishes*

Three hypotheses, namely (1) reduced predation, (2) increased food supply, and (3) increased living space or shelter, have been suggested to explain the attractiveness of usually turbid mangrove areas, as juvenile-fish nurseries (Blaber, 2000). Predation on juvenile fishes in mangroves may be less, because turbid waters reduce the effectiveness of large visual fish predators (Blaber and Blaber, 1980; Cyrus and Blaber, 1987a), shallow waters exclude large fishes (Shulman, 1985), and structure such as seagrass or mangroves enables small fishes to hide from predators (Laegdsgaard and Johnson, 2001). Evidence supporting the turbidity hypothesis comes from comparisons of fish densities across a variety of coastal habitats which show that the abundances of certain species respond positively to increases in turbidity. Further evidence comes from observations of greater abundances of piscivorous species in the creeks of the Dampier mangroves of Northwest Australia that receive no run-off from the land, and thus have much clearer waters (Blaber et al., 1985). Evidence supporting this hypothesis also comes from estuarine systems in which there is little or no mangrove habitat (e.g., the St. Lucia system in South Africa; Cyrus and Blaber, 1987b). However, if fish are responding solely to turbidity, it is possible that mangrove vegetation has little effect on the dependence of fish on estuaries.

Both the quantity and types of food may differ between mangrove areas and adjacent waters (Nagelkerken et al., 2000b). Many of the foods available in sheltered mangrove waters are rare or absent in offshore waters, particularly detritus and microfauna and flora, as well as aquatic macrophytes and their epifauna and flora. The presence of mangroves in tropical estuaries increases the diversity and quantity of food available to juvenile fishes (Blaber, 1980, 1987), and Robertson and Duke (1987, 1990a) have shown highly significant differences in the densities of juvenile fishes between mangrove and other nearshore habitats when they are immediately adjacent to each other. Furthermore, densities of zooplankton in mangrove habitats are greater (by an order of magnitude) during the late dry- to mid-wet season recruitment period of fishes, than in the middle of the dry season. Most newly recruited fish in estuarine or mangrove habitats are zooplanktivores. In intertidal mangroves, fishes typically enter the mangroves at high tide to feed (Vance et al., 1996; Sheaves and Molony, 2000; Lugendo et al., 2006). On Caribbean islands where mangroves are often permanently inundated, on the other hand, fishes mainly shelter in the mangroves during daytime and feed on adjacent seagrass beds at night (Nagelkerken et al., 2000a; Nagelkerken and van der Velde, 2004a). Nevertheless, opportunistic feeding takes place while they shelter in mangroves during daytime (Nagelkerken and van der Velde, 2004b; Verweij et al., 2006b).

The structural significance of mangroves for fishes is well demonstrated by the studies of Thayer et al. (1987) in Florida, Blaber and Milton (1990) in the Solomon Island, Vance et al. (1996) in Australia, and Rönnbäck et al. (1999) in the

Philippines. They showed that the prop-root habitat of mangroves is of major importance to a wide variety of fishes and that the species composition of fishes varies according to the species of mangrove tree, whether the channels are blocked or choked by fallen mangrove tree branches, and the type of substratum. Cocheret de la Morinière et al. (2004) showed in an experimental setup that different densities of prop-root mimics and different degrees of shading (mimicking the above-water mangrove canopy) affected the abundance of fish sheltering in them. It appears that mangrove-associated species inhabit mangrove prop-roots in higher densities than reef-associated species, because their juveniles occur more commonly in shallow-water mangrove areas and not because they possess a greater competitive advantage for mangroves compared the reef-associated species (Nagelkerken and Faunce, 2007). The importance of presence of mangrove-root structure is also shown by the positive effects on abundance and presence of fauna (e.g., crabs, fish, infauna) as a result of mangrove replanting (Bosire et al., 2004; Crona and Rönnbäck, 2005; Walton et al., 2007; Bosire et al., 2008).

The effects of differing structure are illustrated by reference to the physical characteristics of Solomon Islands estuaries, which are similar to those of other tropical Indo-West Pacific estuaries in terms of their salinity, temperature and turbidity regimes (Blaber, 1980; Blaber et al., 1989). There are two different types of mangrove estuaries in the Solomon Islands, based on substrata and mangrove tree species, each with a different fish fauna. Hard substratum estuaries with an abundance of mangrove tree debris are inhabited mainly by species that apparently need the cover or structure provided by the debris, such as Pomacentridae and some species of Apogonidae, together with juvenile Lutjanidae and Serranidae. These species are largely absent from the soft substratum estuaries that have little debris cover, where Gobiidae, including burrowing species are dominant.

The complexity of the interplay among various factors on the distribution of fishes in mangroves is exemplified by the study of Rönnbäck et al. (1999) who showed that the numbers and biomass of fish species were higher among the pneumatophores than in the prop-root areas in Philippine mangroves. This was thought to be because the limited height of pneumatophores allows a larger volume of water free of roots where fish can swim without encountering structural complexity. Also food items associated with mangroves are much more concentrated among pneumatophores compared to among the relatively less dense prop-roots, thereby facilitating feeding (Rönnbäck et al., 1999). For both root types, the densities of small fishes were higher and that of larger carnivores lower than in more seaward habitats. Verweij et al. (2006a) showed that some species mainly utilised prop-roots for shelter whereas other species mainly used them for feeding.

In summary, the three hypotheses of predator avoidance, food and shelter, are probably all important. However, their relative significance, in terms of dependency and utilisation of tropical and subtropical mangroves by fishes, will vary depending upon the fishes and the nature of each system and its mangroves (Pittman et al., 2004; Sheridan and Hays, 2003; Lugendo et al., 2006).

9. The role of litter in the mangrove food web

9.1. Importance of mangrove litter

The idea that mangroves provide a trophic link with the abundant faunal communities within the mangrove ecosystem and in adjacent habitats has been a longstanding issue in the literature and was first proposed by the classical work of Odum and Heald (1972) in their 'outwelling hypothesis'. Odum and Heald suggested that the high productivity of mangroves is partially exported to the aquatic environment, providing an important food source for secondary consumers and thereby supporting adjacent fisheries. It has become increasingly apparent over the past two decades that this hypothesis needs to be revised, since a number of studies using natural tracer techniques (e.g., stable isotopes, fatty acids) have almost invariably found little solid evidence for a significant amount of mangrove-derived carbon in adjacent food webs, and that many of the earlier estimates may have been biased and should be revised (see Bouillon et al., 2008, for a recent overview). Relationships between fisheries or shrimp catch and the presence or extent of nearby mangroves are therefore unlikely to result from a direct trophic link, but rather from the effects of other factors such as the provision of a suitable nursery habitat, refuge from predators, or the provision of other food sources besides mangrove litter (see Sections 5, 8, and 10). The contribution of mangrove-derived organic matter in adjacent systems also appears to vary according to the environmental setting and geomorphology of the system, being more important in riverine/estuarine systems than in lagoon or island settings (Pineda, 2003).

Despite the evidence that mangroves are far less important as a food source for aquatic faunal communities than previously assumed, the assumption that they sustain intertidal food webs has endured much longer, and is often taken for granted. A number of prominent mangrove-dwelling species are indeed known to remove and consume leaf litter, in particular sesarmid crabs (e.g., Lee, 1998) and species such as the crab *Ucides cordatus* (Nordhaus et al., 2005) and the gastropod *Terebralia palustris* (Slim et al., 1997). Subsequently, there is a wealth of literature on the impact of mangrove invertebrates on litter dynamics, and on feeding experiments involving various species of mangrove tree leaves or their state of senescence (see Lee, 1998, for references). The amount of literature exploring the trophic importance of other primary producers, in contrast, is far more limited. The general view emerging from recent studies is that, although faunal communities may have a profound impact on litter dynamics (Lee, 1998; Kristensen et al., 2008), the role of mangrove litter in sustaining epibenthic communities is often fairly limited, and decreases when systems are more open with respect to material exchange with adjacent systems (Bouillon et al., 2004).

9.2. Importance of other carbon sources

When a variety of food sources are available, mangrove fauna show a remarkable diversity in their resource utilisation patterns of the different sources, with different faunal groups each occupying a different trophic niche (Bouillon et al., 2002). Sesarmid crabs, considered to be key consumers of fallen litter, generally show the highest degree of dependency on mangrove carbon in comparison to other faunal taxa. However, in systems where other inputs are considerable, certain species, and in particular juveniles, show a high reliance on imported material and microphytobenthos (Bouillon et al., 2004). Moreover, several studies have indicated that mangrove litter alone would not suffice to meet the nitrogen requirements of sesarmids (Skov and Hartnoll, 2002; Thongtham and Kristensen, 2005). In contrast to sesarmids, fiddler crabs (*Uca* spp.) which are also typically highly abundant in mangrove systems rely mainly on microphytobenthos (France, 1998; Meziane et al., 2002). Other important groups of brachyuran crabs in mangrove systems are known to feed to an important extent on macroalgae (e.g., certain *Metapograpsus* spp.: Dahdouh-Guebas et al., 1999) or forage on other fauna (e.g., *Epixanthus* spp., *Scylla* spp.: Dahdouh-Guebas et al., 1999; Bouillon et al., 2004). Molluscs constitute the second major group of mangrove epifauna, and show equally diverse feeding preferences. This includes grazing on epiphytic algae on tree trunks or pneumatophores (e.g., *Onchidium* spp. and *Littoraria* spp.: Christensen et al., 2001; Lee et al., 2001; Bouillon et al., 2004), utilising surface organic matter and microphytobenthos (e.g., *Assiminea* spp. and *Cerithidea* spp.: Bouillon et al., 2004), selective or unselective filter-feeding on suspended matter (for a number of bivalves: Bouillon et al., 2004), and consuming mangrove leaf or propagule litter (*M. coffeus*: Proffitt and Devlin, 2005). In addition, some molluscs have particular adaptations, such as wood-boring shipworms (*Teredinidae*) which harbour symbiotic bacteria capable of N_2 fixation to supplement their N-poor diet (see Bouillon et al., 2002), and sacoglossan seaslugs, some of which retain functional chloroplasts from their food algae (‘kleptoplasty’: see Bouillon et al., 2008). Previous studies have likely been biased towards more conspicuous groups of fauna, with much less attention to infauna and meiofauna, where recent results suggest that a variety of chemo-symbiotic relationships exist in reduced mangrove sediments (see Bouillon et al., 2008). An integrated view of the importance of different primary sources for consumers, or of the quantitative impact of mangrove fauna on material processing, is still lacking, due to the absence of solid combined datasets on feeding preferences and secondary production or consumption rates. Moreover, there is likely no general ‘mangrove food web’ and the importance of various sources and the impact of fauna on organic matter turnover will significantly depend on the environmental settings and the faunal community composition.

A number of exclusion/inclusion experiments carried out in mangrove systems demonstrate that the presence and activity of macro-epifauna (e.g., gastropods, ocypodid crabs) cause a significant modification of the benthic habitat. The exclusion of fauna may increase the micro-epiphytic biomass due to the absence of grazing (Branch and Branch, 1980; Kristensen and Alongi, 2006) and indirectly cause a modification of meiofaunal communities (Schrijvers and Vincx, 1997; Schrijvers et al., 1998; Carlén and Ólafsson, 2002). Such studies are scarce for mangrove systems, but offer a valuable alternative perspective on trophic interactions and on the mechanisms structuring mangrove faunal communities.

9.3. Linkages with adjacent systems

An important issue in the ecological and habitat function of mangroves is the importance of mangrove areas as feeding habitats for mobile or visiting fauna (Fry and Ewel, 2003). A number of studies suggest that mangroves can provide an important feeding habitat for foraging fish or prawns during high tide, based on observational evidence, gut content analyses, and stable isotope evidence.

For certain mangrove fish species, the importance of predation on mangrove food sources, such as sesarmids and other invertebrates, has been indicated by a number of studies (e.g., Sasekumar et al., 1984; Thong and Sasekumar, 1984; Wilson, 1989; Sheaves and Molony, 2000; Lugendo et al., 2006). The accessibility of the intertidal zone and its potential role as a refuge or feeding habitat is constrained by the tidal regime and system characteristics (Sheaves, 2005; Lugendo et al., 2007b). Lugendo et al. (2007b) showed that feeding by fishes within mangroves is more common when they are permanently accessible than when they are only temporarily accessible due to the tidal regime. Nagelkerken and van der Velde (2004a) and Verweij et al. (2006b) demonstrated that the majority of fish species from a Caribbean mangrove–seagrass–reef system derived little or no food from the mangrove habitat, even though they were permanently inundated, which is consistent with the relatively low tidal amplitude in this region. A probable cause is that Caribbean island mangroves are narrow fringes which provide excellent shelter habitat but little food (Nagelkerken et al., 2000a). As a result, fish that shelter there during the daytime migrate to adjacent seagrass beds at night for most of their feeding activities, while the same species sheltering in seagrass beds derive their food entirely from within that habitat (Nagelkerken and van der Velde, 2004b; Nagelkerken et al., 2006).

9.4. Modelling mangrove food webs

The lack of basic data on the origin of organic matter sustaining different faunal communities is also propagated in modelling approaches to describe the food web structure and energy flows in mangrove systems. A number of studies (e.g., Manickchand-Heileman et al., 1998; Ray et al., 2000; Wolff et al., 2000; Vega-Cendejas and Arreguín-Sánchez, 2001) have used a network analysis approach, typically using Ecopath software (Christensen and Pauly, 1992) to construct an integrated view on energy flow in mangrove systems. While this approach has its own merits and, moreover, has the potential to be an excellent tool to estimate the potential effects of ecosystem changes on overall energy flow, the input data for such models require solid knowledge on the feeding habits of critical ecosystem components. It is worth noting that, while recent studies stress the importance of microphytobenthos and allochtonous carbon sources to intertidal food webs, current models (cited earlier) have not included microphytobenthos in their analyses. The assumption that mangrove litter or mangrove-derived detritus represents the dominant food source for certain major groups of fauna (e.g., fiddler crabs; Wolff et al., 2000) is likely to significantly bias model output, since tracer studies indicate that mangrove-derived carbon contributes only marginally to these organisms' diets (e.g., France, 1998; Meziane et al., 2002; Bouillon et al., 2004). Such bias is inevitably transferred to higher trophic levels. In this context, there is clearly a need for more synergy between specific tracer studies, experimental field studies on trophic interactions, and trophic models in order for these modelling efforts to generate more realistic outputs, and for results from other approaches to generate more added value.

10. Mangroves as drivers of nearshore fishery production

10.1. The role of mangroves and estuaries in relation to fisheries

Over the last four decades, many studies have demonstrated a strong relationship between mangrove presence and fish catch (Turner, 1977; Yáñez-Arancibia, 1985; Pauly and Ingles, 1986; Lee, 2004; Manson et al., 2005; Meynecke et al., 2007), with fishery catch being influenced by the relative abundance of mangroves in a region. Correlations have also been found between the extent (area or linear extent) of mangroves and the catches of prawns (particularly banana prawns) in the fisheries adjacent to the mangroves (Turner, 1977; Staples et al., 1985; Pauly and Ingles, 1986; reviewed in Baran, 1999). Such studies provided important information on the fisheries–mangrove relationship and were the base for economic valuation of mangroves (e.g., Barbier and Strand, 1998; Grasso, 1998; Barbier, 2000). This observed relationship mainly derives from a group of economically important species classified as estuarine-dependent (Cappo et al., 1998) or (non-estuarine) bay-habitat-dependent (Nagelkerken and van der Velde, 2002). Mangroves, or similar environments, are the principal habitat for at least one part of their life cycle (Blaber et al., 1989; Nagelkerken et al., 2000b). Typically, the adults spawn offshore, producing eggs that disperse in the water column for varying lengths of time. The eggs then develop into planktonic larvae which move, or are carried by currents, into inshore and estuarine waters. The subadults or adults migrate out of the estuary or lagoon, and back towards the offshore areas or adjacent coral reefs. Therefore, mangroves could function as an important link in the chain of habitats that provide complementary resources and benefits, e.g., as nursery areas for fish, prawns and crabs (Sheridan and Hays, 2003; Crona and Rönnbäck, 2005), with spatial complexity at a scale that provides refuge to small prey, and abundant food for commercial species at certain stages in their life cycle (Chong et al., 1990).

10.2. Controversy in the literature: nursery ground and outwelling

Opinions vary as to the importance of mangrove habitats to fish and, by extension, to nearshore fisheries (Blaber et al., 1989; Thollot, 1992). Although, studies have documented greater abundances of juvenile species in mangroves than in other estuarine and inshore habitats (Robertson and Duke, 1990a; Nagelkerken and van der Velde, 2002), other studies found a significant contribution by saltmarshes (Connolly, 1999). Controversy also surrounds the measurement of nursery ground values (Sheridan and Hays, 2003). Beck et al. (2001) and Adams et al. (2006) gave a detailed discussion of the nursery habitat concept, where the value of nursery grounds is measured in terms of numbers contributed to adult populations: either the average number of individuals per unit area (Beck et al., 2001) or the total number of individuals per habitat (Dahlgren et al., 2006; see also Layman et al., 2006), in an attempt to simplify the measurement of nursery function and to identify core components (e.g., habitats) that are most important in maintaining overall ecosystem function. Sheaves et al. (2006) argued that this approach is oversimplistic and relates to the value of a nursery from a short-term, fisheries perspective. It is important to develop a better understanding of habitat connection and how these connections can be maintained (Meynecke et al., 2007).

The discussion about the importance of tidal wetlands for fisheries includes the debate on the passive transport of dissolved and particulate nutrients and detritus from productive tidal wetlands to coastal and offshore waters, termed 'outwelling'. Outwelling was considered critical in supporting the secondary production of many coastal fisheries (Nixon, 1980). The transport of nutrients between estuarine and coastal systems is now recognised as a complex and dynamic process (Ford et al., 2005; Webster et al., 2005), and the general model of outwelling appears too simplistic (Kneib, 1997; Ford et al., 2005; see also Section 9). Recent studies using stable isotope analysis and other trophic tracers indicated that offshore fisheries may not be driven through the outwelling of nutrients from estuaries (Loneragan et al., 1997; Connolly, 1999; Chong et al., 2001; Melville and Connolly, 2003) and that, for example, mangrove-derived nutrients only contribute directly to the food webs of some animals within highly restricted areas, e.g., mangrove-lined creeks (Loneragan et al., 1997). Separating the contribution from mangroves, seagrass and salt marshes using casually deployed tracers, such as natural abundance stable isotope analysis, is still problematic since benthic and pelagic organisms seem to rely on different mixes of organic matter sources.

10.3. Studies linking fish catches with mangroves and estuaries

The most direct approach to search for links between mangroves and fisheries is to use fish catch data in comparison with mangrove or estuarine parameters. Manson et al. (2005) found a significant influence of mangrove forest characteristics (e.g., perimeter and area) on mangrove-related and estuarine fishery species, while latitude was the only variable influencing catch of offshore species along the north-eastern Australian coast. The earliest studies in this field were completed by Macnae (1974) who showed that inshore fish production in Malaysia was related to mangrove area. Turner (1977) found a positive correlation between penaeid shrimp catches and the vegetated surface area of estuaries in the Gulf of Mexico. Martosubroto and Naamin (1977), working in Indonesia, showed a positive correlation between annual fish landings and mangrove area. They implied that a certain minimum mangrove area is necessary for high production, a point also noted by Pauly and Ingles (1986) who suggested that the impact of destroying a mangrove area might be greater if the area is small and residual. A review of literature (Baran and Hambrey, 1998) demonstrated the dependence of fish harvests on estuarine environments, and showed the importance of these systems in terms of sustainable management of the coastal resource. Rönnbäck (1999) and Barbier (2000) identified and synthesised ecological and biophysical links of mangroves that sustain seafood production from an economic perspective, and Manson et al. (2005) tried to go beyond the correlative approach and developed a new framework on which evaluations can be based.

The review presented here found a total of 27 studies comparing commercial catch with estuarine habitats, in particular mangroves in tropical and subtropical zones, over the last four decades. Most of the analyses in these studies have resulted in positive correlations, assuming that the area of mangroves or tidal wetland habitat directly translates to the catch of commercial fisheries (Manson et al., 2005; Meynecke et al., 2007). Estimates of the amount of commercial catch explained by the presence of mangroves or estuaries range from 20 to 90% (Fig. 1). The most common variables used were mangrove area, followed by linear extent and intertidal area or estuarine size. Over 15 studies used mangroves as a proxy and seven studies used the extent of estuaries, coastal vegetation or shallow water. Most studies were undertaken in Australia, Asia and the U.S.A., whereas West Africa and South America were under-represented (see also Faunce and Serafy, 2006, in their review on mangroves–fish studies). Estimates in studies covering worldwide tropical commercial catch range between 21% (Houde and Rutherford, 1993) and 30% (Naylor et al., 2000) for an estuarine–fish catch relationship, 38% for a mangrove–prawn catch relationship (Lee, 2004), 53% for a mangrove area–fish catch relationship (Pauly and Ingles, 1986), and 54% for an intertidal wetlands–prawn catch relationship (Turner, 1977).

Depending on species, location and time scale, the relationships between commercial catch and mangroves vary largely, indicating that the link is more complex than a linear function. The predictors used in the regression analyses are themselves strongly correlated, and catch statistics are often not well delineated. There is high variation within the data sets (mangrove forest distribution, commercial records, effect of stock size and fishing pressure) and difficulty in distinguishing links against a background of highly variable temperature, rainfall, ocean currents, and fishing effort.

On the other hand, estuarine or lagoonal habitats and the strong links between them have been neglected in past studies (Sheridan and Hays, 2003). A certain combination of habitats and their accessibility is likely to explain the importance of estuaries to nekton (Cappo et al., 1998). Evidence is mounting that permanently inundated fringing mangroves in the Caribbean primarily serve as daytime refugia for a major component of fishes occupying various habitats in lagoons or bays (Nagelkerken et al., 2000a; Valdés-Muñoz and Mochek, 2001), while fishes from adjacent habitats feed in large intertidal mangroves at high tide (Sheaves, 2005; Lugendo et al., 2007b). This suggests for some species that fish production attributed to mangroves may not necessarily be derived from this habitat alone. Evidence exists, for example, that fish abundance and species richness are higher when mangroves and seagrass beds occur together rather than in isolation (Robertson and Blaber, 1992; Nagelkerken et al.,

Fig. 1. World map showing the percentage of commercial fish catch explained by either mangroves or estuarine presence from 27 reviewed studies of which 22 provided quantitative data for this linkage. For countries where more than one study was conducted the conservative number has been chosen for display (for a detailed listing see Manson et al., 2005; Meynecke et al., 2007).

2001; Dorenbosch et al., 2006a,b; Jelbart et al., 2007). Many fish species occupying lagoons appear to show ontogenetic fish movements between seagrass beds, tidal channels and mangroves (Rooker and Dennis, 1991; Nagelkerken et al., 2000c; Nagelkerken and van der Velde, 2002, 2003; Eggleston et al., 2004; Lugendo et al., 2005), making the individual contribution of mangroves difficult to determine (Adams et al., 2006).

Worldwide, most studies on mangrove fish communities and their linkages with offshore fisheries have been done in estuarine mangrove systems (Nagelkerken, 2007). However, there are hundreds to thousands of small islands in the Caribbean and Indo-Pacific which only harbour non-estuarine mangroves located in marine embayments and lagoons. Although their surface area is mostly much smaller than that of large estuarine mangrove forests, they may be important on an island scale for coral-reef associated fisheries. Only in this millennium have studies started focusing in more detail on the connectivity between non-estuarine mangroves (and seagrass beds) and adjacent coral reefs with regard to fish movement (Nagelkerken, 2007), mostly based on multiple habitat density comparisons using a single census technique and distinguishing between fish size classes. This has resulted in the identification of several (commercial) reef fish species which appear to depend on mangroves while juvenile (e.g., Nagelkerken et al., 2000b,c; Cocheret de la Morinière et al., 2002; Christensen et al., 2003; Serafy et al., 2003; Eggleston et al., 2004; Dorenbosch et al., 2007). Studies comparing reef fish communities near and far from mangrove habitats, and with the presence or absence of island mangroves, have shown that the dependence on mangroves is species-specific, but appears to be high for various reef species (Nagelkerken et al., 2000b, 2001, 2002; Mumby et al., 2004; Dorenbosch et al., 2004, 2005, 2006a,b, 2007). Otolith microchemistry studies have also suggested a linkage between mangroves and coral reefs (Chittaro et al., 2004). Mumby (2006) developed algorithms to describe various aspects of mangrove–reef connectivity that can be used for management purposes.

Future investigations of tidal wetlands–fisheries links, should be based on an understanding of connectivity and should use standardised data collection. More research is required documenting the natural temporal and spatial variability of assemblages in fish habitats. Although there is no direct evidence of the fish catch–mangrove dependence, studies so far clearly infer a strong link emphasising the need to reverse the loss of mangroves and tidal wetlands (FAO, 2003) from both natural and anthropogenic causes.

11. Mangroves as habitats for amphibians and reptiles

Several independent evolutionary lines of reptiles and amphibians have successfully colonised, and are variously dependent on, mangrove ecosystems. These include frogs, marine and freshwater turtles, crocodilians, lizards, and marine and terrestrial snakes.

11.1. Frogs

Globally, little is known of the amphibian fauna inhabiting mangroves (Kathiresan and Bingham, 2001). Amphibians are generally intolerant of saline conditions found within mangroves, although many species are associated with estuarine habitats such as frog species from the genus *Eleutherodactylus* (Hedges and Thomas, 1992). Notable exceptions include the crab-eating frog *Rana cancrivora* from Southeast Asia that is adapted to salt water during all stages of its life cycle (Dunson, 1977), and *E. caribe* which is unique among species in the genus by inhabiting the flooded, *Rhizophora mangle*-dominated mangrove habitat of the Tiburon Peninsula of Haiti in the Caribbean (Hedges and Thomas, 1992).

11.2. Turtles

Freshwater turtles are known to inhabit estuaries, but little is known of their specific habitat requirements. The mangrove terrapin *Batagur baska* (from Central and Southeast Asia), and the painted terrapin *Callagur borneoensis* (from the Sundarbans, Bangladesh) are large freshwater chelonians that are known to inhabit tidal creeks and rivers (Blanco et al., 1991). Both species are listed as critically endangered and rely on riparian vegetation, including mangrove fruit, as a food source (IUCN, 2006; UNEP-WCMC, 2007). *Callagur borneoensis* nests on ocean beaches and the hatchlings have to swim through seawater to reach the river mouths; however, they are not physiologically adapted to the high water salinity in estuaries for extended periods (Dunson and Moll, 1980).

Five species of marine turtles have global distributions in tropical and temperate waters ranging from the lower reaches of estuaries to oceanic/pelagic habitats, while two species have relatively restricted ranges: the flatback turtle *Natator depressus* is endemic to the Australian-New Guinea continental shelf (Limpus and Chatto, 2004), and the Kemp's ridley turtle *Lepidochelys kempii* is restricted to the warm temperate zone of the North Atlantic Ocean (Bowen et al., 1997). Marine turtles occupy different habitats at different stages of their life cycle: natal beaches, mating areas, inter-nesting habitat, feeding areas and pelagic waters (EA, 2003). Juvenile movements in neritic developmental habitats are little known compared to adult reproductive migrations. There is also a lack of knowledge of life history and habitat requirements away from nesting beaches. Habitat selection may be significantly influenced by biotic factors such as the availability and/or quality of food or the co-occurrence of predators. In nearshore waters, abiotic factors such as tidal flux, water temperature and depth, salinity and turbidity may influence the occurrence of marine turtles via direct (physiological tolerance) or indirect (effects on prey or predators) mechanisms (EA, 2003). Habitat quality for *L. kempii* in the nearshore waters of the north-western Gulf of Mexico was influenced by water temperature and depth, salinity, dissolved oxygen and turbidity, which influenced the distribution and abundance of predators and prey (Metz, 2004). In general, there is a lack of detailed studies of the habitat requirements of in-water life history stages of marine turtles (Metz, 2004).

Many animals alter their movements and home range in relation to the particular type and quality of the habitat occupied. Fidelity of marine turtles to foraging areas has been demonstrated in several studies (Limpus and Limpus, 2000; Godley et al., 2002). Green turtles (*Chelonia mydas*) have a pelagic existence for the first 3–5 years, after which they recruit to coastal waters and occupy a series of developmental habitats, including mangroves, until sexual maturity (Makowski et al., 2005). These movements coincide with an ontogenetic dietary shift from an omnivorous to a herbivorous diet including *Avicennia marina* fruit (Pendoley and Fitzpatrick, 1999), cotyledons and propagules (Limpus and Limpus, 2000; H.M. Penrose, unpublished data). Indirectly, mangroves can provide a food source for marine turtles by providing habitat for macroalgae that grow on roots, trunks (Cribb, 1996) and pneumatophores (H.M. Penrose, unpublished data). *Rhizophora mangle* is also known as a developmental foraging ground for Kemp's ridley turtles in the coastal waters of their range (Schmid, 2000). Despite a paucity of data, evidence suggests that mangroves are important to marine turtles and further research is needed to determine species-specific differences in mangrove use in a range of environmental settings.

11.3. Crocodilians

The 23 extant crocodilian species (crocodiles, alligators, caimans and gharials) are integral components of aquatic, wetland and marine/estuarine ecosystems in tropical and subtropical regions, with most species requiring large areas of undisturbed habitat to maintain viable populations (Hutton and Webb, 1990). The relative importance of mangroves as a habitat for crocodilians, compared with other habitats, is variable, due to the wide diversity in their biology and ecology. However, as nurseries for fish and other marine animals on which crocodilians feed, mangroves provide an abundance of food sources at all life history stages. The estuarine crocodile *Crocodylus porosus* is one of the most notable species associated with mangroves. Generally, *C. porosus* do not nest in mangroves but are found nesting in vegetation fringing mangrove areas (Webb et al., 1977; Magnusson, 1980; Webb et al., 1983). However, the indirect importance of mangroves for *C. porosus* has been demonstrated in Sri Lanka where the decline of this species is linked to an increase in coastal runoff due to clearing of mangrove trees, resulting in the destruction of crocodile nests and eggs (Santiapillai and de Silva, 2001). Prop-roots of *Rhizophora* spp. are also known to provide an important structural refuge for hatchlings (Santiapillai and de Silva, 2001).

11.4. Lizards

Many lizard species, ranging from geckos to iguanas, are known to inhabit intertidal mangrove forests. Some lizards are terrestrial species that enter mangroves on an opportunistic basis to access resources, whereas others live a semi-aquatic existence, with the monitor lizards *Varanus* spp. being the most notable. The rusty monitor *Varanus semiremex*, which is restricted to the east coast of Queensland, Australia, are particularly dependent on *Avicennia marina*, utilising hollow limbs of living mature as well as dead trees (Wilson and Knowles, 1988).

11.5. Snakes

Pythons (*Python morolus*) and king cobras (*Ophiophagus hannah*) make opportunistic movements from terrestrial to intertidal mangrove habitats to feed (Macintosh and Ashton, 2002). Some sea snakes (family Hydrophiidae) access mangroves during high tide, whereas others, such as the 'primitive' *Ephalophis greyae* of Western Australia, which has retained its terrestrial mode of locomotion, undertake foraging migrations across the dry mangrove substrate during low tide in search of gobiid fish (Storr et al., 1986; H.M. Penrose, unpublished data). Other snake species rely on mangrove trees as a physical habitat structure, such as *Myron richardsonii* that is endemic to Northern Australia (Guinea et al., 2004), and *Boiga dendrophila* of Southeast Asia and Australia, both members of the family Colubridae (Macintosh and Ashton, 2002). The structure of snake communities in the mangroves of south-eastern Nigeria was described by Luiselli and Akani (2002). Eighteen snake species were recorded in mangroves, whereas 43 species inhabited neighbouring habitats (rainforest and forest-plantation mosaics). Of these 18 species, 50% were arboreal, 22% terrestrial, 11% terrestrial–arboreal, 11% semi-aquatic, and 6% described as very generalist. Species preyed on a wide range of organisms including lizards, birds, bird eggs, frogs, mammals and fish. The relative frequency of the African rock python *Python sebae* in the mangroves, compared with other habitats, suggest that mangroves may represent an important refuge or dispersal corridor for this threatened species. Luiselli and Akani (2002) highlight the need for further research on the rich diversity of the high trophic level arboreal snake species, and the preservation of the habitat mosaics within mangrove creeks, where the great majority of snakes are found.

12. Mangroves as habitats for birds

Mangrove habitats play host to a moderate number of bird species around the globe. Most diverse are the Queensland mangroves of Australia which host 186 bird species (Noske, 1996). Other counts are 135 in Peninsular Malaysia (Nisbet, 1968), 125 in Guinea-Bissau, West Africa (Altenburg and van Spanje, 1989), 104 in north-western Australia (Noske, 1996), 94 in Surinam (Haverschmidt, 1965), and 84 in Trinidad (Ffrench, 1966). The forests are strongly zoned with few tree species and a sparse understory producing a simple vertical profile.

When considering the bird faunas of these and other mangrove habitats around the globe, it is interesting to speculate on the sources of the species that make up these communities. To what extent have mangrove forests played the role of independent sites of species diversification, to what extent have they been recipient habitats, and to what extent have they been the source of colonists for other habitats? What ecological forces may have driven these processes? This suggests a way to review the avifauna of mangroves, namely those that have a tolerance for a narrow range of habitats (stenotopic species), mangrove invaders, and mangrove species that move out into other habitats.

12.1. Mangrove specialists

The first interesting observation is that there are few true mangrove specialists. No African species has been found to be exclusively mangrove-dependent, the closest being the insectivorous sunbird *Anthreptes gabonicus* which is found in mangroves but also in riverine woods hundreds kilometres inland. Mangrove habitats in Surinam host 94 bird species, while in Trinidad these habitats support 84 bird species. Only one species, the rufous crab–hawk (*Buteogallus aequinoctialis*) is restricted there to mangrove habitats (Haverschmidt, 1965; Ffrench, 1966). In north-western Australia, 16 of 104 species are more or less confined to mangroves, in eastern Australia, 9 of 106. Just 11 species are mangrove-dependent there, namely great-billed heron *Ardea sumatrana*, striated heron *Butorides striata*, chestnut rail *Eulabeornis castaneoventris*, collared kingfisher *Todiramphus chloris*, mangrove robin *Peneoenanthe pulverulenta*, kimberley flycatcher *Microeca flavigaster tormenti*, white-breasted whistler *Pachycephala lanioides*, dusky gerygone *Gerygone tenebrosa*, yellow silver-eye *Zosterops lutea*, red-headed myzomela *Myzomela erythrocephala*, and mangrove honeyeater *Lichenostomus fasciogularis*.

In Peninsular Malaysia, Wells (1999) cites nine species (brown-winged kingfisher *Pelargopsis amauroptera*, ruddy kingfisher *Halcyon coromanda*, greater goldenback *Chrysocolaptes lucidus*, mangrove pitta *Pitta megaryncha*, black-hooded oriole *Oriolus xanthornus*, great tit *Parus major*, dusky warbler *Phylloscopus fuscatus* (a non-breeding visitor), mangrove blue flycatcher *Cyornis rufigastra*, and copper-throated sunbird *Leptocoma calcostetha*) that depend exclusively on mangrove forests, or mangrove forest out to an immediate fringe of Nipa palm swamp or strand or plantation woodland. Three others (great-billed heron *Ardea sumatrana*, great egret *Ardea alba*, and milky stork *Mycteria cinerea*) depend on it exclusively for nesting but feed elsewhere. Grey heron *Ardea cinerea*, striated heron, and black-crowned night heron *Nycticorax nycticorax* now also breed inland. Only the brown-winged kingfisher, mangrove pitta, and copper-throated sunbird are global mangrove specialists. In regions outside the peninsula some of these specialists use other habitats. Ruddy kingfishers and great tits inhabit inland forests in Thailand, and the laced green woodpecker enters inland forest north of latitude 60°N. The fact that none of these birds has invaded inland non-forest habitats suggests that the peninsular populations have become specialised for mangrove habitats. The abundant, mainly frugiverous, families of adjacent dipterocarp evergreen forest are conspicuously rare, namely babblers, barbets, bulbuls, leafbirds, hornbills, and pheasants.

12.2. Mangrove invaders

In some cases, species may be better adapted to non-mangrove habitats but use mangrove either because their preferred habitats are not available locally, or because some mangrove forests provide marginal habitat for some individuals whose principal populations occupy other adjacent forest habitats. Wells (1999) analysed the species origins of the birds in mangroves of Peninsular Malaysia, where inland forests once abutted with mangrove trees over long stretches of the coast until well into the 20th century. Around one-third of the avian mangrove community (mainly kingfishers, sunbirds, warblers and woodpeckers) is shared with its former inland forest habitats which may indicate how marginal mangroves were for at least some of the inland forest species that used their back zone. Leafbirds, broadbills, giant woodpeckers, and others formerly reported in the mangroves are now scarce or absent. Wells (1999) suggested that if more of the interface between mangroves and inland forests had been explored before the interface had been destroyed, more shared species may have been found in the mangroves. The same may be true in Western Australia, where the proximity of mangroves and so-called vine forests may maintain species in mangroves (Noske, 1996).

Given the nature of some current mangrove specialists, it seems likely that mangroves were attractive for some open-forest adapted species. The latter habitats would have been much drier during the Pleistocene glacial periods, while the mangroves were probably more extensive providing an essential refuge for birds from shrinking open forests. Noske (1996) cites the existence of mangrove specialists such as mangrove fantail *Rhipdura phasiana*, broad-billed flycatcher *Myiagra ruficollis*, kimberley flycatcher, mangrove gerygone *Gerygone levigaster*, and mangrove honeyeater, species with relatives in these open forest regions, and even inland regions. However, given the huge linear continuity of continental mangrove forests, it is almost impossible to guess where any particular specialist originated.

12.3. Species that move out to non-mangrove habitats

Some scientists suggest that the mangrove assemblage is an exporter of bird species to non-forest habitats. This assumption is based on the birds having niches that developed in an environment of low plant species diversity, itself derived from instability of the habitat over various time scales. This, in turn, results in a relatively simple structure and reduced niche space. Bird species niches are broad enough to predispose mangrove birds to simplicity and instability elsewhere (Noske, 1995; Ward, 1968). Noske (1995) revealed that certain groups (woodpeckers, passerines) found both in mangroves and non-forest habitats have narrower niches than those species that still live exclusively within the mangroves, perhaps because of competition once outside the mangrove habitat, or because the simplicity of the mangroves precluded such specialisation.

Ward (1968) remarked how mangroves have contributed many bird species to rural and urban habitats in Peninsular Malaysia, and suggested that this may be due to the simple floristic and habitat structure shared by mangroves and these anthropogenic habitats. Broad niches and tolerances by mangrove bird species may enable them to exploit these newer habitats. Noske (1995) related broad niches of mangrove bird species to fluctuations in food availability driven by tidal cycles. He interpreted the absence of colonisation of Australian urban and exurban habitats by mangrove bird species as being a consequence of the sharp contrast between the stable, evergreen, fire-protected mangroves, and the highly seasonal, deciduous, and fire-prone savannas that abut them. An alternative explanation could be that such savannas never were empty of species as the suddenly deforested sub-coastal lowlands of Peninsular Malaysia, which provided the opportunity for colonisation (D.R. Wells, personal communication).

As a rule, most bird species found in mangroves are also found in other habitats, but how would we tell in which direction colonisation took place: into or out of mangroves? We know that most of the West African mangrove bird species in Guinea-Bissau were more common in adjoining forests and rice fields. Some use the mangrove for roosting only (Altenburg and van Spanje, 1989), and in Peninsular Malaysia 46 residents and at least 6 non-breeding visitors to mangroves also occur in 1 or more of the original inland forest formations (Wells, 1999). Some kinds of birds, such as aerial insectivores (nightjars, tree swifts, rollers, swallows), may nest in mangroves but feed over a wider range of habitats while others (white-vented myna *Acridotheres javanicus*, java sparrow *Lonchura oryzivora*) may nest in mangroves but never feed there (Medway and Wells, 1976).

Almost as many bird species that we now find in mangroves can also be found in open coastal areas, agricultural, and urban areas that meet the truncated mangrove succession inland. In Australia, the floristically rich north-eastern mangroves have fewer mangrove specialist bird species than the north-western mangroves, though it is unclear why. Mangrove habitats may have remained widespread during the Pleistocene glacial periods when rainforests may have contracted to small patches, providing places for many of the rainforest species to survive, and then have been a source for re-populating re-expanding rain forests.

12.4. Synthesis

The most intriguing insights of the role of mangroves for bird communities come from a consideration of mangroves in their broader context, namely their relationships with other habitats, both current and historic. We should also ask why there are so few true mangrove specialists. It is interesting to speculate on what current species may tell us about past habitat relationships. What roles may mangroves have served as stable habitats during times of climatic change in the past? We do not have an accepted model of how mangrove forest might have behaved in response to sea-level changes. While one can envisage the mangrove system extending seaward as sea levels fall, observation shows that a simple change in local long-shore currents can eliminate the forest, while a rising sea level would probably reduce mangroves. So what was the distribution and availability of mangroves in the past? How did changes in mangrove availability push species out into non-mangrove habitats? We can imagine a scenario where mangroves change sequentially from becoming refugia for drying forests to expellers of birds as they shrink with rising sea levels, and a resulting two-way flow of species into and out of these habitats over time.

It is not clear to what extent mangrove forests support relict populations. Noske (1995) reports that one of his transects in Malaysia still retained small areas of original back-mangrove forest, and several decades after the link with inland forest was broken this still contained a few ‘inland forest’ birds, such as velvet-fronted nuthatch *Sitta frontalis*. Bird species of adjacent inland habitats, and those habitats formerly adjacent before their destruction, use mangroves in different ways.

As one would predict, the greatest bird species diversity occurred in the more plant-species diverse back-mangrove zones, where colonisation of the mangrove from the inland species once occurred, and where it interfaces with habitats inland (Wells, 1999). Nisbet (1968) suggested that the current scarcity of overlapping forest bird species in the mangroves of Peninsular Malaysia is the result of the near-total clearance of the transition zone between mangrove and inland forests. Some formerly widespread species of this zone, such as the giant woodpeckers, have all but disappeared from their mangrove haunts. Noske (1996) suggested that the relatively small number of mangrove bird specialists in Peninsular Malaysia resulted from long historical and continuous contact between mangrove and other forest habitats and so no geographical block to gene flow was present. However, Peninsular Malaysia has more species than West Africa and Surinam. This could in turn be explained by the direct contact of its mangrove ecosystem with that of the rest of tropical Asia, acting as a corridor for immigrants from outside rather than by generation of species from within the habitat.

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