

Managing mangroves with benthic biodiversity in mind: Moving beyond roving banditry

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Abstract

This review addresses mangrove management activities in the broader context of the diversity of the mangrove benthos. Goals for mangrove ecosystem management include silviculture, aquaculture, or ‘ecosystem services’ such as coastal protection. Silvicultural management of mangroves generally neglects the benthos, although benthic invertebrates may affect tree establishment and growth, and community composition of benthic invertebrates may be a reliable indicator of the state of managed mangrove forests. Similarly, mangrove aquaculture focuses on particular species with little attention paid either to impacts on other trophic levels or to feedbacks with the trees. Exploitation of mangrove-associated prawns, crabs, and molluscs has a total economic value >US \$4 billion per year. These aquaculture operations still rely on wild-collected stock; world-wide patterns of exploitation fit the well-known process of ‘roving banditry’, where mobile agents move from location to location, rapidly exploiting and depleting local resources before moving on to other, as-yet unprotected grounds. Collection of brood stock and fishing for other external inputs required by aquaculture (e.g., ‘trash fish’) removes intermediate trophic levels from marine food webs, may destabilize them, and lead to secondary extinctions of higher-order predators. Increased attention being paid to the role of mangroves in coastal protection following the 2004 Indian Ocean tsunami provides an opportunity to reassess the relative merits of management focused on short-term economic gains. Managing for ecosystem services may ultimately preserve benthic biodiversity in mangrove ecosystems.

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1. Introduction

Mangroves are salt-tolerant trees that grow on sheltered tropical coastlines throughout the world. These trees - ~70 species in ~27 genera and ~19 flowering plant families (Tomlinson, 1986) - once covered nearly 200 000 km² of riverbanks, estuaries, and seacoasts as well as carbonate sands and coral rubble islands (Ellison and Farnsworth, 2001). Their extraordinary high rates of

productivity, often exceeding 2 t ha⁻¹ y⁻¹, support both terrestrial and marine (both pelagic and benthic) food webs and contribute significant carbon to some offshore fisheries (Manson et al., 2005a,b). Mangrove forests significantly reduce coastal erosion and may provide protection from tropical cyclones and tidal waves (UNESCO, 1979; Danielsen et al., 2005). And like other forested ecosystems throughout the world, mangrove forests are disappearing at 1–2% y⁻¹ (Farnsworth and Ellison, 1997; Alongi, 2002). What are the consequences of this rapid deforestation for the biodiversity and management of the marine benthic fauna that is

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associated with mangrove forests for all or part of their life cycle?

Mangroves and non-timber products from mangrove ecosystems have been exploited for centuries (Watson, 1928; Biagi and Nisbet, 1992; Kathiresan and Bingham, 2001). Until the 1970s, management schemes focused almost exclusively on wood products, especially charcoal, lumber, and pulpwood, but by the 1980s, it was generally recognized by ecologists, fisheries scientists, managers and policy-makers that mangrove forests are tightly linked with adjacent ecosystems, and that managing them in isolation is unsustainable (Rao, 1987). Thus the 1992 Charter for Mangroves explicitly asserted that *[m]angrove ecosystems that are utilized by people shall be managed to achieve and maintain sustainable productivity without degrading the integrity of other ecosystems with which they coexist* (ISME, 1992). Despite this clarion call, degradation and outright destruction of mangroves has continued virtually unabated (Alongi, 2002). Although the 2003 global assessment of mangrove forests suggested a modest decline in their deforestation rates (Wilkie and Fortuna, 2003), this overall ‘improvement’ is due only to the substantial slowing of mangrove deforestation in two countries - Brazil and Pakistan - each of which had lost ~50% of their mangroves in the preceding decade (Fig. 1). Nonetheless, renewed optimism in the ability of people to manage mangroves was reiterated in 2005: *The fundamental objective of mangrove management is to promote conservation, restoration or rehabilitation and sustainable use of mangrove ecosystems and their associated habitats, supported where necessary by ecological restoration and rehabilitation* (World Bank et al., 2004).

In this review, I examine the consequences of ongoing mangrove forest loss for the diversity and sustainable management of the communities of the benthic invertebrates that are associated with mangroves. Some of these benthic invertebrates, such as tiger prawns and mud crabs themselves are exploited or managed for profits exceeding US \$4 Billion per year. Because our understanding of the distribution and ecology of the mangrove macrobenthos in general lags well behind our knowledge of mangrove forests, the impact of managing the mangrove macrobenthos for overall benthic biodiversity in mangrove ecosystems is largely unknown. I thus evaluate current knowledge on the biodiversity of the mangrove macrobenthos, and discuss whether or not we can manage, conserve, restore, or rehabilitate the mangrove macrobenthos and provide for their sustainable use. I also assess some of the broader consequences of managing the mangrove macrobenthos for mangrove-associated food webs. Throughout the text, I identify key

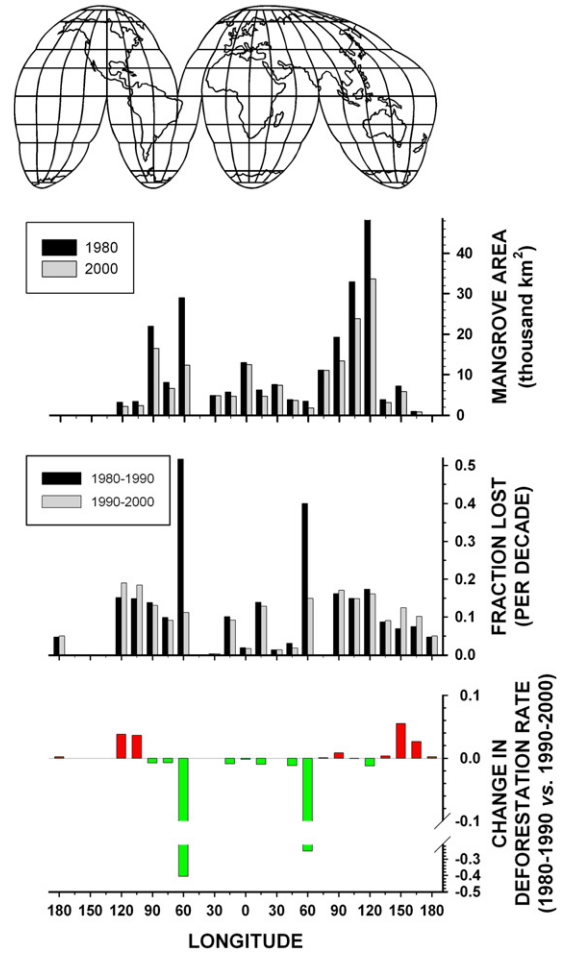


Fig. 1. Loss of mangroves 1980–2000. The **top** graph shows estimated mangrove area per 15° of longitude in 1980 (black bars) and 2000 (grey bars). The **middle** graph shows the fraction of mangroves area lost per 15° of longitude between 1980–1990 (black bars) and between 1990–2000 (grey bars). The two extreme values are Brazil, which lost 56% of its mangrove area between 1980 and 1990, and Pakistan, which lost 40% of its mangrove area in the same decade. The **bottom** graph shows the change in deforestation rate between the two decades. The value shown is the simple difference between deforestation rates 1990–2000 and 1980–1990. A positive value (shown in red) indicates a faster deforestation rate, and a negative value (shown in green) indicates a slower deforestation rate in 1990–2000 than in 1980–1990. All data are derived from 113 country-by-country summaries published by Wilkie and Fortuna (2003).

data gaps and priorities for research that are required before we can realistically conserve and sustainably manage the mangrove macrobenthos.

2. Biodiversity of the mangrove macrobenthos

The mangrove macrobenthos - those species that live in mangrove muds or depend on mangroves for all or

part of their life-cycle - encompasses a number of phyla, including Porifera (sponges), Mollusca (molluscs), Arthropoda (crabs, lobsters, prawns, etc.), Annelida (segmented worms), Nematoda (roundworms), Sipunculoidea (peanutworms), Platyhelminthes (flatworms), and ascidians within the Chordata. Although species inventories exist for some groups within each of these phyla in select mangrove ecosystems around the world, there exist comprehensive global data only for some gastropod molluscs and the major families of brachyuran crabs (Fig. 2). Although the taxonomy and nomenclature of the gastropods, especially the littorinids, are relatively stable, nomenclature and systematic relationships among the Brachyura are regularly revised. Bringing order to this chaos is needed to better quantify the impacts of mangrove loss and management of benthic species on overall benthic biodiversity.

Species richness of mangrove gastropods and brachyuran crabs parallel species richness not only of the mangrove tree species themselves (Lee, 1998), but also of the total area of mangrove forest in 1980; all of these metrics reach their maximum in the Indo-West Pacific (Fig. 3). Mangrove sponges have been enumerated only in the neotropics, in areas where tidal amplitudes <1 m permit the development of a species-rich fouling community on permanently submerged roots of *Rhizophora mangle* (Rützler, 1969; Sutherland, 1980; Farnsworth and Ellison, 1996). In the Caribbean Basin, species richness of mangrove-root fouling sponges is highly correlated with the area of mangrove forest (1980 data) at individual localities (Fig. 3). All these data suggest that both slowing deforestation rates and rehabilitating mangrove stands may limit loss of species in these three major benthic groups. Geographic coverage for other macrobenthic taxa is so sparse, and studies of lower taxa are so idiosyncratic that any global synopses would be premature and misleading. This is clearly an opportunity for future large-scale research.

3. Mangrove forest management and its effects on the benthos

3.1. History of mangrove forest management

Mangrove forest management has developed most extensively in Malaysia (the Matang mangroves in the state of Perak) and in the Sundarbans of Bangladesh. In these forests, the long-term goal has been to provide a consistent volume of extractable wood for timber, pulp, and charcoal production, primarily for local use. Outside of Malaysia and Bangladesh, the available data suggest that use of mangrove forests for forest products is best

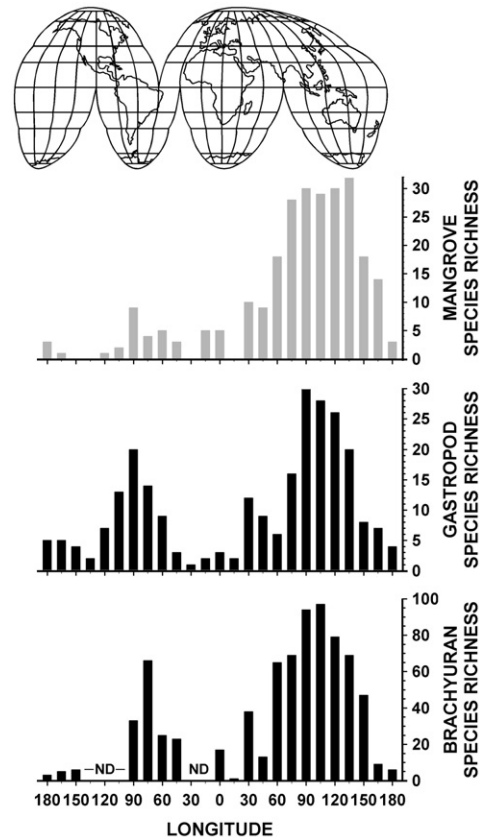


Fig. 2. Global species richness per 15° of longitude of mangroves, mangrove gastropods (in eight genera: *Littoraria*, *Pythia*, *Cassidula*, *Melampus*, *Ellobium*, *Cerithidea*, *Telescopium*, and *Terebralia*) and brachyuran crabs (in five families: Grapsidae [including Sesarminae and Varuninae]; Ocypodidae, Portunidae, Xanthidae, and Gecarcinidae). ND — no data available. Mangrove and gastropod data summarized from Ellison et al. (1999) and Reid (1986, 1999). Brachyuran data assembled from a variety of sources. The major references are Crane (1975), Davie (1982), Jones (1984), and Tan and Ng (1994). The complete list of sources and the raw data (species × site matrices) are available on request from the author.

described as ‘exploitation’ or ‘liquidation’ rather than as management, sustainable or otherwise (Wilkie and Fortuna, 2003; Walters, 2004).

An objective analysis of regular forest inventories in Matang and the Sundarbans suggests that current long-term management practices involving mangrove trees also are not sustainable in these regions (Ellison and Farnsworth, 2001). In the 40 000-ha forest at Matang, which accounts for ~40% of the total mangrove area of Malaysia, yields have declined steadily from 296 t/ha from the virgin stands of the late 19th century to 158 t/ha in the late 1960s to 136 t/ha from the late 1970s to the present (Gong and Ong, 1995; FDP, 2006). A recent analysis of market values of products other than charcoal and timber that are derived from mangroves suggests that

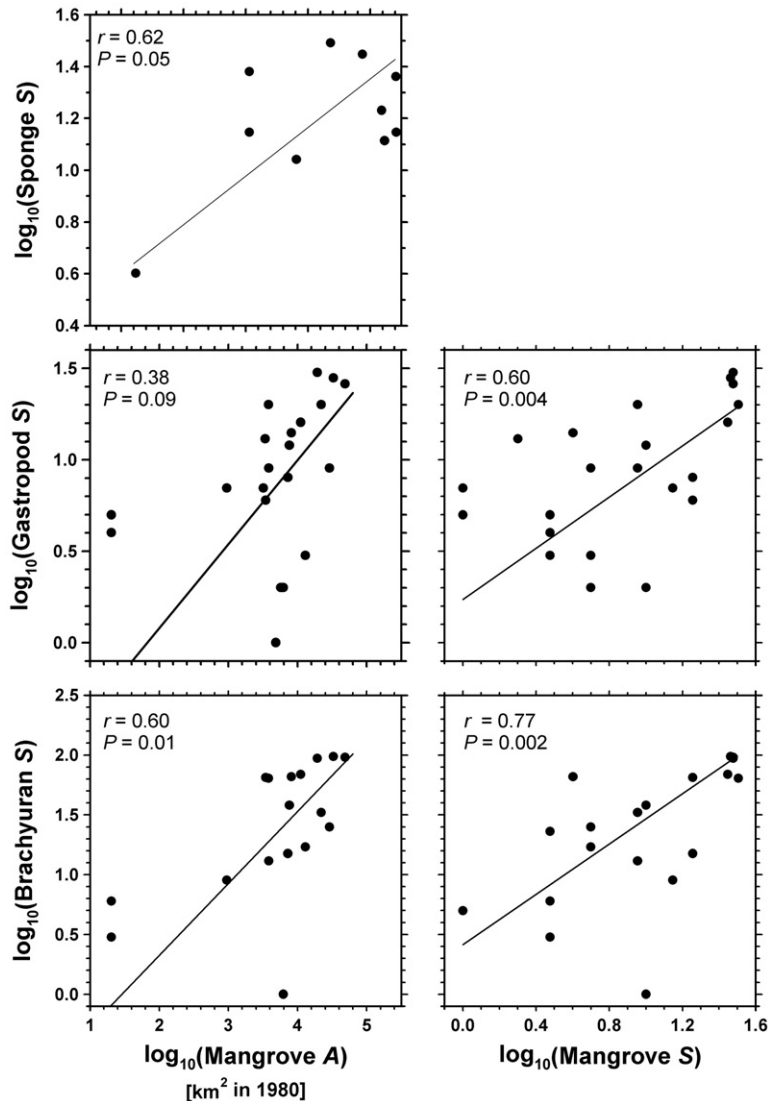


Fig. 3. Relationship between gastropod, brachyuran crab, and sponge species richness (S), and mangrove species richness (S) or mangrove area (A) (all per 15° of longitude; both on \log_{10} -scale to normalize and equalize variances). Gastropod and brachyuran data are global; sponge data are for 10 locations in the Caribbean Basin. Sponges are only associated with *Rhizophora mangle*, so the sponge S vs. mangrove S plot is not drawn. Because there is measurement error in both variables, reduced major axis regression (Sokal and Rohlf, 1995) was used to fit the regression lines. See Fig. 2 legend for sources of data for gastropods and brachyura; sponge data compiled from Van Soest (1978, 1980, 1984), Díaz et al. (1985), Rützler and his colleagues (De Weerd et al., 1991; Rützler and Smith, 1992; Hajdu and Rützler, 1998; Alvarez et al., 1999), Alvarez-León (1993), Farnsworth and Ellison (1996), and Alleng (1997). The raw data (species \times site matrices) are available on request from the author.

people living in communities around Matang would prefer a modified management regime that devoted more area to ‘environmental’ forests (currently the 20% of the Matang mangroves not used for wood and charcoal production), protection of migratory bird species, increased eco-tourism, and consequent increased employment for local residents (Othman et al., 2004). Economic analyses routinely illustrate that mangroves managed for multiple uses provide more value than mangroves

managed for single (forestry) products (Rönnbäck, 1999; Barbier, 2000; Sathirathai and Barbier, 2001).

Management of the Sundarbans mangroves has followed a similar trajectory. Successive management plans have consistently decreased the minimum tree size and rotation time at which mangroves could be cut. The net result was a decline in timber volume by $\sim 50\%$ by the early 1980s, leading to an end of economically-viable mangrove forestry and a temporary ban on mangrove cutting in

Bangladesh in 1994 (Hussain and Acharya, 1994; Iftekhar and Islam, 2004).

3.2. Impact of forest management on benthic species of commercial importance

The direct impact on the benthos of mangrove forest management is rarely quantified (Manson et al., 2005b). Landings of wild-caught shrimp (generally *Penaeus merguensis*) are generally correlated with available mangrove area in Malaysia (Loneragan et al., 2005) and elsewhere in Southeast Asia (Rönnbäck, 1999). During the 1980s and 1990s, landings remained stable around Matang, where mangrove area has been maintained, but actually increased in adjacent states (Selangor and Penang) despite rapid loss of mangroves there (Loneragan et al., 2005). This finding, which is at odds with general findings elsewhere in the world (Rönnbäck, 1999; Manson et al., 2005b) may be due to: (1) migration of prawns from adjacent areas (Loneragan et al., 2005); (2) catches of additional species that do not rely on mangroves as nurseries (Dall et al., 1990); or (3) recording of prawns as local catches when in fact they were landed elsewhere.

In the Sundarbans of Bangladesh, extraction of oyster (*Crassostrea* spp.) shells for production of lime and poultry feed declined by nearly 75%, from $\sim 6 \times 10^6$ t y^{-1} to $\sim 1.5 \times 10^6$ t y^{-1} (Iftekhar and Islam, 2004). Concurrently, mangrove production declined at only 0.04% y^{-1} , suggesting that available mangrove area is not the best predictor of oyster abundance. This may result from a non-linear relationship between mangrove cover and oyster abundance or over-exploitation of oysters, or that alternative measures of mangrove forest extent (e.g., length of coastline) may be a better predictor of faunal abundance (cf. Manson et al., 2005b). Similarly, a non-linear relationship between mangrove area and prawn yields was found by Pauly and Ingles (1986). Their data suggest that the rate of decline in prawn yields will accelerate as mangrove area decreases. Further research is needed to determine appropriate spatial scales for analyzing and elucidating interactions between mangroves and benthic fauna.

3.3. The mangrove macrobenthos as an indicator of forest management

Species diversity, density, and biomass of brachyuran crabs and gastropods appear to respond predictably to disturbance, exploitation, management, or rehabilitation of mangroves (Skilleter, 1996; Skilleter and Warren, 2000; Macintosh et al., 2002; Ashton et al., 2003; Bosire et al., 2004), and it has been suggested that structure of

benthic assemblages may be a useful indicator for measuring the progress of rehabilitation efforts (Macintosh et al., 2002; Ashton et al., 2003). Along the western coasts of Malaysia and Thailand, degraded sites (e.g., former tin mines, replanted clearcuts) are dominated by the grapsid crab, *Metaplax elegans* (Macintosh et al., 2002). Young (often replanted) stands are dominated by ocypodid crabs (especially fiddler crabs, *Uca* spp.) and snails in the families Littorinidae, Potamidae, and Assimineidae, whereas mature stands are dominated by sesarmid crabs and elobiid and neritid snails (Sasekumar and Chong, 1998; Macintosh et al., 2002; Ashton et al., 2003). In these systems, which are dominated by mangroves in the Rhizophoraceae, density and biomass of crabs and snails are higher in young stands than in intermediate-aged (15-year-old) forests. Sasekumar and Chong (1998) report a further increase in biomass and density of snails from intermediate-aged forests to mature stands, whereas Ashton et al. (2003) do not.

In Australian systems dominated by *Avicennia* spp., removal of pneumatophores following disturbances (e.g., for boardwalk construction) leads to a decline in mollusc density and abundance, but promotes an increase in density and abundance of the burrowing ocypodid and grapsid crabs that use pilings as structures to increase stability of their burrows (Kelaheer et al., 1998a,b; Skilleter and Warren, 2000). In all studies of responses of benthic fauna to mangrove structure, there are simultaneous changes in environmental characteristics (e.g., salinity, pH, tidal amplitude, percent silt) that parallel changes in forest structure, tree species composition, and structure of benthic assemblages. Teasing apart the relationships between the structure of faunal assemblages, historical land-use, environmental conditions, and mangrove species composition presents a set of open questions that need to be resolved before faunal composition can be used reliably as an indicator of success of mangrove rehabilitation or restoration schemes (cf. Macintosh et al., 2002; Ashton et al., 2003).

4. Direct management of the mangrove macrobenthos

4.1. Prawns

Few benthic taxa are actively managed in mangrove ecosystems, but those that are provide significant economic returns. Most attention has focused on aquaculture of shrimp and prawns, especially the tiger prawn *Penaeus monodon*, for which the commodity value in 2004 was US\$3.3 Billion (FAO, 2006). The literature on prawn aquaculture is vast and no attempt is

made to review it here, but prawn aquaculture appears to be inherently unsustainable for at least four reasons. First, prawn aquaculture generally requires destruction of mangroves for construction of rearing ponds (Sathirathai and Barbier, 2001; Barbier and Cox, 2004; Islam and Wahab, 2005). Although integrated mangrove silviculture-prawn aquaculture systems have been proposed in Viet Nam and have been shown to have higher economic returns than prawn aquaculture in the absence of mangroves (Binh et al., 1997; Trong, 1999), available evidence suggests that integrated mangrove-prawn aquaculture has not been widely adopted and mangroves in the Mekong Delta (and elsewhere) continue to be lost to prawn ponds (Tong et al., 2004). Second, water pollution from intensive prawn farms negatively impacts adjacent mangrove ecosystems. Economic returns of prawn farms decline dramatically if pollution controls are required (Sathirathai and Barbier, 2001), but there are few legal requirements anywhere that prawn-pond effluent be treated prior to its release. Third, the area of mangrove required to support a ‘fishery’ of gravid *P. monodon* spawners for generating prawn ‘seed’ for stocking ponds in which intensive prawn aquaculture is practiced is ~11 times the pond area (Rönnbäck et al., 2003). Given the rapid loss of mangrove forests world-wide, especially in areas of intensive aquaculture (Figs. 1 and 4), the long-term sustainability of prawn aquaculture that relies on wild-caught females for stocking ponds is unlikely. Fourth, white-spot syndrome virus (WSSV) is now established in shrimp ponds throughout the world. Following the rapid spread of the virus in the mid-1990s, production of *P. monodon* declined; with better control of the virus, overall production in Southeast Asia increased to historic highs in recent years; unsurprisingly, mangrove area concurrently declined as forests continued to be converted to aquaculture ponds (Fig. 4).

The rapid overall growth in tiger prawn production (Fig. 4) masks the fact that it is declining rapidly in half of the major producing countries. Peak production in the Philippines occurred in 1994, in Sri Lanka in 1998, in Thailand in 2000, and in Singapore in 2002 (Fig. 4). Production by China, Indonesia, India, and especially Viet Nam made up the difference in global production lost by the aforementioned countries through 2004. Whether or not the newly dominant producers of *P. monodon* can maintain these outputs is unknown. What is clear is that patterns of *P. monodon* production are similar to ‘slash-and-burn’ agriculture in rain forests and similar to patterns seen in other fisheries with global markets, where multinational producers (or fishing fleets) move from location to location, rapidly exploit-

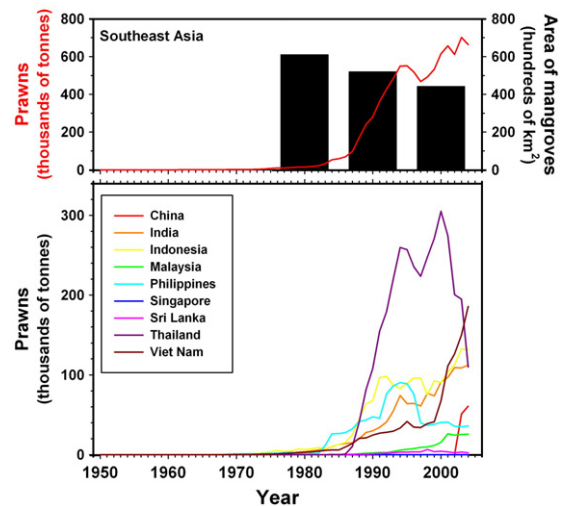


Fig. 4. Production of prawns in mangroves. **Top** — Remaining mangrove area in hundreds of km² (black bars) and total production of giant tiger prawns (thousand tonnes of *Penaeus monodon*; red line) in Southeast Asia (China, India, Indonesia, Malaysia, Philippines, Singapore, Sri Lanka, Thailand, and Viet Nam). As prawn production has increased, mangrove area has decreased. **Bottom** — Prawn production of each country (thousand tonnes of *P. monodon* per year). Mangrove data from Wilkie and Fortuna (2003); prawn production data from FAO (2006), except for Vietnamese production data from Lindner (2005).

ing local resources and then moving on to other, unprotected areas (Berkes et al., 2006). Such ‘roving bandits’ can persist because they have no connection to local communities and no incentive to manage sustainably a local resource. They cut mangroves, establish prawn ponds, exhaust them before regulators can catch up and respond appropriately, and then move on to another country and repeat the process.

4.2. Molluscs

Blood cockles (*Anadara granosa*) and oysters (*Crassostrea* spp.) are farmed or harvested in mangroves in Southeast Asia and the Caribbean, respectively. Although the Matang mangrove forest is managed at a constant 40 000 ha, cockle production in 2004 was only 50% of its historic high of 121 000 tonnes in 1980 and accounted for only 14% of Southeast Asian production (total production value: US \$435 Million [FAO, 2006]) in that same year (Fig. 5 top). For Matang, these data suggest that either continued management of the mangroves is altering cockle production; that cockle producers are opting out of culturing this species in favour of others; or that other factors, as yet undetermined, are driving production figures down. A similar pattern is observed for oyster production among the five major Caribbean producers

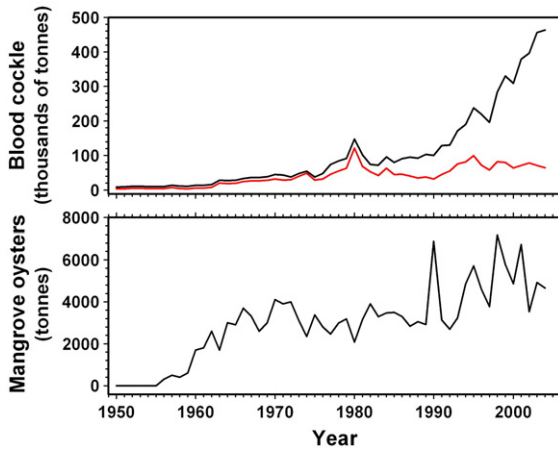


Fig. 5. Production of mangrove molluscs. **Top** — Production of blood cockles (*Anadara granosa*) in Southeast Asia (black line: sum of China, Malaysia, Taiwan, Thailand) and by Malaysia alone (red line). **Bottom** — Total production of mangrove oysters (*Crassostrea rhizophorae*) in the Caribbean (Colombia, Cuba, Dominican Republic, Jamaica, and Venezuela).

(Colombia, Cuba, Dominican Republic, Jamaica, and Venezuela). Total production in 2004 was 65% of its historic high of 6 900 tonnes in 1990 (Fig. 5 bottom), and had a production value of US \$1.2 Million (FAO, 2006). During this same period, total mangrove area across these countries declined by 5%, from 12 000 km² to 11 400 km² (Wilkie and Fortuna, 2003). As with cockle production in Matang and declines in oyster-lime yields in Bangladesh, direct causes of decline in mangrove oyster production in the Caribbean are unknown.

4.3. Crabs

Among the more than 300 species of brachyuran crabs reported from mangroves worldwide, two families, the Grapsidae and Ocypodidae, account for over 80% of the species diversity (Tan and Ng, 1994). Yet it is a mangrove-dwelling portunid crab, the Indo-West Pacific swamp crab (*Scylla* spp.) that is actively managed. Management is similar for the four species of mud crab, *S. serrata*, *S. olivacea*, *S. tranquebarica*, and *S. paramamosain* (taxonomy follows Keenan et al., 1998). Overall production of *Scylla* has grown exponentially since 1950 (Fig. 6), and in 2004 had a production value of US \$252 Million (FAO, 2006). As with prawn production, however, optimistic overall production trends mask substantial within-country changes indicative of roving banditry. Of the seven countries with significant production data in the FAO (2006) database (excluding Brunei Darussalam, Mauritius, and Sri Lanka, each of which did not produce more than 2 t/y between 1950 and 2004), five

have passed their peaks of production (Fig. 6): Taiwan in 1983, Thailand in 1986, Singapore in 1993, Malaysia in 1995, and Australia in 1998. Production in Indonesia may have peaked in 2002, and production in the Philippines has only recently recovered to 1993 levels. China and Viet Nam currently dominate world production of *Scylla* (Fig. 6). Throughout the Indo-West Pacific, *Scylla* production is done either in open ponds (mangroves cut) or in ponds within mangroves, possibly with parallel silvicultural management; the latter is considered to be commercially viable (Minh et al., 2001; Triño and Rodriguez, 2002).

Despite several decades of active research into hatchery technology to enable commercial production of crab larvae for *Scylla* ponds, all countries engaged in *Scylla* production still produce the vast majority (70–100% of production) of marketable crabs from wild-caught crablets. Viable hatcheries have been achieved on a commercial scale only in Viet Nam, where they are heavily subsidized by the government yet still account for only ~30% of marketable production (Felder, 2004;

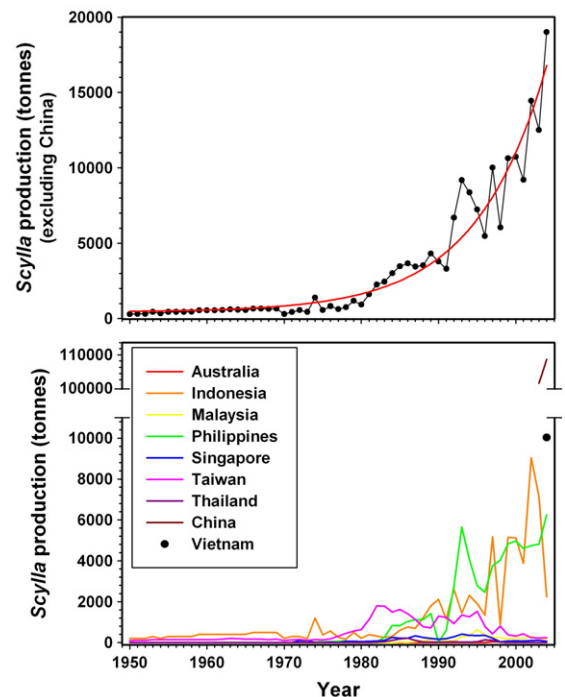


Fig. 6. Production of mud crabs (*Scylla* spp.). **Top** — Total production (tonnes per year) in the Indo-West Pacific (including the countries of Australia, Indonesia, Malaysia, Philippines, Singapore, Taiwan, Thailand, and Vietnam). Data for China (100 870 tonnes in 2003 and 108 503 tonnes in 2004 [FAO, 2006]) are not included to more clearly illustrate the trend. Production is growing at approximately 10% per year ($r^2=0.91$). **Bottom** — Production by country. Note axis break to illustrate Chinese production in 2003 and 2004.

Lindner, 2005). New production facilities, such as in Kosrae, Federated States of Micronesia, often begin with wild-caught crablets and only later may begin to develop hatchery technology (Wortel, 2005). All hatchery operations require heavy use of antibiotics (especially tetracycline derivatives) to reduce mortality, and WSSV also infects at least *Scylla serrata* (Vaseeharan et al., 2003). Further, whether reared from hatchery-produced or wild-collected crablets, intensive pond production of *Scylla* requires fishmeal consisting of various amounts of shrimp, squid, high-valued soft-shelled crabs, ‘Chilean fish’, ‘trash fish’, and a number of unidentified benthic species (e.g., ‘worm meal’) (Hutabarat, 1999; Millamena and Qunitio, 1999; Williams and Primavera, 2001; Christensen et al., 2004).

In the neotropics, the ocypodid crab *Ucides cordatus* is the major non-timber resource that is artisanally extracted from Brazilian mangroves (Glaser and Diele, 2004; Alves et al., 2005; Diele et al., 2005). Most of Brazil’s 10 000 km² mangroves are in the northern states of Pará, Paraíba, and Maranhão (Kjerfve and Lacerda, 1993) where the majority of coastal residents rely on mangrove products for subsistence and commercial

extraction (Glaser, 2003). Although the *Ucides* fishery is considered biologically sustainable in the Caeté estuary (Diele et al., 2005) because large male crabs account for 98% of the harvest, there has still been a notable decline in population size of marketable-size crabs. Catch per unit effort declined 16% from 1997 to 2001 and economic return from the crab fishery declined by 20% during the same period (Glaser and Diele, 2004). Harvesting of *U. cordatus* in Caeté is now subject to a co-management plan developed jointly by local communities and the Brazilian federal government (Glaser and da Silva Oliveira, 2004), so long-term sustainability of this fishery is possible.

In contrast, the *Ucides* fishery in the ‘permanently protected area’ of Barra do Rio Mamanguape in Paraíba is declining rapidly (Alves et al., 2005). Local residents collect undersized crabs and a substantial number of female crabs. Most of the crabs are sold for regional (and urban) markets; the economically marginal residents rely heavily on income garnered from crab collection, income that is paid to them by non-residents. As with prawn and *Scylla* aquaculture, regional and global markets increasingly are driving the population dynamics and harvesting

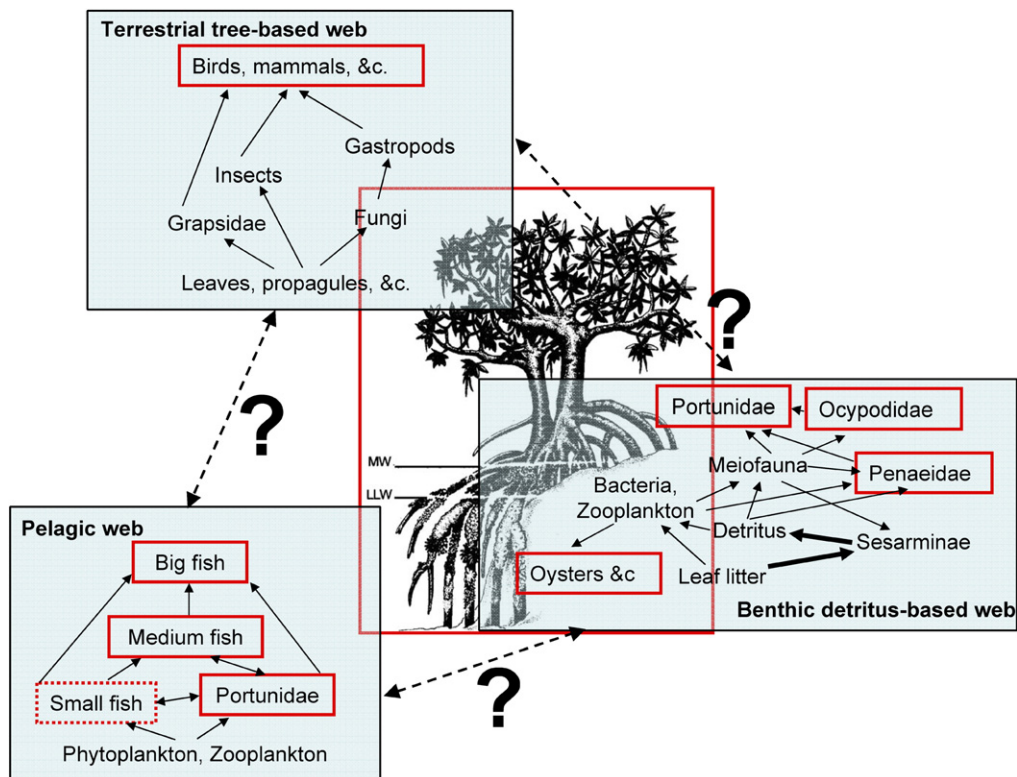


Fig. 7. Generic mangrove food webs. Mangrove trees support terrestrial, tree-based webs; benthic, detritus-based webs that span tidal elevations from mean water (MW) through low water (LW); and through some degree of carbon export, pelagic, mixed detritus- and producer-based web.

of *Ucides*. Crab populations also appear to be declining due to run-off of pollutants into mangrove areas from nearby sugar-cane plantations.

5. Broader consequences of managing the mangrove macrobenthos

5.1. Are we fishing out the mangrove food web?

Mangrove food webs were studied intensively and in great detail by Odum and Heald (1972), who reconstructed a mangrove food web for southern Florida based on analysis of gut contents of 52 fish, 4 molluscs, 2 mysids, 2 cumaceans, 2 isopods, 3 amphipods, 2 palaemonid shrimp, a penaid shrimp, a snapping shrimp, 2 brachyuran crabs, at least 4 chironimids, 16 ciliated protozoan species, and with a host of unidentified hydroids, nematodes, and polychaetes. Although their vision of off-shore fisheries supported by carbon export from the detritus-based, mangrove food web is now regarded as inaccurate - the processing of leaf litter by grapsid and ocypodid crabs limits export of mangrove carbon (Robertson et al., 1992; Lee, 1998; Schories et al., 2003) and stable-isotope studies indicate that off-shore fisheries are supported principally by carbon from algae, seagrasses, and the latter's epiphytes (Kieckbusch et al., 2004; Manson et al., 2005a,b; Guest et al., 2006) - there has been no comparable study of a mangrove food web anywhere in the world. Available studies of one or a few species allow only broad and assuredly inaccurate generalizations (cf. Alongi and Sasekumar, 1992).

Mangrove ecosystems have both detritus-based food webs based on decaying plant tissue (leaf litter and coarse woody debris) and production-based food webs based on living mangrove tissue (Fig. 7). Arthropods and gastropods occur in the middle of each of these food webs. For example, littorinid snails graze on fungi or algae that grow on leaves and trunks (Kohlmeyer and Bebout, 1986; Alongi and Sasekumar, 1992) whereas cerithids and elobiids are detritivores. Some crabs (e.g., *Aratus pisonii*) consume living leaves and propagules (Warner, 1967; Smith et al., 1989; Farnsworth and Ellison, 1991), whereas others (e.g., *Ucides cordatus*, *Perisesarma messa*) remove and shred leaf litter (Lee, 1998). Prawns are omnivorous, with diets consisting of bacteria, algae, protozoa, copepods, nematodes, and other meiofauna living on sediment surfaces (Odum and Heald, 1972; Dall et al., 1990). Crabs feed omnivorously on both lower (e.g., leaves, decaying organic matter) and higher trophic levels (insects, molluscs, fish) (Jones, 1984; Alongi and Sasekumar, 1992). Although crabs have often been considered to be 'keystone species' (sensu Holling,

1992) in mangroves because of their role in carbon recycling (Schories et al., 2003) and selective propagule predation leading to zonation of tree species (Smith et al., 1989), there is as yet no evidence that they are 'keystone predators' (sensu Paine, 1966) whose removal would lead to an increase in diversity of lower trophic levels.

All these data suggest that mangrove food webs share many characteristics with other, marine and terrestrial food webs (Fig. 7). They have identifiable subsystems (e.g., pelagic, benthic, terrestrial) with many linkages within subsystems and few (potentially strong but unresolved) linkages between subsystems (Allesina et al., 2005). They have a mixture of omnivores and dietary specialists. And both their species composition and abundance, and the energy flows through them are likely to change when particular species are fished to low levels or removed entirely (Eklöf and Ebenman, 2006). Food-web ecologists have devoted much time and energy in recent years in developing an understanding of how changes in the abundance of top predators and basal resources alter food-web structure (see review in Eklöf and Ebenman, 2006). Consequences of 'fishing down' marine food webs as top predators are over-harvested are well understood (Pauly et al., 2000) and show up in the choices and costs of seafood available in markets.

For mangroves, however, the crucial question at hand is to determine the consequences for benthic biodiversity and food web structure of management activities that dramatically reduce or remove completely species that occupy *intermediate* trophic levels, such as shrimp, crabs, and molluscs. First, we need detailed descriptions of mangrove food webs from around the world. Only then can we answer key questions such as: what are the effects on benthic food webs and carbon dynamics of harvesting gravid 'stock' or crablets over broad areas of mangroves for intensive culture of prawns and crabs? How are off-shore food webs changed by harvesting 'trash fish' and lower trophic levels for production of aquaculture meal? Models suggest that losses of trophically intermediate species that are energetically linked to many other species have large effects on overall food web structure. Removal of a well-connected species at an intermediate trophic level can lead to rapid losses of species at both higher and lower trophic levels (Eklöf and Ebenman, 2006), but data to test this hypothesis are lacking for *any* food web. Broadly speaking, we need to refocus food web research to determine whether the removal of intermediate trophic levels can destabilize food webs in general. Elucidating these impacts on mangrove food webs is of particular importance because of the economic value of both mangrove forests and the benthic and pelagic fisheries that they support.

5.2. *Feedbacks from the benthos to the forest*

Macrobenthic organisms have direct impacts on individual trees and on overall forest structure. In the neotropics, damage caused by burrowing isopods (Perry, 1988) is ameliorated by root-fouling sponges (Ellison and Farnsworth, 1992), which also stimulate root growth through transfer of nitrogen (Ellison et al., 1996). Throughout the world, grapsid crabs eat leaves and recycle essential nutrients within mangrove forests (Robertson et al., 1992). These crabs also eat propagules, with attendant reduction in reproductive output of trees (Farnsworth and Ellison, 1991) and, through species-specific propagule predation, establish zonation patterns common in mangroves throughout the world (Smith et al., 1989; Dahdouh-Guebas et al., 1998). Oysters, clams, and other filter-feeders remove pollutants and toxins from the water column, but their effects on plant production are unknown. Because research has focused on what benefits (or costs) mangroves (or their loss) provide to benthic aquaculture and off-shore fisheries, much less is known about how the benthos and fisheries reciprocally affect mangroves. This knowledge gap should be filled.

6. Future prospects

In most ecosystems, management plans tend to be developed for a single commodity, and mangroves are no exception. Forestry departments develop management plans for wood and charcoal production; fisheries departments develop management plans to maximize yields of oysters, crabs, or prawns; and tourism departments focus on attracting wealthy tourists to view charismatic megafauna, such as birds and tigers. An encouraging development in recent years is the development of integrated management plans that attempt to manage simultaneously multiple facets of an ecosystem. Examples include co-management of extractive reserves in mangrove ecosystems on the northern coast of Brazil (Glaser and da Silva Oliveira, 2004); collaborative management of mangroves, coral reefs, and fisheries in Tanzania (Verheij et al., 2004); integrated silviculture-prawn (Binh et al., 1997) or silviculture-mud crab (Triño and Rodriguez, 2002) systems in Southeast Asia; and multiple-use planning for the Matang mangroves (Othman et al., 2004). These plans are in accord with current fundamental objectives for management of mangrove ecosystems (World Bank et al., 2004) and if similar plans are implemented world-wide, it could reduce the ability of roving bandits to continue to over-exploit mangroves and the mangrove benthos.

Integrated management plans cannot succeed without additional economic intervention and regulation,

and an increasing degree of local control over the design and implementation of these plans (Barbier, 2006a). Key changes required include: the termination of economic subsidies for aquaculture; enforced, legal requirements that effluent from aquaculture ponds be treated prior to release into surrounding ecosystems; and restrictions on the ability of ‘roving bandits’ to convert untitled mangrove forests to private aquaculture operations serving the global marketplace. Local residents, unlike roving bandits, have a stake in the sustainable management of their own resources. Currently, local communities are encouraged to bear the costs of conserving (and often replanting) mangroves after they have been ravaged and abandoned by roving bandits. But local communities and stakeholders will not bear this cost, and will only participate in mangrove conservation and restoration, if they also can realize economic gain from their efforts (Barbier, 2006a).

Perhaps more promisingly, since the Asian tsunami of December 2004, the role of mangroves in providing coastal protection has received increased attention (Adger et al., 2005; Dahdouh-Guebas et al., 2005; Danielsen et al., 2005; Roy and Krishnan, 2005; Barbier, 2006a; for pre-tsunami discussion of the protective value of mangroves, see UNESCO, 1979; Roth, 1992; Othman, 1994; Mazda et al., 1997). Plans to plant mangroves and (re)vegetate coastlines have been promulgated throughout Southeast Asia, although often with little attention paid to whether or not sites chosen for planting efforts supported mangroves in the past (Dahdouh-Guebas et al., 2005; Barbier, 2006a). It is critical that mangrove restoration efforts be sited appropriately, and that diverse stands be favoured over monocultures. Mangrove afforestation on previously unvegetated mudflats is rarely successful (Ertfemeijer and Lewis, 2000), and monocultures have lower structural complexity (Ellison, 2000) and therefore are less likely to support a full complement of benthic species than would mixed stands. Although replanting mangroves alone will not ensure future protection from tsunamis or cyclonic storms, a deeper appreciation of indirect economic values (e.g., Barbier, 2000,b) of mangrove ecosystems and careful attempts to rehabilitate and restore mangrove forests (Field, 1998a,b; Ellison, 2000; Lewis, 2005) may nonetheless provide a refuge for benthic diversity and lead to true sustainable management of mangrove ecosystems.

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