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Preface

The continual significant loss of mangrove forests to urbanisation, coastal aquaculture and pollution is an unwelcome fact confronting ecologists and coastal managers in the 21st century. Despite the widely acknowledged ecological and economic values of mangrove forests, this devastating trend on one of the world's most productive and dynamic ecosystems will unlikely be reversed, at least not in the near future. Mangrove research has a long history, but major gaps of knowledge that are crucial to mangrove conservation and management still exist. Early research on mangroves focussed strongly on their floristics and potential as an economic resource. While there has been much effort in the last four to five decades to quantify mangrove primary production, and more recently, its fate, relatively little is known about the assemblages and ecological roles of animals associated with mangrove forests. Further, the macrobenthos are clearly one poorly understood group of animals associated with mangroves, largely due to the difficulties of sampling and observing them in this spatially complex environment. The first Meeting on Mangrove Macrobenthos (MMM1) was held in Mombasa, Kenya, in September 2000 to address this gap. Selected papers presented in the meeting were published in *Wetlands Ecology and Management*, Volume 10 (2002).

Six years after MMM1, mangroves have continued to decline and we now face the regrettable, but likely, prospect of a world without (functional) mangroves. While scientists and managers debate the actual significance of mangroves to society and world ecology, fundamental aspects of mangrove biology and ecology, such as the faunal biodiversity resources associated with the forests and their role in ecosystem function, are yet to be explored. This special issue comprises 10 papers presented at the second Meeting on Mangrove Macrobenthos (now renamed 'Mangrove Macrobenthos Meeting II' or MMM2) held in Coolangatta, Queensland, Australia, 26th – 30th June 2006. The diversity of topics presented at MMM2 ranged from documentation and analysis of the macrobenthic assemblages to understanding their roles in organic matter dynamics, and fisheries resources management. This diversity of interest is also reflected in the papers published in this special issue, which represent the four keynote presentations and selected submitted papers from the conference.

Papers in this special issue fall into the following three themes: (a) Research tools for studying mangrove macrobenthos ecology: Bouillon et al.; (b) Mangrove macrobenthos assemblages and their ecological roles: Erickson et al.; Imgraben and Dittmann; Kristensen; Lee; Mchenga and Tsuchiya; Metcalfe and Glasby; Mfilinge and Tsuchiya; and (c) Management of mangrove macrobenthic biodiversity resources: Ellison; Ewel. Hopefully these papers will not only provide valuable overviews of these aspects of mangrove macrobenthos research, but also contribute to the protection and management of this poorly studied component of our dwindling mangroves.

MMM2 would not have been possible without the financial and logistical support of the following organisations: Griffith University, the University of Queensland, James Cook University, the Ian Potter Foundation, and Queensland Department of Primary Industries and Fisheries. Other members of the Organising Committee, namely, Rod Connolly, Peter Davie, Norm Duke, Tarik Meziane and Michaela Irvebrant provided indispensable and cheerful team support. We also gratefully acknowledge the assistance many colleagues have provided through reviews of the manuscripts submitted for publication in this special issue.

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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.

Keywords: Aquaculture; Brachyura; Food web; Management; Mangroves; *Penaeus*; Roving bandits; *Scylla*

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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 km^2 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 cylones 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 data gaps and priorities for research that are required before we can realistically conserve and sustainably manage the mangrove macrobenthos.

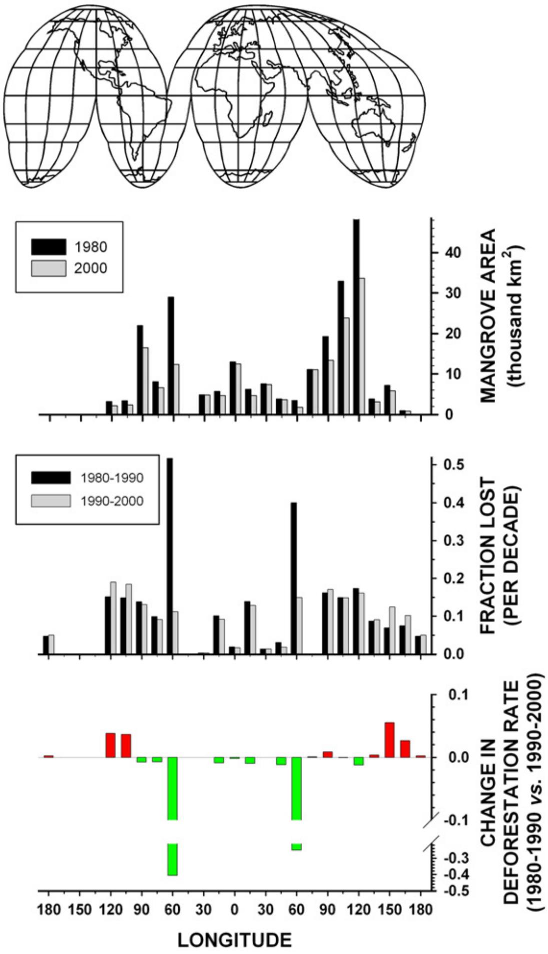

Fig. 1. Loss of mangroves 1980–2000. The **top** graph shows estimated mangrove area per 15° of longitude in 1980 (black bars) and 2000 (grey bars). The **middle** graph shows the fraction of mangroves area lost per 15° of longitude between 1980–1990 (black bars) and between 1990–2000 (grey bars). The 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).

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.

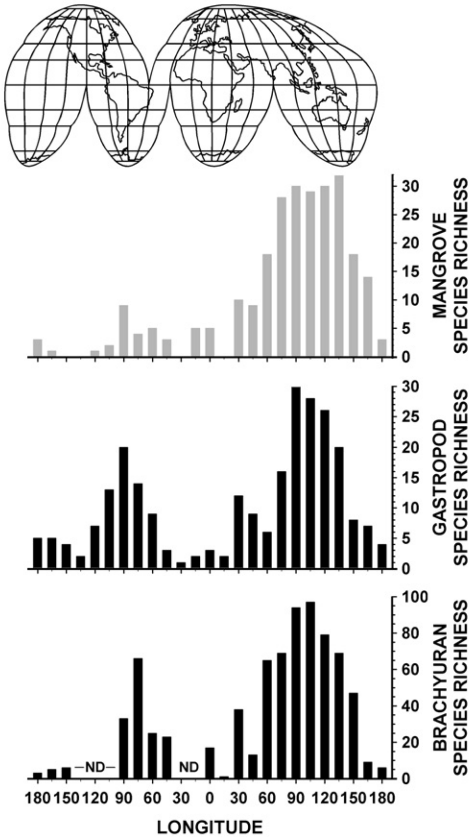

Fig. 2. Global species richness per 15° of longitude of mangroves, mangrove gastropods (in eight genera: *Littoraria, Pythia, Cassidula, Melampus, Ellobium, Cerithidea, Telescopium*, and *Terebralia*) and brachyuran crabs (in five families: Grapsidae [including Sesarminae and Varuninae]; Ocypodidae, 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.

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 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; FDPM, 2006). A recent analysis of market values of products other than charcoal and timber that are derived from mangroves suggests that

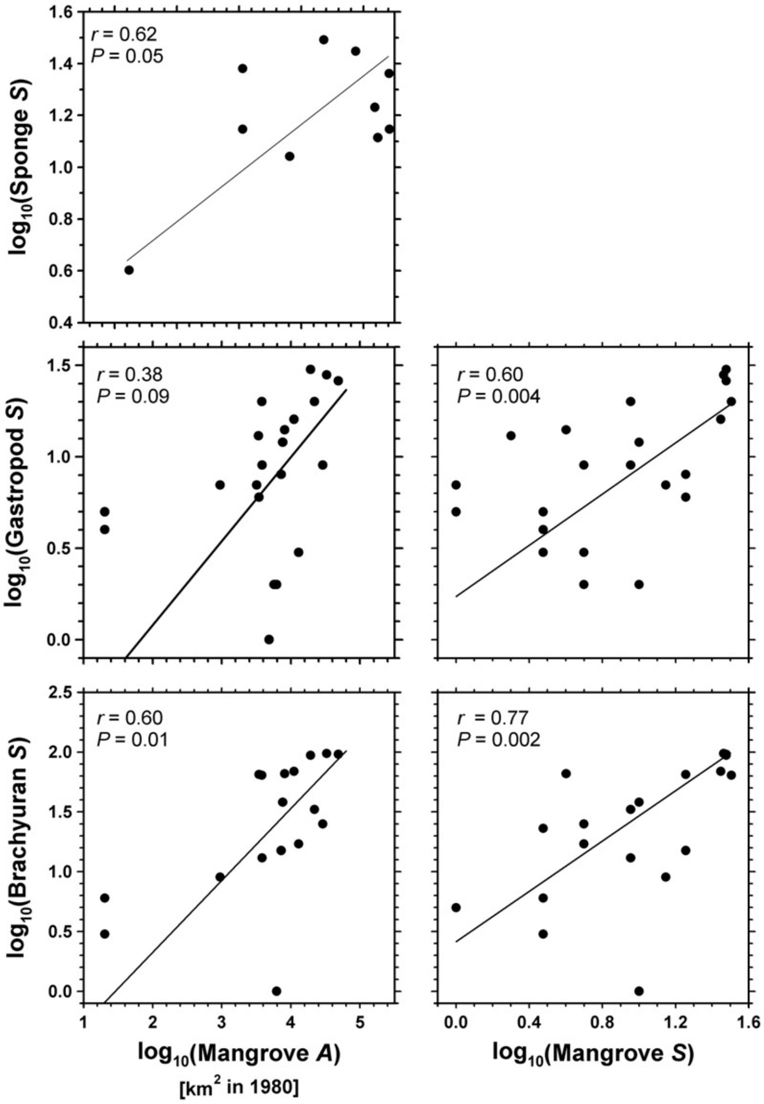

Fig. 3. Relationship between gastropod, brachyuran crab, and sponge species richness (*S*), and mangrove species richness (*S*) or mangrove area (*A*) (all per 15° of longitude; both on $\log_{10}$-scale to normalize and equalize variances). Gastropod and brachyuran data are global; sponge data are for 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 Weerdt 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 × 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 ~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 merguiensis*) 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 $\sim 6\times10^6$ t y^{-1} to $\sim 1.5\times10^6$ 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 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 (Kelaher 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 exploiting 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.

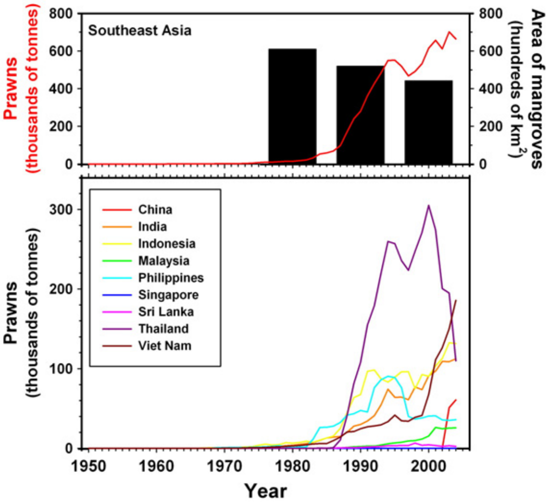

Fig. 4. Production of prawns in mangroves. **Top** — Remaining mangrove area in hundreds of km^2 (black bars) and total production of giant tiger prawns (thousand tonnes of *Penaeus monodon*; red line) in Southeast Asia (China, India, Indonesia, Malaysia, Philippines, Singapore, Sri Lanka, Thailand, 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).

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

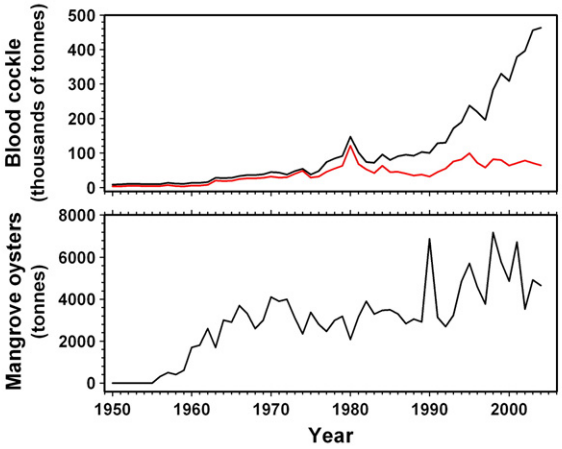

Fig. 5. Production of mangrove molluscs. **Top** — Production of blood cockles (*Anadara granosa*) in Southeast Asia (black line: sum of China, Malaysia, Taiwan, Thailand) and by Malaysia alone (red line). **Bottom** — Total production of mangrove oysters (*Crassostrea rhizophorae*) in the Caribbean (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 km^2 to 11 400 km^2 (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 (Fielder, 2004;

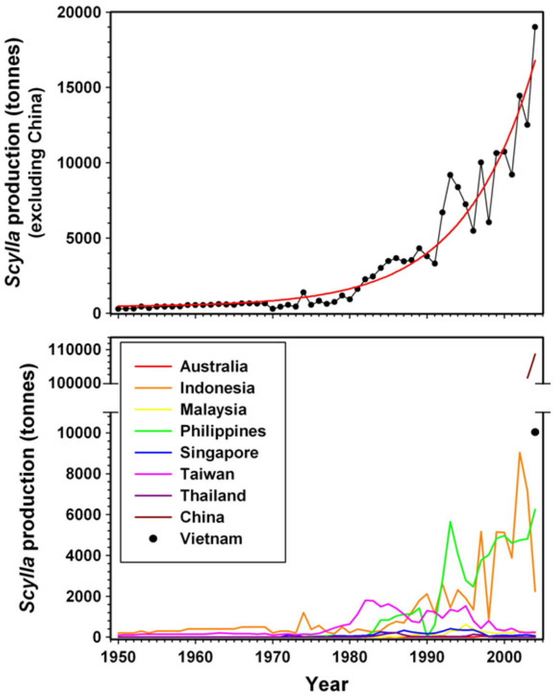

Fig. 6. Production of mud crabs (*Scylla* spp.). **Top** — Total production (tonnes per year) in the Indo-West Pacific (including the countries of Australia, Indonesia, Malaysia, Philippines, Singapore, Taiwan, Thailand, and Vietnam). Data for China (100 870 tonnes in 2003 and 108 503 tonnes in 2004 [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 Quinitio, 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 km^2 mangroves are in the northern states of Pará, Paraiba, and Maranhão (Kjerfve and Lacerda, 1993) where the majority of coastal residents rely on mangrove products for subsistance 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 Paraiba 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

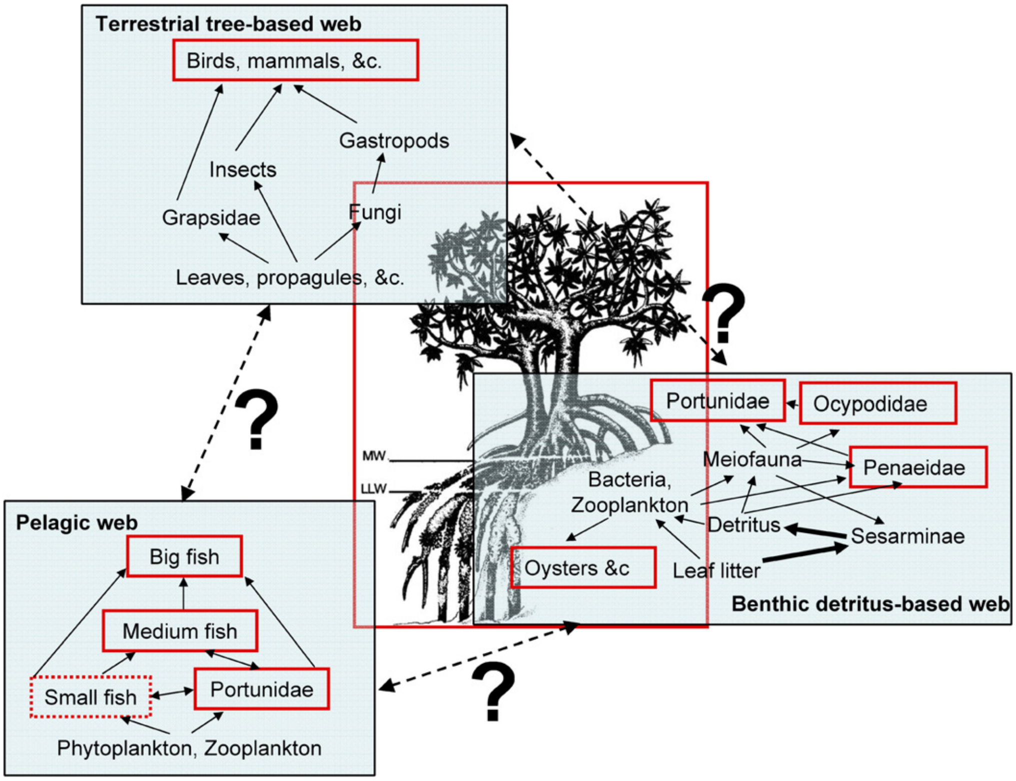

Fig. 7. Generic mangrove food webs. Mangrove trees support terrestrial, tree-based webs; benthic, detritus-based webs that span tidal elevations from mean water (MW) through low water (LW); and through some degree of carbon export, pelagic, mixed detritus–and producer–based web.

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 destablize 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 (Erftemeijer 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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References

Adger, W.N., Hughes, T.P., Folke, C., Carpenter, S.R., Rockström, J., 2005. Social-ecological resilience to coastal disasters. Science 309, 1036–1039.

Alleng, G.P., 1997. The fauna of the Port Royal mangal, Kingston, Jamaica. Stud. Nat. Hist. Caribb. Reg. 73, 23–42.

Allesina, S., Bodini, A., Bondavelli, C., 2005. Ecological subsytems via graph theory: the role of strongly connected components. Oikos 110, 164–176.

Alongi, D.M., 2002. Present state and future of the world's mangrove forests. Environ. Conserv. 29, 331–349.

Alongi, D., Sasekumar, A., 1992. Benthic communities. In: Robertson, A.I., Alongi, D.M. (Eds.), Tropical Mangrove Ecosystems. American Geophysical Union, Washington, DC, pp. 137–173.

Alvarez, B., Van Soest, R.W.M., Rützler, K., 1999. A revision of Axinellidae (Porifera: Demospongiae) of the Central West Atlantic Region. Smithson. Contrib. Zool. 598, 1–47.

Alvarez-León, R., 1993. Mangrove ecosystems of Colombia. In: Lacerda, L.D. (Ed.), Conservation and Sustainable Utilization of Mangrove Forests in Latin America and Africa Regions. Part I - Latin America. International Society for Mangrove Ecosystems, Okinawa, Japan, pp. 75–114.

Alves, R.R.N., Nishida, A.K., Hernández, M.I.M., 2005. Environmental perception of gatherers of the crab 'caranguejo-uçá' (*Ucides cordatus*, Decapoda, Brachyura) affecting their collection attitudes. J. Ethnobiol. Ethnomed. Volume 1, article 10 (3 November 2005). doi:10.1186/1746–4269–1–10 (http://www.ethnobiomed.com/content/1/1/10).

Ashton, E.C., Hogarth, P.J., Macintosh, D.J., 2003. A comparison of brachyuran crab community structure at four mangrove locations under different management systems along the Melaka Straits-Andaman Sea Coast of Malaysia and Thailand. Estuaries 26, 1461–1471.

Barbier, E.B., 2000. Valuing the environment as input: review of applications to mangrove-fishery linkages. Ecol. Econ. 35, 47–61.

Barbier, E.B., 2006a. Natural barriers to natural disasters: replanting mangroves after the tsunami. Front. Ecol. Env. 4, 124–131.

Barbier, E.B., 2006b. Valuing ecosystem services as productive inputs. Paper presented at the 43rd Panel Meeting of Economic Policy, 21–22 April 2006, Vienna, Austria.

Barbier, E.B., Cox, M., 2004. An economic analysis of shrimp farm expansion and mangrove conversion in Thailand. Land Econ. 80, 389–407.

Berkes, F., Hughes, T.P., Steneck, R.S., Wilson, J.A., Bellwood, D.R., Crona, B., Folke, C., Gunderson, L.H., Leslie, H.M., Norberg, J., Nyström, M., Olsson, P., Österblom, H., Scheffer, M., Worm, B., 2006. Globalization, roving bandits, and marine resources. Science 311, 1557–1558.

Biagi, P., Nisbet, R., 1992. Environmental history and plant exploitation at the aceramic sites of RH5 and RH6 near the mangrove swamp of Qurm (Muscat - Oman). Bull. Soc. Bot. Fr. 138, 571–578.

Binh, C.T., Phillips, M.J., Demaine, H., 1997. Integrated shrimp-mangrove farming systems in the Mekong delta of Vietnam. Aquac. Res. 28, 599–610.

Bosire, J.O., Dahdouh-Guebas, F., Kairo, J.G., Cannicci, S., Koedam, N., 2004. Spatial variations in macrobenthic fauna recolonisation in a tropical mangrove bay. Biodivers. Conserv. 13, 1059–1074.

Christensen, S.M., Macintosh, D.J., Phuong, N.T., 2004. Pond production of the mud crabs *Scylla paramamosain* (Estampador) and S. *olivacea* (Herbst) in the Mekong Delta, Vietnam, using two different supplementary diets. Aquac. Res. 35, 1013–1024.

Crane, J., 1975. Fiddler crabs of the world. Ocypodidae: genus *Uca*. Princeton University Press, Princeton, New Jersey.

Dahdouh-Guebas, F., Verneirt, M., Tack, J.F., Van Speybroeck, D., Koedam, N., 1998. Propagule predators in Kenyan mangroves and their possible effect on regeneration. Mar. Freshw. Res. 49, 345–350.

Dahdouh-Guebas, F., Jayatissa, L.P., DiNitto, D., Bosire, J.O., Lo Seen, D., Koedam, N., 2005. How effective were mangroves as a defence against the recent tsunami? Curr. Biol. 15, R443–R447.

Dall, W., Hill, B.J., Rothilsberg, P.C., Staples, D.J., 1990. The biology of the Penaeidae. Adv. Mar. Biol. 27, 1–461.

Danielsen, F., Sørensen, M.K., Olwig, M.F., Selvam, V., Parish, F., Burgess, N.D., Hiraishi, T., Karunagaran, V.M., Rasmussen, M.S., Hansen, L.B., Quarto, A., Suryadiputra, N., 2005. The Asian tsunami: a protective role for coastal vegetation. Science 310, 643.

Davie, P.J.F., 1982. A preliminary checklist of the Brachyura (Crustacea: Decapoda) associated with Australian mangrove forests. Operculum 5, 204–207.

De Weerdt, W.H., Rützler, K., Smith, K.P., 1991. The Chalinidae (Porifera) of Twin Cays, Belize, and adjacent waters. Proc. Biol. Soc. Wash. 104, 189–205.

Díaz, H., Bevilacqua, M., Bone, D., 1985. Esponjas en manglares del Parque Nacional Morrocoy. Fondo Editorial, Acta Cientifica Venezolana, Caracas, Venezuela.

Diele, K., Koch, V., Saint-Paul, U., 2005. Population structure, catch composition and CPUE of the artisanally harvested mangrove crab *Ucides cordatus* (Ocypodidae) in the Caeté estuary, North Brazil: Indications for overfishing? Aquat. Living Resour. 18, 169–178.

Eklöf, A., Ebenman, B., 2006. Species loss and secondary extinctions in simple and complex model communities. J. Anim. Ecol. 75, 239–246.

Ellison, A.M., 2000. Mangrove restoration: do we know enough? Restor. Ecol. 8, 219–229.

Ellison, A.M., Farnsworth, E.J., 1992. The ecology of Belizean mangrove-root fouling communities: patterns of distribution and abundance and effects on root growth. Hydrobiologia 247, 87–98.

Ellison, A.M., Farnsworth, E.J., 2001. Mangrove communities. In: Bertness, M.D., Gaines, S.D., Hay, M.E. (Eds.), Marine Community Ecology. Sinauer Associates, Sunderland, Massachusetts, USA, pp. 423–442.

Ellison, A.M., Farnsworth, E.J., Twilley, R.R., 1996. Facultative mutualism between red mangroves and root-fouling sponges in Belizean mangal. Ecology 77, 2431–2444.

Ellison, A.M., Farnsworth, E.J., Merkt, R.E., 1999. Origins of mangrove ecosystems and the mangrove biodiversity anomaly. Glob. Ecol. Biogeogr. 8, 95–115.

Erftemeijer, P.L.A., Lewis III, R.R., 2000. Planting mangroves on intertidal mudflats: habitat restoration or habitat conversion? Proc. Regional Seminar for East and Southeast Asian Countries: ECOTONE VIII, Ranong and Phuket, Thailand, 23–28 May, 1999. Royal Forestry Department, Bangkok, Thailand, pp. 156–165.

FAO, 2006. FISHSTAT Plus: Universal software for fishery statistical time series, version 2.3.1. FAO Fisheries Department, Fishery Information, Data and Statistics Unit.

Farnsworth, E.J., Ellison, A.M., 1991. Patterns of herbivory in Belizean mangrove swamps. Biotropica 23, 555–567.

Farnsworth, E.J., Ellison, A.M., 1996. Scale-dependent spatial and temporal variability in biogeography of mangrove-root epibiont communities. Ecol. Monogr. 66, 45–66.

Farnsworth, E.J., Ellison, A.M., 1997. The global conservation status of mangroves. Ambio 26, 328–334.

Field, C., 1998a. Rationales and practices of mangrove afforestation. Mar. Freshw. Res. 49, 353–358.

Field, C.D., 1998b. Rehabilitation of mangrove ecosystems: an overview. Mar. Pollut. Bull. 37, 383–392.

Fielder, D., 2004. Crab aquaculture scoping study and workshop. In: Allan, G., Fielder, D. (Eds.), Mud Crab Aquaculture in Australia and Southeast Asia: Proc. ACIAR Crab Aquaculture Scoping Study and Workshop, 28–29 April 2003, Joondooburri Conference Center, Bribie Island. Australian Centre for International Agricultural Research, Canberra, Australia, pp. 10–30.

FDPM (Forestry Department Peninsular Malaysia), 2006. Management and policy strategies for mangrove forests. http://www.forestry.gov.my/eManagement.html.

Glaser, M., 2003. Interrelations between mangrove ecosystem, local economy and social sustainability in Caeté Estuary, North Brazil. Wetlands Ecol. Manag. 11, 265–272.

Glaser, M., da Silva Oliveira, R., 2004. Prospects for co-management of mangrove ecosystems on the North Brazilian coast: whose rights, whose duties and whose priorities? Nat. Resour. Forum 28, 224–233.

Glaser, M., Diele, K., 2004. Asymmetric outcomes: assessing central aspects of the biological, economic and social sustainability of a mangrove crab fishery, *Ucides cordatus* (Ocypodidae), in North Brazil. Ecol. Econ. 49, 361–373.

Gong, W.K., Ong, J.E., 1995. The use of demographic studies in mangrove silviculture. Hydrobiologia 295, 255–261.

Guest, M.A., Connolly, R.M., Lee, S.Y., Loneragan, N.R., Breitfuss, M.J., 2006. Mechanism for the small-scale movement of carbon among estuarine habitats: organic matter transfer not crab movement. Oecologia 148, 88–96.

Hajdu, E., Rützler, K., 1998. Sponges, genus *Mycale* (Poecilosclerida : Demospongiae: Porifera), from a Caribbean mangrove and comments on subgeneric classification. Proc. Biol. Soc. Wash. 111, 737–773.

Holling, C.S., 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. Ecol. Monogr. 62, 447–502.

Hussain, Z., Acharya, G., 1994. Mangroves of the Sundarbans. IUCN Wetlands Programme, Gland, Switzerland, vol. 2. Bangladesh.

Hutabarat, J., 1999. Suitability of local raw materials for mud crab feed development. In: Keenan, C.P., Blackshaw, A. (Eds.), Mud Crab Aquaculture and Biology: Proc. International scientific forum held in Darwin, Australia, 21–24 April 1997. Australian Centre for International Agricultural Research, Canberra, Australia, pp. 109–113.

Iftekhar, M.S., Islam, M.R., 2004. Degeneration of Bangladesh's Sundarbans mangroves: a management issue. Int. For. Rev. 6, 123–135.

ISME (International Society for Mangrove Ecosystems), 1992. Charter for Mangroves. http://www.mangrove.or.jp/isme/english/charter.pdf.

Islam, M.S., Wahab, M.A., 2005. A review on the present status and management of mangrove wetland habitat resources in Bangladesh with emphasis on mangrove fisheries and aquaculture. Hydrobiologia 542, 165–190.

Jones, D.A., 1984. Crabs of the mangal ecosystem. In: Por, F.D., Dor, I. (Eds.), Hydrobiology of the Mangal. Junk, The Hague, The Netherlands, pp. 89–110.

Kathiresan, K., Bingham, B.L., 2001. Biology of mangroves and mangrove ecosystems. Adv. Mar. Biol. 40, 81–251.

Keenan, C.P., Davie, P.J.F., Mann, D.L., 1998. A revision of the genus *Scylla* de Haan, 1833 (Crustacea: Decapoda: Brachyura: Portunidae). Raffles Bull. Zool. 46, 217–245.

Kelaher, B.P., Chapman, M.G., Underwood, A.J., 1998a. Changes in benthic assemblages near boardwalks in temperate urban mangrove forests. J. Exp. Mar. Biol. Ecol. 228, 291–307.

Kelaher, B.P., Underwood, A.J., Chapman, M.G., 1998b. Effect of boardwalks on the semaphore crab Heloecius cordiformis in temperate urban mangrove forests. J. Exp. Mar. Biol. Ecol. 227, 281–300.

Kieckbusch, D.K., Koch, M.S., Searfy, J.E., Anderson, W.T., 2004. Trophic linkages among primary producers and consumers in fringing mangroves of subtropical lagoons. Bull. Mar. Sci. 74, 271–285.

Kjerfve, B., Lacerda, L.D., 1993. Mangroves of Brazil. In: Lacerda, L.D. (Ed.), Conservation and Sustainable Utilization of Mangrove Forests in Latin America and Africa Regions. Part I- Latin America. International Society for Mangrove Ecosystems, Okinawa, Japan, pp. 245–272.

Kohlmeyer, J., Bebout, B., 1986. On the occurrence of marine fungi in the diet of *Littorina angulifera* and observations on the behavior of the periwinkle. Mar. Ecol. 7, 333–343.

Lee, S.Y., 1998. Ecological role of grapsid crabs in mangrove ecosystems: a review. Mar. Freshw. Res. 49, 335–343.

Lewis, R.R., 2005. Ecological engineering for successful management and restoration of mangrove forests. Ecol. Eng. 24, 403–418.

Lindner, B., 2005. Impacts of mud crab hatchery technology in Viet Nam (Impact assessment series report no. 36). Australian Centre for International Agricultural Research, Canberra, Australia.

Loneragan, N.R., Ahmad Adnan, N., Connolly, R.M., Manson, F.J., 2005. Prawn landings and their relationship with the extent of mangrove and shallow waters in western peninsular Malaysia. Estuar. Coast. Shelf Sci. 63, 187–200.

Macintosh, D.J., Ashton, E.C., Havanon, S., 2002. Mangrove rehabilitation and intertidal biodiversity: a study of the Ranong mangrove ecosystem, Thailand. Estuar. Coast. Shelf Sci. 55, 331–345.

Manson, F.J., Loneragan, N.R., Harch, B.D., Skilleter, G.A., Williams, L., 2005a. A broad-scale analysis of links between coastal fisheries production and mangrove extent: a case-study for northeastern Australia. Fish. Res. 74, 69–85.

Manson, F.J., Loneragan, N.R., Skilleter, G.A., Phinn, S.R., 2005b. An evaluation of the evidence for linkages between mangroves and fisheries: A synthesis of the literature and identification of research directions. Oceanogr. Mar. Biol. Ann. Rev. 43, 483–513.

Mazda, Y., Magi, M., Kogo, M., Hong, P.N., 1997. Mangroves as a coastal protection from waves in the Tong King Delta, Vietnam. Mangroves and Salt Marshes 1, 127–135.

Millamena, O.M., Quinitio, E.T., 1999. Reproductive performance of pond-sources *Scylla serrata* fed various broodstock diets. In:

Keenan, C.P., Blackshaw, A. (Eds.), Mud Crab Aquaculture and Biology: Proc. International scientific forum held in Darwin, Australia, 21–24 April 1997. Australian Centre for International Agricultural Research, Canberra, Australia, pp. 114–117.

Minh, T.H., Yakupitiyage, A., Macintosh, D.J., 2001. Management of the integrated mangrove-aquaculture farming systems in the Mekong Delta of Vietnam (ITCZM Monograph No. 1). Asian Institute of Technology: Integrated Tropical Coastal Zone Management, School of Environment, Resources and Development, Pathumthani, Thailand.

Odum, W.E., Heald, E.J., 1972. Trophic analyses of an estuarine mangrove community. Bull. Mar. Sci. 22, 671–738.

Othman, J., Bennett, J., Blamey, R., 2004. Environmental values and resource management options: a choice modelling experience in Malaysia. Environ. Dev. Econ. 9, 803–824.

Othman, M.A., 1994. Value of mangroves in coastal protection. Hydrobiologia 285, 277–282.

Paine, R.T., 1966. Food web complexity and species diversity. Am. Nat. 100, 65–75.

Pauly, D., Ingles, J., 1986. The relationship between shrimp yields and intertidal vegetation (mangrove) areas: a reassessment. Workshop Rep. - Intergov. Oceanogr. Comm. 44, 277–283 (Suppl.).

Pauly, D., Christensen, V., Froese, R., Palomares, M.L., 2000. Fishing down aquatic food webs. Am. Sci. 88, 46–51.

Perry, D.M., 1988. Effects of associated fauna on growth and productivity in the red mangrove. Ecology 69, 1064–1075.

Rao, A.N., 1987. Mangrove ecosystems of Asia and the Pacific. In: Umali, R. (Ed.), Mangroves of Asia and the Pacific: Status and Management. Technical Report of the UNDP/UNESCO Research and Training Pilot Programme on Mangrove Ecosystems in Asia and the Pacific, Quezon City, Philippines, pp. 1–48.

Reid, D.G., 1986. Molluscs of mangrove forests in the Indo-Pacific region. British Museum (Natural History), London.

Reid, D.G., 1999. The genus *Littoraria* Griffith and Pidgeon, 1834 (Gastropoda: Littorinidae) in the tropical eastern Pacific. Veliger 42, 21–53.

Robertson, A.I., Alongi, D.M., Boto, K.G., 1992. Food chains and carbon fluxes. In: Robertson, A.I., Alongi, D.M. (Eds.), Tropical Mangrove Ecosystems. American Geophysical Union, Washington, DC, pp. 293–326.

Rönnbäck, P., 1999. The ecological basis for economic value of seafood production supported by mangrove ecosystems. Ecol. Econ. 29, 235–252.

Rönnbäck, P., Troell, M., Zetterström, T., Babu, D.E., 2003. Mangrove dependence and socio-economic concerns in shrimp hatcheries of Andhra Pradesh, India. Environ. Conserv. 30, 344–352.

Roth, L.C., 1992. Hurricanes and mangrove regeneration: effects of Hurricane Joan, October 1988, on the vegetation of Isla del Venado, Bluefields, Nicaragua. Biotropica 24, 275–284.

Roy, S.D., Krishnan, P., 2005. Mangrove stands of Andamans *vis-à-vis* tsunami. Curr. Sci. 89, 1800–1804.

Rützler, K., 1969. The mangrove community, aspects of its structure, faunistics and ecology. In: Castanares, A.A., Phleger, F.B. (Eds.), Lagunas Costeras, un Simposio. UNAM-UNESCO, Mexico City, pp. 515–535.

Rützler, K., Smith, K., 1992. Guide to Western Atlantic species of *Cinachyrella* (Porifera: Tetillidae). Proc. Biol. Soc. Wash. 105, 148–164.

Sasekumar, A., Chong, V.C., 1998. Faunal diversity in Malaysian mangroves. Glob. Ecol. Biogeogr. Lett. 7, 57–60.

Sathirathai, S., Barbier, E.B., 2001. Valuing mangrove conservation in southern Thailand. Contemp. Econ. Policy 19, 109–122.

Schories, D., Barletta-Bergan, A., Barletta, M., Krumme, U., Mehlig, U., Rademaker, V., 2003. The keystone role of leaf-removing crabs in mangrove forests of North Brazil. Wetlands Ecol. Manag. 11, 243–255.

Skilleter, G.A., 1996. Validation of rapid assessment of damage in urban mangrove forests and relationships with molluscan assemblages. J. Mar. Biol. Assoc. UK 76, 701–716.

Skilleter, G.A., Warren, S., 2000. Effects of habitat modification in mangroves on the structure of mollusc and crab assemblages. J. Exp. Mar. Biol. Ecol. 244, 107–129.

Smith III, T.J., Chan, H.T., McIvor, C.C., Robblee, M.B., 1989. Comparisons of seed predation in tropical tidal forests from three continents. Ecology 70, 146–151.

Sokal, R.R., Rohlf, F.J., 1995. Biometry, 3rd ed. W.H. Freeman and Co, New York.

Sutherland, J.P., 1980. Dynamics of the epibenthic community on roots of the mangrove *Rhizophora mangle*, at Bahia de Buche, Venezuela. Mar. Biol. 58, 75–84.

Tan, C.G.S., Ng, P.K.L., 1994. An annotated checklist of mangrove brachyuran crabs from Malaysia and Singapore. Hydrobiologia 285, 75–84.

Tomlinson, P.B., 1986. The Botany of Mangroves. Cambridge Univ. Press, Cambridge.

Tong, P.H.S., Auda, Y., Populus, J., Aizpuru, M., Al Habshi, A., Blasco, F., 2004. Assessment from space of mangroves evolution in the Mekong Delta, in relation to extensive shrimp farming. Int. J. Remote Sens. 25, 4795–4812.

Triño, A.T., Rodriguez, E.M., 2002. Pen culture of mud crab *Scylla serrata* in tidal flats reforested with mangrove trees. Aquaculture 211, 125–134.

Trong, N.V., 1999. Mixed shrimp farming-mangrove forestry models in the Mekong Delta: ACIAR PN 9412. In: Keenan, C.P., Blackshaw, A. (Eds.), Mud Crab Aquaculture and Biology: Proc. International scientific forum held in Darwin. Australia, 21–24 April 1997. Australian Centre for International Agricultural Research, Canberra, Australia, pp. 21–24.

UNESCO, 1979. The mangrove ecosystem: scientific aspects and human impact. UNESCO Rep. Mar. Sci., vol. 9.

Van Soest, R.W.M., 1978. Marine sponges from Curacao and other Caribbean localities. Part I. Keratosa. Stud. Fauna of Curacao and Other Caribbean Islands 56, 1–94.

Van Soest, R.W.M., 1980. Marine sponges from Curacao and other Caribbean localities: Part II. Haplosclerida. Stud. Fauna of Curacao and Other Caribbean Islands 62, 1–78.

Van Soest, R.W.M., 1984. Marine sponges from Curacao and other Caribbean localities. Part III. Poecilosclerida. Stud. Fauna of Curacao and Other Caribbean Islands 66, 1–167.

Vaseeharan, B., Jayakumar, R., Ramasamy, P., 2003. PCR-based detection of white spot syndrome virus in cultured and captured crustaceans in India. Lett. Appl. Microbiol. 37, 443–447.

Verheij, E., Makoloweka, S., Kalombo, H., 2004. Collaborative coastal management improves coral reefs and fisheries in Tanga, Tanzania. Ocean Coast. Manag. 47, 309–320.

Walters, B.B., 2004. Local management of mangrove forests in the Philippines: successful conservation or efficient resource exploitation? Hum. Ecol. 32, 177–195.

Warner, G.F., 1967. The life history of the mangrove tree crab, *Aratus pisonii*. J. Zool. 153, 321–335.

Watson, J.G., 1928. Mangrove forests of the Malay Peninsula. Malay. For. Rec. 6, 1–275.

Wilkie, M.L., Fortuna, S., 2003. Status and trends in mangrove area extent worldwide. Food and Agriculture Organization of the United Nations, Rome, Italy.

Williams, M.J., Primavera, J.H., 2001. Choosing tropical portunid species for culture, domestication and stock enhancement in the Indo-Pacific. Asian Fish. Sci. 14, 121–142.

World Bank, International Society for Mangrove Ecosystems, cenTER Aarhus, 2004. Principles for a code of conduct for the management and sustainable use of mangrove ecosystems. The World Bank, Washington, D.C.

Wortel, O., 2005. Kosrae's mangrove crabs prove tasty export. Federated States of Micronesia Government News and Public Statements, April 7, 2005. http://www.fsmgov.org/press/nw040705.htm.

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Mangrove macrobenthos: Assemblages, services, and linkages

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Abstract

Macrobenthic assemblages are relatively poorly known compared to other components of the mangrove ecosystem. Tropical mangroves support macrobenthic biodiversity resources yet to be properly documented and interpreted. Some methodological challenges, such as the generally high spatial heterogeneity and complexity of the habitat, evidently reduce sampling efficiency and accuracy, while also leaving some microhabitats under-sampled. Macrobenthic assemblage structure seems to be influenced by local environmental conditions, such as hydroperiod, organic matter availability and sediment characteristics. Brachyurans, gastropods and oligochaetes dominate in the sediment, with the former two groups also common on hard surfaces provided by tree trunks, while insects and arachnids inhabit the canopy. Traditionally, studies of mangrove macrobenthos have focused on assemblage structure or the biology of individual species, but more complex inter-specific interactions and the inter-relationship between habitat and the biota are recently being addressed. Brachyuran crabs are the best-studied macrobenthos group, but many issues about their role in mangrove ecosystem dynamics are still controversial. Despite many species of mangrove macrobenthos being referred to as ‘trophic dead ends’, most serve as important links between recalcitrant mangrove organic matter and estuarine secondary production, through feeding excursion by mobile nekton during the high tide, and macrobenthos-mediated processing and exportation of organic matter. A significant difference in the standing crop biomass of forests between the Indo-west-Pacific (IWP)’ and Atlantic-east-Pacific (AEP) mangroves may be related to the difference in species richness of mangrove as well as macrobenthos diversity in the two bioregions. Such differences in assemblage structure may also result in different ecosystem functioning, but the nature of the links is, however, yet to be explored. There is also a strong need for evaluating mangrove macrobenthos assemblages as a component of the connected biotic resources in the land-sea continuum, rather than as an isolated faunal group.

Keywords: Ecosystem services; Ecosystem function; Organic matter dynamics; Crabs; Gastropods; Diversity

1. Introduction

The macrobenthos of mangroves are relatively poorly known compared to other aspects of these productive ecosystems, such as floristics and trophic ecology. The classical account of Macnae (1968) demonstrates, qualitatively, the diversity of the mangrove fauna, particularly the macrobenthos, in rich tropical forests in the Indo-West-Pacific, but advancement in the understanding of assemblage structure and the role of these animals in ecosystem function has since stagnated for a few decades. Mangroves have often been regarded as one of the most productive ecosystems in the world, but discussion has rarely been focussed on the contribution from the resident mangrove macrofauna.

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Table 1
The abundance and dominant taxa of macrobenthos assemblages reported from selected studies on mangroves, and factors thought to exert strong influence on abundance and structure

Location	Species richness	Numerically dominant taxa	Density (m^{-2})	Factors shaping assemblage	Reference
Port Swettenham, Malaysia	85	Polychaetes Gastropods Crustaceans	<507 ('stream' station)	Tidal regime, sediment (grain size, pH)	Sasekumar (1974)
Sydney, Australia	17 – 29	Molluscs Crustaceans Annelids	<790	Disturbance due to boardwalk	Kelehar et al. (1998)
Kenya, Africa	ND	Oligochaetes (94%) Polychaete	23,058*	Detritus availability, predation	Schrijvers et al. (1998)
Port Hacking estuary, Australia	ND	Oligochaete Molluscs	37 – 45 per core*	No effect of urbanisation	Lindegarth and Hoskin (2001)
Mai Po, Hong Kong	46	Crustaceans Gastropods	998*	Salinity, season	Lui et al. (2002)
Puhinui Creek, New Zealand	ND	Oligochaetes Gastropods	17 – 80 per core*	Stand age (on species richness)	Morrisey et al. (2003)
Sydney, Australia	22 – 31	Oligochaetes Polychaetes	ND	No effect of sediment, high within-site variation	Chapman and Tolhurst (2004)
Matapouri estuary, northern New Zealand	29.4 per core	Oligochaetes Gastropods	8,000*	Sampling date, location	Alfaro (2006)

*- Average density for all taxa recorded in study; other values refer to maximum densities attained by individual taxa or stations. Numbers for species richness refer to totals recorded in the study, unless otherwise stated. ND - no data.

Interest in the non-fishery value of mangrove fauna rekindled in the mid 1980s when grapsid crabs were found to play an important role in leaf litter turnover (Robertson, 1986, 1991, see Robertson et al., 1992), significantly retaining mangrove organic production and reducing direct export. Subsequently, the role of the macrobenthos in shaping the structure and function of mangrove forests has been demonstrated through activities such as bioturbation, organic matter processing and propagule predation. This overview attempts to examine the current knowledge of the mangrove macrobenthos assemblages, the ecosystem services they provide and the linkage with communities and processes in adjoining habitats.

2. The assemblages

2.1. Species richness and abundance

The microhabitats offered by mangrove forests cover a wide range of coarse to fine-grained environments. Microhabitats that are occupied by macrobenthos in mangroves include the hard substrata offered by the trunk, aerial roots and foliage of mangrove trees, and the soft sediment, which is often heavily ramified by fine and shallow nutritive roots. Additional microhabitats are created for smaller benthos through the habitat modifying activities of other taxa, such as the burrows of large crustaceans. Some macrofaunal groups have been particularly successful as components of the mangrove macrobenthos, with members being important inhabitants of all available microhabitats. For example, brachyuran crabs, particularly Grapsidae, display arboreal as well as epipelic and burrowing habits (Vannini and Ruwa, 1994; Lee, 1998; Sivasothi, 2000).

Faunal assemblages of mangroves are significantly less studied and documented than the forests they inhabit. Methods for studying mangrove forest structure are well established (e.g. Cintron and Schaeffer-Novelli, 1984) and procedures for characterising the complexity and heterogeneity of mangroves are available (e.g. Lugo and Cintron, 1975). The macrobenthos of mangroves are, however, much more difficult to characterise and problems in quantifying macrobenthic abundance exist even for the most apparent groups (e.g. crabs - Nobbs and McGuinness, 1999; Skov et al., 2002).

The mangrove epibenthos are generally dominated by decapod crustaceans (especially brachyuran crabs) and gastropods, while polychaetes, oligochaetes and insect larvae make up the bulk of the infauna (Table 1). Other taxa such as sipunculids can also be locally abundant (Sasekumar and Chong, 1998). Composition of the assemblages may differ significantly depending on whether some taxa, such as nematodes, are included. Nematodes are the most abundant metazoans in estuarine sediments (Alongi, 1987; Gwyther, 2003; Gwyther and Fairweather, 2005) but most are considered to be meio-rather than macrofauna. Although traditionally attention has been focused on benthos of the sediment, the sessile epibionts of mangrove trees (e.g. barnacles) have been investigated in perspectives of recruitment and assemblage dynamics (Satumanatpan et al., 1999; Ross, 2001; Satumanatpan and Keough, 2001), as have the diet and behaviour of tree-climbing crabs (Vannini et al., 1995; Erickson et al., 2003). Comparison with adjoining lower intertidal flats suggests shift in dominance towards taxa that are more dependent on tidal immersion, e.g. filter-feeding bivalves (Dittmann, 2002). Less is known about the functional organisation of the mangrove macrobenthos.

Studies on mangrove macrobenthos have generally reported assemblages with lower species richness than the adjoining habitats such as seagrass meadows and open sand/mudflats, but abundance levels are usually similar (Dittmann, 2001; Alfaro, 2006) (Table 1). Despite the lower species richness, abundance of mangrove macrobenthos is generally high. Natural drivers such as stand age (Morrisey et al., 2003), substrate elevation and salinity (Lui et al., 2002) have been identified as influencing assemblage structure and abundance, while anthropogenic influence such as chemical pollution and sedimentation are important in populated areas (Inglis and Kross, 2000; Skilleter and Warren, 2000; Ellis et al., 2004). High small-scale spatial variability is usually detected (Chapman and Tolhurst, 2004) while equivocal results were recorded for the effect of urban runoff on assemblage structure (Inglis and Kross, 2000; Lindegarth and Hoskin, 2001; Courtenay et al., 2005).

The mangrove habitat has a low degree of environmental favourableness, due to stresses arising from tidal fluctuations (hypersaline sediment), or hypoxia (production of toxins from reductive metabolism). Mangroves have remarkable adaptations to these conditions and are able to attain high levels of primary productivity. Part of the adaptation, however, is to minimise nutrient drain through organic matter loss. The nutritional quality of leaf litter, the largest component of mangrove organic matter input to estuarine food chains, is generally poor. This trophic limitation, together with the physical environmental stresses, may have limited the proliferation of species in the mangrove macrobenthos. The assemblages are therefore dominated by large populations of few species that are adapted to these limitations, e.g. possession of cellulases that can help digest structural polysaccharides (Neilson et al., 1986; Neilson and Richards, 1989) or an ability to synthesise polyunsaturated fatty acids from simpler precursors (unpubl. data).

2.2. Methodological issues

Many factors contribute to the methodological hurdles for quantifying macrobenthos abundance in mangroves, one of which is structural complexity of the habitat. McCoy and Bell (1991) identified three elements of habitat structure: complexity (the absolute abundance of individual structural components), heterogeneity (the relative abundance of components) and scale (size or volume used to measure heterogeneity and complexity). Mangrove forests have no shortage of structures that define the benthic environment: prop roots, pneumatophores, knee joints create a complex epibenthic landscape, while the shallow but widespread cable and fibrous root systems result in a fine-grained and often impenetrable substrate to sample from. The spatial occurrence of these structures is highly irregular, thus contributing to both the complexity and heterogeneity of the habitat. These structures prevent the use of most devices commonly deployed for quantitative sampling of the benthos, such as trawls, coring devices, and pop nets; also making direct counting difficult. As a result of these barriers, indirect and inaccurate methods are often used, e.g. counting of burrows for estimating crab density (e.g. Steinke et al., 1993; Skov and Hartnoll, 2001; Skov et al., 2002), which are known to present biases (e.g. Warren, 1990; Nobbs and McGuinness, 1999). Macrobenthic assemblage data must therefore be viewed with some caution, as these problems with sampling affect the mangroves significantly more than other structurally less complex habitats, such as mudflats.

The difficulty in sampling particular microhabitats in the mangrove environment may have contributed to the apparent low species richness. Sediments of established mangrove forests are often impenetrable due to the myriad of fine shallow roots. Selective sampling of more easily penetrable areas to coring devices would underestimate species richness, as would the omission of other structural components of the habitat. Pneumatophores, tree trunks, prop roots and leaf litter have been, for example, demonstrated to support distinct and sometimes obscure (e.g. Morton, 1976; Gillikin et al., 2001; Proches et al., 2001) faunal assemblages that might develop intricate interactions with their mangrove hosts (Ellison et al., 1996; Gwyther, 2003; Gwyther and Fairweather, 2005). In fringing mudflats, burrows made by macrofauna such as crabs also support local assemblages (Dittmann, 1996). Failure to include these microhabitats will seriously underestimate species richness.

The lack of a satisfactory approach to measuring mangrove habitat complexity and heterogeneity also hampers efforts in relating macrobenthos assemblages to habitat conditions. Traditional complexity indices developed for terrestrial forests over-rely on above-

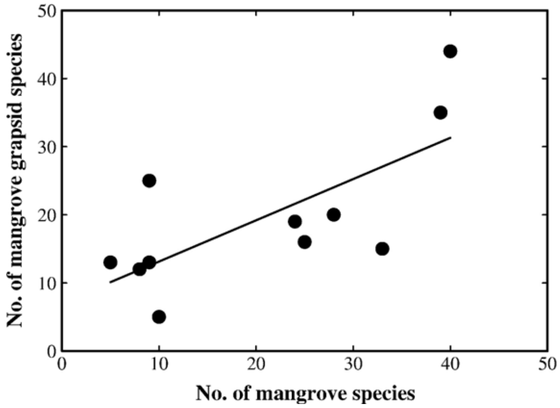

Fig. 1. Correlation between the species richness of grapsid crabs and mangroves at a regional scale. Data based on Lee (1998) with additional information from Australia (Davie, 2002), Malaysia (Ashton et al., 2003b) and Hong Kong (Lee and Leung, 1999). Regression has an r^2 value of 0.508, $p<0.02$.

ground characteristics such as tree height and stem density (Blanco et al., 2001). These factors are relatively irrelevant to macrobenthos of mangroves, which are more responsive to forest floor level structures (e.g. prop roots, pneumatophores). Many species of mangroves produce dense root structures both above and below the sediment surface that are primarily used for assisting with respiration and anchorage. In addition to modifying the oxygen availability of surface sediment, these root \structures greatly increase the complexity of the epibenthic and shallow endo-benthic environment. Such an increase in complexity through provision of additional microhabitats should be expected to result in positive effects on biodiversity but, as mentioned earlier, no such benefits have been demonstrated for mangroves.

The spatial scale of the studies also influences the apparent pattern. Chapman (1998) and Chapman and Tolhurst (2004) attempted to relate sediment properties such as water content, colloidal carbohydrate and chlorophyll-a concentration with the abundance pattern of macrobenthic assemblages, but failed to detect correlation at any spatial scale. The latter study, however, detected significant differences in the spatial scale of variation of the sediment parameters and the benthos. It is unclear at which spatial scale macrobenthic organisms respond to broad physical habitat conditions; it is likely that relevance of physical habitat structures and conditions depends on their sizes, which would correlate positively with the size of the faunal groups concerned (Hixon and Beets, 1989, 1993). Feeding efficiency of predatory fish, for example, is dependent on habitat complexity relative to their sizes (Laegdsgaard and Johnson, 2001; Meager et al., 2005).

2.3. Species interaction

The close relationship between the macrobenthos and the mangroves can be illustrated by significant correlations between the species richness of the two. Lee (1998) reported a positive correlation between grapsid crab and mangrove species richness at a regional scale,

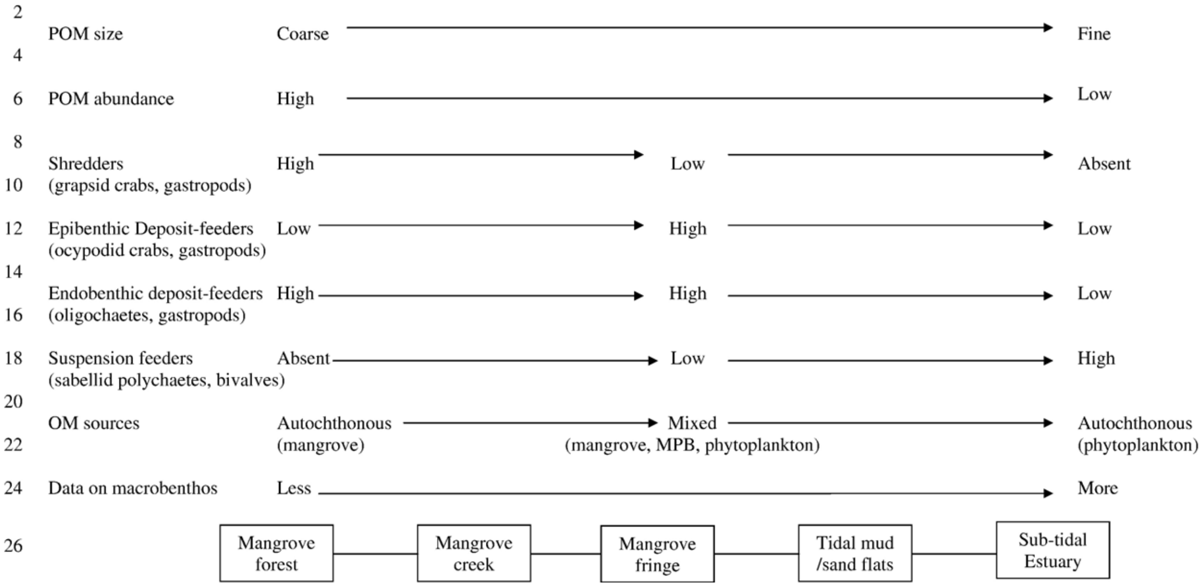

Fig. 2. A conceptual model depicting the pattern of particulate organic matter (POM) availability and utilisation in mangrove dominated estuaries, with indication of the relative abundance of the different guilds of macrobenthos involved in organic matter processing.

and the relationship seems to hold with additional recent data (Fig. 1), some of which also suggest a positive correlation at the local forest scale (e.g. Ashton et al., 2003a). The underlying explanation for such a correlation deserves more attention. It is also interesting to see at what spatial scale (e.g. local forest versus regional) the correlation is strongest, as this may shed light on the nature of the association. Correlation at the larger spatial scales is probably more a result of broad biogeographic patterns, whereas functional associations should be revealed by correlations at smaller spatial scales. A causal relationship should not be ruled out, as there is evidence of some mutual ecological dependence between mangrove and their macrobenthos, such as crabs (e.g. Smith et al., 1991; Lee and Kwok, 2002). Data on the other major macrobenthic taxa such as polychaetes and molluscs are scanty, and the lack of sufficient taxonomic resolution in most studies has further made comparisons unreliable.

In terms of functional organisation, macrobenthos associated with mangrove and adjacent environments (e.g. mud flats, subtidal estuary) are strongly influenced by the form and availability of organic matter. Large particulate organic matter (POM, e.g. leaf litter) produced by mangroves is initially processed by shredders such as grapsid crabs and gastropods in the shaded mangrove forest, where grazers of benthic microalgae are relatively rare. Shredded POM is utilised by endobenthic deposit-feeders such as oligochaetes. Tidal export of fine POM resulting from this processing then partly fuels the epibenthic consumer assemblages on the exposed banks and open sand/mud flats, dominated by deposit-feeders and grazers (e.g. ocypodids, opisthobranchs and microgastropods), which also utilise autochthonous microphytobenthos (MPB) production (Dittmann, 2000; Dittmann and Vargas, 2001). These habitats also support high densities of deposit-feeder infauna, dominated by polychaetes and oligochaetes. Further down the tidal gradient, where MPB production is limited by water column turbidity and mangrove POM contributions are diminished, the assemblage will be dominated by filter-feeders, e.g. sabellid polychaetes and bivalves (Fig. 2).

The hostile mangrove sediment environment (low oxygen penetration, high toxins, e.g. sulfide) often limits the abundance of large infauna that do not maintain burrows to assist aeration. Some groups have, however, developed specific trophic adaptations that enable them to tap from the normally unavailable nutrient sources. Bivalves of the family Lucinidae (e.g. *Austriella*) often attain high local densities in anoxic and sulfidic mangrove sediments, their nutrition probably assisted by their chemoautotrophic symbionts (bacteria). Their link to the mangrove food chain is, however, obscure.

Species interaction among the mangrove macrobenthos and its role in shaping faunal community structure has received little attention to date. Biotic influences such as competition and mutualism generally are more important in favourable, stable and productive habitats. Although mangroves are highly productive, environments in which they flourish cannot be described as favourable (e.g. salinity stress, high concentration of interstitial biotoxins) or stable (e.g. fluctuation in riverine input). Biotic processes are thus unlikely to exert overriding influence on community structure compared to physical factors. Activities of the macrobenthos have been shown, however, to directly or indirectly influence the other faunal components of mangroves. Numerically and functionally dominant species such as burrowing crabs have been reported to exert large influence on the distribution and abundance of other species. In most cases such influences are probably mediated through alteration of organic matter availability both spatially and in terms of quality (e.g. Lee, 1997; Botto and Iribarne, 1999), but direct evidence demonstrating such links is scanty. Such interactions could lead to secondary effects on processes such as foraging success of higher predators but the effect seems to depend on the nature of the predator-prey pair (e.g. Palomo et al., 2003; Martinetto et al., 2005). Schrijvers et al. (1995, 1998) found significant positive effects of exclusion of epibenthos on the infaunal meio- and macrobenthos, probably due to predation. Examples of facilitation have not been directly reported, but the apparent dependence on macrobenthos burrows by other invertebrates (e.g. Dittmann, 1996; Gillikin et al., 2001) suggests the existence of positive interactions. Very little is known about species interaction among the mangrove macrobenthos and much is yet to be learnt from processes shaping community structure and function in this spatially complex and productive environment. In some groups such as grapsid crabs, cannibalism can be an important process regulating species density and abundance (e.g. Kneib et al., 1999).

3. Role of macrobenthos in mangrove ecosystem services

Macrobenthos have been demonstrated to regulate the structure and function (e.g. productivity) of mangrove forests. Grapsid crabs have been proposed to influence forest structure through selective propagule predation (Smith, 1987; Osborne and Smith, 1990;

Smith et al., 1991; Frusher et al., 1994; Mcivor and Smith, 1995), with an inverse relationship between predation pressure and mangrove species dominance (the 'Predation-dominance hypothesis') but recent studies dispute the general significance of this relationship (Mckee, 1995; McGuinness, 1997; Sousa and Mitchell, 1999). Manipulative experiments in northeastern Australia have demonstrated that crab predation plays a more important role in maintaining forest structure than micro-habitat condition or differences in growth between species (Clarke and Kerrigan, 2000, 2002; Clarke, 2004). At the tree level, wood borers and epibionts mostly exert negative impacts on tree growth and productivity (Perry, 1988; Brooks and Bell, 2002; Svavarsson et al., 2002). Crab activities have also been suggested to regulate forest productivity through physical modification of the habitat (e.g. increased aeration due to burrow construction) or biological influence on nutrient turnover (e.g. Smith et al., 1991).

3.1. Organic matter dynamics and biogeochemistry

By far the most studied contribution of macrobenthos to mangrove ecosystem function is their role in organic matter dynamics. Molluscan and, particularly, decapod macrobenthos have been reported to process large quantities of mangrove leaf litter (Robertson, 1986; Slim et al., 1997; Lee, 1998; Fratini et al., 2004; Proffitt and Devlin, 2005), profoundly changing the physical and chemical nature of this organic matter. Leaf litter is the most important component of mangrove primary production that is readily available to consumers, but nutritional accessibility is often limited by poor quality. Mangrove leaf litter is a rich source of carbon, but nitrogen availability is poor (C/N ratio often >100) and feeding deterrents such as polyphenolics and tannins are abundant (Neilson and Richards, 1989), making it an unattractive organic matter source. One adaptation shown by mangrove macrobenthic detritivores is that these animals seem to have developed an ability to profitably consume this nutritively poor food source, and in the process turning the material into a form that is more conducive to further consumption by themselves and other animals. Grapsid crabs, for example, shred large amounts of fresh litter in the Indo-Pacific mangroves, transforming the material partly into crab biomass, and produce faecal material with a much increased surface area to volume ratio that will facilitate microbial colonisation (Lee, 1997; Werry and Lee, 2005). In this respect, these macrobenthic consumers of fresh mangrove leaf litter perform a role intermediate between the shredders in low order streams and the deposit-feeders in subtidal marine environments in terms of their contribution to organic matter flow and food generation for other consumers in the adjoined habitats, e.g. estuaries (Fig. 2).

Stable isotope and other tracer studies indicate that the crabs, as with most other mangrove animals, apparently do not depend heavily on the mangrove leaf organic matter for their nutritional needs (Lee, 2005; Hall et al., 2006). Many hypotheses have been proposed to explain this paradox (e.g. Skov and Hartnoll, 2002; Thongtham and Kristensen, 2005) but the most effective supplemental source is through occasional predation of other invertebrates and carrion. This model suffers, however, from the fact that this pathway will not work with molluscan detritivores such as *Terebralia palustris*, which also demonstrate significant dependence on mangrove leaf litter (Slim et al., 1997; Fratini et al., 2004).

Underground processes involving mangrove macrobenthos are virtually unknown. In mudflats, the burrows of macrobenthos such as crabs house distinct associated meio-and macrofauna (Dittmann, 1996), probably supported by local organic matter sources, e.g. cached leaves and faecal material of crabs. Irrigation and passive flushing by tidal flow, and pore water circulation may help shape the micro-environment of the burrow chambers, leading to different nutrient and organic matter dynamics. Again, this is a poorly known area of mangrove macrobenthos ecology.

Coastal wetlands are generally low-energy, depositional environments promoting sedimentation of fine particles that create a substrate with poor aeration. Mangroves demonstrate numerous adaptations for countering the hypoxia associated with the protected sediment, but the role of the macrobenthos is highly significant. Burrowing macrofauna greatly increase the surface area of the sediment-air/water interface, thus altering fundamental biogeochemical processes that are sensitive to redox conditions (Fenchel, 1996; Williamson et al., 1999; Rosenberg and Ringdahl, 2005). This change may also be mediated through vertical redistribution of sediment during burrow maintenance and construction (e.g. Warren and Underwood, 1986; Bortolus and Iribarne, 1999; Botto and Iribarne, 2000). Burrows built by large infauna also greatly modify tidal and porewater flow, contributing to materials exchange (Ridd, 1996; Stieglitz et al., 2000). The latter study demonstrated that multiple openings exist for a single burrow of the grapsid crab *Sesarma messa*, and the close spacing (<20 cm) of burrow chambers results in efficient removal of salt from sediments around mangrove roots through tidal flushing. It can be expected that exchange of other bioactive materials such as

Table 2
Predictions on aspects of ecosystem function in mangroves with contrasting levels of keystone species abundance (using the grapsid crabs as an example), such as between the Indo-west-Pacific (IWP) and Atlantic-east-Pacific (AEP) mangroves

Ecosystem attributes	Low crab richness and abundance (AEP)	High crab richness and abundance (IWP)
Forest structure	Determined mainly by propagule supply and factors such as light gap occurrence - more stochastic in nature	Determined mainly by survival upon crab predation - deterministic interaction
Organic matter retention	High OM retention especially in high-intertidal forests; export of OM mainly as coarse POM	High crab consumption especially in high-intertidal forests, significant OM retention; export of OM also as shredded micro-POM'
Organic matter turnover and mineralisation rates	Slow turnover (months), mainly mediated by microbial decomposition; slower mineralisation	Fast turnover (days to months); mediated by shredders and microbes; faster mineralisation
Secondary production in forest	Low	High
Forest productivity	Low, limited by phytotoxins and nutrient mineralisation (?)	High, facilitated by bioturbation effects of crabs

phytotoxins and dissolved organic matter between mangrove sediments and tidal water may also be facilitated by the same mechanism. Macrobenthos such as fiddler crabs may work synergistically with the aerating action of *Avicennia marina* pneumatophores in regulating microbe-mediated nutrient processes in mangrove sediments (Kristensen and Alongi, 2006).

A recent study on south Atlantic estuaries has revealed that sediments with high density of the crab *Chasmagnathes granulatus* had significantly more enriched δ^{15}N signatures (by 3 – 7‰) compared to no-crab areas (Botto et al., 2005). These authors attributed the difference to increased rate of denitrification mediated by the crabs and suggest that the source and turnover of N are thus altered beyond what is usually achievable through 'external' drivers, such as anthropogenic influences. Direct evidence of such an effect is yet to be reported.

3.2. Ecosystem services and macrobenthos diversity

The ecological implications of the striking difference in the richness and abundance of the crab fauna between the Indo-west-Pacific (IWP) and Atlantic-east-Pacific (AEP) (the 'Eastern' and 'Western' mangroves, respectively, *sensu* Tomlinson, 1986) deserve more attention. Given the range of ecosystem services deliverable by grapsid crabs, it may be hypothesized that this difference may result in fundamental differences in energy flow efficiency, organic matter dynamics and productivity. In the AEP mangroves, there is evidence that some of the roles played by grapsid crabs in the IWP mangroves are performed by gastropods (e.g. Proffitt and Devlin, 2005). Mcivor and Smith (1995) documented significantly lower rates in mangrove leaf consumption in a Florida mangrove compared to northeast Australia, and attributed the difference to the much impoverished grapsid crab fauna in the former. There is evidence that grapsid crab involvement in detrital dynamics greatly enhances mangrove leaf litter turnover rates, accelerates microbial detrital processing (Lee, 1997, 2005; Werry and Lee, 2005), and forest productivity might be influenced by crab bioturbation (Smith et al., 1989).

Much research effort has been paid to the relationship between terrestrial biodiversity and ecosystem services and function (Knops et al., 1999; Bunker and Naeem, 2006), but aquatic, particularly marine, ecosystems have received relatively less attention (Duarte, 2000; Naeem, 2006). Recent studies on stream and seagrass ecosystems have demonstrated linkages between species mix and

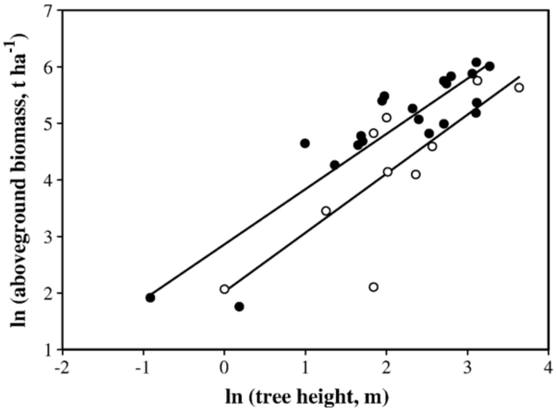

Fig. 3. The relationship between above-ground biomass and tree height in the IWP (●) and AEP (○) mangroves, based on the data from Table 5 of Fromard et al. (1998). Both variables are ln-transformed before analysis, i.e. the regression is based on the allometric relationship biomass= a (height)^b, where a and b are constants (or ln(biomass)= ln $a + b$ ln(height) after ln-transformation). The regressions cover forests of the same height range and are both significant at $p<0.001$. The slopes (b) of the regression lines for the IWP and AEP mangroves are, respectively, 0.977 and 1.043 and are equal ($p>0.1$). The elevations (ln a) of the two lines are, however, different ($t=2.94$, $p<0.01$), meaning that IWP mangroves have significantly higher above-ground biomass than AEP mangroves of the same tree height.

richness on ecological processes such as litter decomposition (Duarte et al., 2006; Moore and Fairweather, 2006). Both studies, however, identified stronger influence from the presence of specific species than sheer species number. The positive effect of species mixture over single species in controlling the rate of ecological processes is thought to be derived from complementarity of species roles (Hector, 1998; Hooper et al., 2005). The function of critical transitional zones such as intertidal wetlands may suffer significantly from loss of diversity (Levin et al., 2001). These authors have, however, suggested considerable levels of functional redundancy amongst the resident invertebrate fauna of estuarine and coastal wetlands. Functional redundancy is suggested to be inversely proportional to species richness in functional groups, with groups such as detritivores and deposit-feeders having high redundancy (Levin et al., 2001). This notion is, however, potentially problematic, as high diversity is often a reflection of good resource partitioning, food web complexity and thus high ecosystem stability and efficiency (Balvanera et al., 2006). The global differences in mangrove species richness have stimulated discussion on the relationship between mangrove biodiversity and ecosystem function (Field et al., 1998). There is, however, still no explicit study demonstrating this relationship to date. Predictions can similarly be made on the differences in ecosystem function resulting from the difference in species richness and abundance of important ('keystone') macrobenthos components, such as grapsid crabs (Table 2).

A preliminary comparison of the regression relationship between above-ground biomass of mangrove forests and average tree height of the IWP and AEP mangroves using the general allometric equation Biomass= a (Height)^b results in a significant difference in the value of a, which has a significantly higher value for the IWP mangroves (Fig. 3). As mature forests are expected to demonstrate P/B ratios ≈1, this difference potentially reflects higher levels of primary productivity in the IWP mangroves. The difference could be a result of difference in climate, tree density, stand age, species architecture and anthropogenic disturbances (Clough, 1992; Clough et al., 1997; Alongi, 2002), but contrary to the conclusion of Alongi (2002), latitude was not significant in causing the difference when tree height was already in the model. This difference between the IWP and AEP mangroves is unlikely to be a result of different tree architecture but, rather, of stand characteristics, because congeners of *Rhizophora* and *Avicennia* in the IWP and AEP mangroves have comparable allometry (and thus similar mass in relation to tree height) (Clough et al., 1997). This difference may also be a direct consequence of the diversity of the mangrove systems, demonstrating a similar relationship to other ecosystem types (Hooper et al., 2005). Since the relatively species-poor AEP mangroves still comprise genera that are the major elements in the IWP assemblage, the difference is unlikely due to difference in growth form linked to species identity. To what extent this pattern is caused by differences in ecosystem services due to different macrobenthic diversity levels in the two biogeographic regions deserves attention. A positive role of specific groups of macrobenthos, i.e. the brachyuran crabs, on mangrove productivity, has been suggested (Smith et al., 1991; Koch and Wolff, 2002). The significance of these effects is expected to vary according to factors such as local environmental gradients in salinity and human impact.

Positive species interactions, though acknowledged as common in communities and their importance highlighted in certain soft sediment environments (e.g. Reise, 2002), have been largely ignored in contemporary models of community dynamics (Bertness and Leonard, 1997). Even less is known about the importance of positive species interactions in the function (e.g. energy flow pattern) of ecosystems (Jones et al., 1997). Mangrove productivity is influenced by many factors related to drivers of geomorphic (e.g. tidal regime, hydrologic connectivity), environmental (e.g. latitude, rainfall) and ecological (e.g. macrobenthos diversity) nature, which also operate on dissimilar temporal and spatial scales (Farnsworth, 1998). It is therefore a challenging task to measure the presumably weaker effects of ecological drivers. There is no *a priori* reason why IWP and AEP mangroves should differ in how they are shaped by physical drivers; the apparent difference in biomass-tree height relationship is likely to be influenced by biotic processes related to biodiversity patterns. Issues such as functional redundancy and species functional complementarity are generally poorly documented (Hooper et al., 2005), and even less understood of macrobenthos in mangroves, and should be explored. Long-term stand-scale manipulative experiments (e.g. exclusion of key macrobenthos) conducted in different biogeographic regions with different levels of mangrove/macrobenthos diversity, and with due reference to the spatial and temporal scales of variation (Farnsworth, 1998), may contribute to assessing the effects of macrobenthos diversity on ecosystem function.

3.3. Secondary production

The contribution of mangroves to near-shore secondary production has predominantly been attributed to the outwelling of mangrove organic matter by tidal export (Lee, 2004) while little is known about the significance of mangrove macrobenthic secondary production. Compounded by the same methodological issues limiting estimation of macrobenthos abundance, production by mangrove macrobenthos has rarely been measured and is one of the least studied areas of mangrove ecology (Alongi, 2002). Very little is known about infaunal secondary production in mangroves. Infaunal macrobenthos are probably less efficiently utilised by estuarine predators because of the limitation in access, both in terms of time and the difficulty of extraction. Schrijvers et al. (1998) suggested that since predator exclusion did not significantly benefit many infaunal macrobenthos, such as oligochaetes, they represent trophic 'dead ends' and contribute little to the mangrove food web. It is unclear, however, to what extent these organisms are involved in below-ground species interactions, e.g. those occurring in crab burrows. There is also the possibility that the exclusion cages did not prevent entry by intermediate predators tapping these small macrobenthos prey. The epibenthos, however, provide a significant food source to estuarine predators and may serve as an additional indirect export pathway of mangrove/marsh production to near-shore systems (Kneib, 1997; Sheaves and Molony, 2000). An evaluation of the contributions from these different components of secondary productivity may shed light on the relative significance of the short and long food chains they fuel, and the implication for estuarine nutrient dynamics.

Macintosh (1984) reported overall minimum production by *Metaplax, Uca* and *Sesarma* populations between 10.5 – 126 kJ $m^{-2}y^{-1}$, with figures varying widely dependent on species. Koch and Wolff (2002) estimated epibenthic secondary productivity of a Brazilian mangrove to be 456 kJ m^{-2} y^{-1}, with >95% of the biomass contributed by seven brachyuran crabs and one gastropod. Although much attention has been accorded to brachyuran crabs, given the high density (e.g. 10.5 individuals m^{-2}, Fratini et al., 2004) attained by gastropods in some forests, their contribution to secondary productivity should not be neglected.

The significance of the trophic link between macrobenthos and mangrove production is that some animals are adapted to digesting nutritionally poor food sources that are very low in nitrogen but high in structural carbon. Few animals have developed abilities to derive enough nutrition from such poor food sources, making the services provided by these initial processors of mangrove carbon particularly important in estuarine food chains.

One of the key issues in ascertaining the trophic link between mangrove and near-shore secondary productivity is hydrologic connectivity of the estuarine habitats, and the degree to which near-shore consumers utilise the connection for extension of their feeding habitats into the mangroves. Estuarine habitats providing good connectivity tend to support higher fish yield (Meynecke et al., 2007). In Australia, both tropical and temperate mangroves support significant presence of fish, especially juveniles (Robertson and Duke, 1990; Hindell and Jenkins, 2004; Manson et al., 2005). While feeding by these predators on mangrove macrobenthos during the high tide has not been extensively studied, similar trophic utilisation by fish has been demonstrated for Australian salt marsh habitats (Thomas and Connolly, 2001; Hollingsworth and Connolly, 2006).

4. Linkages

4.1. Mangrove-estuary linkage through animal biomass movement

Mangrove macrobenthos influence the dynamics of other adjoining ecosystems through linkages that are mediated by tidal flow, animal migrations, and direct and indirect nutrient movement and trophic relationships. Tidal flow provides the primary driving force for most material movement in mangroves, including passive movement of propagules, larval stages, litter, and vital nutrients sustaining the biota. Mangrove macrobenthos influence such material movement through their impact on organic matter retention, bioturbating activities, and also active migration. Most attention on macrobenthos-mediated material export from mangroves focussed on mangrove organic matter processing, while little is known about export in terms of animal biomass, such as eggs and larval stages. Mangrove decapod larval stages have been recorded in the plankton up to 15 km offshore (Schwamborn et al., 1999) and show salinity adaptation for this dispersal (Diele and Simith, 2006), thus contributing to the offshore food chain. Recruitment back to the adult habitat after a significant offshore planktonic larval phase is basically a stochastic process dependent on co-occurrence of conditions controlled by numerous factors, such as wind direction and current flow, as has been demonstrated for the blue crab (*Callinectes sapidus*) on the Atlantic coast of the US (Epifanio, 1995). The temporal variability of these factors is responsible for the usually large fluctuations in recruitment back to the estuarine habitats (Queiroga et al., 2006).

The potential contribution of this link to near-shore pelagic ecosystems can be estimated based on the density and fecundity of the major groups of macrobenthos demonstrating the same life history pattern. While this information is not readily available for most groups, the brachyuran crabs provide sufficient data for an exploratory assessment. Small (<3 cm carapace width, CW, e.g. *Perisesarma* spp.) species of mangrove grapsids produce typically 10 000 – 25 000 eggs or 0.05 g AFDW per brood (Lee and Kwok, 2002; Colpo and Negreiros-Fransozo, 2003) while the fecundity of larger species (e.g. *Ucides*) may be up to 10x higher (Pinheiro et al., 2003). Mangrove grapsids can attain considerably high densities (>1 female m^{-2}) and females typically produce at least 2 – 3 broods per year (some studies in the tropics, e.g. Macintosh (1984), have reported >10 broods for some sesarmine species) . The reproductive output from the brachyuran crabs can therefore be a significant indirect export pathway of mangrove organic production to supply near-shore pelagic systems. A small (20 mm CW) and relatively sparse (~ 1 individual m^{-2}) species such as *Perisesarma bidens* exports ~ 0.13 g AFDW m^{-2} y^{-1} of larvae to estuarine waters and beyond. A species-rich assemblage of brachyuran crabs in tropical Australia may comprise 40 species occurring at densities averaging ~ 5 individuals m^{-2}, producing a total export of larval biomass of ~ 25 g AFDW m^{-2} y^{-1}. This quantity may appear small compared to particulate carbon export from mangroves (e.g. ~ 330 g C m^{-2} y^{-1} for a northeastern Australian mangrove, Robertson et al., 1992) but the figures are likely to be similar in terms of N, given the large difference in the C/N ratios of animal biomass (~ 10) and senescent mangrove leaf litter (~ 100). A large proportion of the mangrove organic production consumed by these brachyuran crabs is therefore made available through this export pathway, in a form much more accessible to offshore pelagic consumers compared to senescent mangrove litter.

This link between mangrove macrobenthos and offshore communities is bi-directional. The macrobenthos of mangroves also provide crucial trophic linkage to a wide range of estuarine and coastal consumers through their occasional or regular feeding excursions into the mangroves. The degree of dependence on the macrobenthos resources, especially the infauna, by these occasional predators is still largely unknown, contributing to notions that some mangrove infauna (e.g. oligochaetes, nematodes) may be regarded as trophic 'dead-ends' (Schrijvers et al., 1998), i.e. the biomass is not further transferred to a higher trophic level but is only returned to the nutrient pool through natural mortality and decay. Again, this notion is probably more a consequence of the ignorance than a true representation of the nature of mangrove food webs. Juvenile fish seem to associate with mangroves because of the feeding efficiency they enjoy in this environment (Laegdsgaard and Johnson, 2001), but there are both spatial (biogenic structures, sediment) and temporal (limited inundation time) refuges that are available to especially the infauna of mangroves. The value of the temporal refuge to the epibenthos is apparent from the behaviour that most taxa are behaviourally adapted to the tidal inundation cycle: most are active only during the low tide and would retreat to spatial refuges such as burrows or supratidal structures (e.g. tree trunk) at high tide. Individuals trying to lengthen their foraging time into the inundation period present themselves to significantly higher predation risk (Lee and Kneib, 1994).

The degree of dependence of estuarine fish and crustaceans on mangroves as feeding and nursery grounds has significant management implications, but few assessments have been made. Although juvenile fish and crustaceans undoubtedly utilise mangrove trophic resources, it is unclear if there is an obligatory dependence, i.e. mortality of the juveniles, and thus a reduction in future recruitment due to a particular cohort, would be increased when mangroves are absent. Assessing the relationship between the catch data of 31 commercially important fish species and wetland habitats in 13 independent Queensland estuaries, Meynecke et al. (2007) have found that structural connectivity of wetlands is of crucial importance to commercial catch of these species.

Linkage between the mangrove macrobenthos and coastal pelagic systems is not limited to trophic links that involve macrofauna. Dissolved material, both organic (mainly DOC) and inorganic (mainly DIN), originated from the macrobenthos in salt marsh has been demonstrated to enhance pelagic bacterioplankton production in estuarine environments (Hopkinson et al., 1998). Similar linkages are emerging from recent studies of mangroves (Dittmar and Lara, 2001; Dittmar et al., 2001, 2006), with influence of mangrove DOM extending to offshore oceanic environments.

5. Conclusive remarks

Due to difficulties in sampling and quantifying the mangrove habitat, the diversity and abundance of mangrove macrobenthos are yet to be fully documented. Some members of the mangrove macrobenthos, such as brachyuran crabs, have been demonstrated as important functional components in mangroves, particularly in terms of organic matter and nutrient processing, through their feeding and bioturbation activities. To what extent biogeographic and anthropogenic differences in macrobenthic diversity may affect mangrove ecosystem function and services presents a significant research question.

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References

Alfaro, A.C., 2006. Benthic macro-invertebrate community composition within a mangrove/seagrass estuary in northern New Zealand. Estuar. Coast. Shelf Sci. 66, 97–110.

Alongi, D.M., 1987. Inter-estuary variation and intertidal zonation of free-living nematode communities in tropical mangrove systems. Mar. Ecol. Prog. Ser. 40, 103–114.

Alongi, D.M., 2002. Present state and future of the world's mangrove forests. Environ. Conserv. 29, 331–349.

Ashton, E.C., Hogarth, P.J., Macintosh, D.J., 2003a. A comparison of brachyuran crab community structure at four mangrove locations under different management systems along the Melaka straits-Andaman sea coast of Malaysia and Thailand. Estuaries 26, 1461–1471.

Ashton, E.C., Macintosh, D.J., Hogarth, P.J., 2003b. A baseline study of the diversity and community ecology of crab and molluscan macrofauna in the Sematan mangrove forest, Sarawak, Malaysia. J. Trop. Ecol. 19, 127–142.

Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.-S., Nakashizuka, T., Raffaelli, D., Schmid, B., 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. Ecol. Lett. 9, 1146–1156.

Bertness, M.D., Leonard, G.H., 1997. The role of positive interactions in communities: Lessons from intertidal habitats. Ecology 78, 1976–1989.

Blanco, J.F., Bejarano, A.C., Lasso, J., Cantera, J.R., 2001. A new look at computation of the complexity index in mangroves: Do disturbed forests have clues to analyze canopy height patchiness? Wetlands Ecol. Manag. 9, 91–101.

Bortolus, A., Iribarne, O., 1999. Effects of the SW Atlantic burrowing crab *Chasmagnathus granulata* on a *Spartina* salt marsh. Mar. Ecol. Prog. Ser. 178, 79–88.

Botto, F., Iribarne, O., 1999. Effect of the burrowing crab *Chasmagnathus granulata* (Dana) on the benthic community of a SW Atlantic coastal lagoon. J. Exp. Mar. Biol. Ecol. 241, 263–284.

Botto, F., Iribarne, O., 2000. Contrasting effects of two burrowing crabs (*Chasmagnathus granulata* and *Uca uruguayensis*) on sediment composition and transport in estuarine environments. Estuar. Coast. Shelf Sci. 51, 141–151.

Botto, F., Valiela, I., Iribarne, O., Martinetto, P., Alberti, J., 2005. Impact of burrowing crabs on C and N sources, control, and transformations in sediments and food webs of sw Atlantic estuaries. Mar. Ecol. Prog. Ser. 293, 155–164.

Brooks, R.A., Bell, S.S., 2002. Mangrove response to attack by a root boring isopod: Root repair versus architectural modification. Mar. Ecol. Prog. Ser. 231, 85–90.

Bunker, D.E., Naeem, S., 2006. Species diversity and ecosystem functioning. Science 312, 846–847.

Chapman, M.G., 1998. Relationships between spatial patterns of benthic assemblages in a mangrove forest using different levels of taxonomic resolution. Mar. Ecol. Prog. Ser. 162, 71–78.

Chapman, M.G., Tolhurst, T.J., 2004. The relationship between invertebrate assemblages and bio-dependant properties of sediment in urbanized temperate mangrove forests. J. Exp. Mar. Biol. Ecol. 304, 51–73.

Cintron, G., Schaeffer-Novelli, Y., 1984. Methods for studying mangrove structure. In: Snedaker, S.C., Snedaker, J.G. (Eds.), The Mangrove Ecosystem: Research Methods. Unesco, Paris, pp. 91–113.

Clarke, P.J., 2004. Effects of experimental canopy gaps on mangrove recruitment: Lack of habitat partitioning may explain stand dominance. J. Ecol. 92, 203–213.

Clarke, P.J., Kerrigan, R.A., 2000. Do forest gaps influence the population structure and species composition of mangrove stands in northern Australia? Biotropica 32, 642–652.

Clarke, P.J., Kerrigan, R.A., 2002. The effects of seed predators on the recruitment of mangroves. J. Ecol. 90, 728–736.

Clough, B.F., 1992. Primary productivity and growth of mangrove forests. In: Robertson, A.I., Alongi, D.M. (Eds.), Tropical Mangrove Ecosystems. American Geophysical Union, New York, pp. 225–249.

Clough, B.F., Dixon, P., Dalhaus, O., 1997. Allometric relationships for estimating biomass in multi-stemmed mangrove trees. Aust. J. Bot. 45, 1023–1031.

Colpo, K.D., Negreiros-Fransozo, M.L., 2003. Reproductive output of *Uca vocator* (Herbst, 1804) (Brachyura, Ocypodidae) from three subtropical mangroves in Brazil. Crustaceana 76, 1–11.

Courtenay, G., Gladstone, W., Schreider, M., 2005. Assessing the response of estuarine intertidal assemblages to urbanised catchment discharge. Environ. Monit. Assess. 107, 375–398.

Davie, P.J.F., 2002. Crustacea: Malacostraca: Eucarida (part 2): Decapoda- Anomura, Brachyura. In: Wells, A., Houston, W.W.K. (Eds.), Zoological Catalogue of Australia, 19.3B. CSIRO Publishing, Melbourne.

Diele, K., Simith, D.J.B., 2006. Salinity tolerance of northern Brazilian mangrove crab larvae, *Ucides cordatus* (Ocypodidae): Necessity for larval export? Estuar. Coast. Shelf Sci. 68, 600–608.

Dittmann, S., 1996. Effects of macrobenthic burrows on infaunal communities in tropical tidal flats. Mar. Ecol. Prog. Ser. 134, 119–130.

Dittmann, S., 2000. Zonation of benthic communities in a tropical tidal flat of north-east Australia. J. Sea Res. 43, 33–51.

Dittmann, S., 2001. Abundance and distribution of small infauna in mangroves of Missionary Bay, north Queensland, Australia. Rev. Biol. Trop. 49, 535–544.

Dittmann, S., 2002. Benthic fauna in tropical flats of Hinchinbrook Channel, NE Australia: Diversity, abundance and their spatial and temporal variation. Wetlands Ecol. Manag. 10, 323–333.

Dittmann, S., Vargas, J.A., 2001. Tropical tidal flat benthos compared between Australia and Central America. In: Reise, K. (Ed.), Ecological Comparisons of Sedimentary Shores. Springer, Berlin, pp. 275–293.

Dittmar, T., Lara, R.J., 2001. Driving forces behind nutrient and organic matter dynamics in a mangrove tidal creek in north Brazil. Estuar. Coast. Shelf Sci. 52, 249–259.

Dittmar, T., Lara, R.J., Kattner, G., 2001. River or mangrove? Tracing major organic matter sources in tropical Brazilian coastal waters. Mar. Chem. 73, 253–271.

Dittmar, T., Hertkorn, N., Kattner, G., Lara, R.J., 2006. Mangroves, a major source of dissolved organic carbon to the oceans. Glob. Biogeochem. Cycles 20, GB1012. doi:10.1029/2005GB002570.

Duarte, C.M., 2000. Marine biodiversity and ecosystem services: An elusive link. J. Exp. Mar. Biol. Ecol. 250, 117–131.

Duarte, S., Pascoal, C., Cassio, F., Barlocher, F., 2006. Aquatic hyphomycete diversity and identity affect leaf litter decomposition in microcosms. Oecologia 147, 658–666.

Ellis, J., Nicholls, P., Craggs, R., Hofstra, D., Hewitt, J., 2004. Effects of terrigenous sedimentation on mangrove physiology and associated macrobenthic communities. Mar. Ecol. Prog. Ser. 270, 71–82.

Ellison, A.M., Farnsworth, E.J., Twilley, R.R., 1996. Facultative mutualism between red mangroves and root-fouling sponges in Belizean mangal. Ecology 77, 2431–2444.

Epifanio, C.E., 1995. Transport of blue crab (*Callinectes sapidus*) larvae in the waters off mid-Atlantic states. Bull. Mar. Sci. 57, 713–725.

Erickson, A.A., Saltis, M., Bell, S.S., Dawes, C.J., 2003. Herbivore feeding preferences as measured by leaf damage and stomatal ingestion: A mangrove crab example. J. Exp. Mar. Biol. Ecol. 289, 123–138.

Farnsworth, E.J., 1998. Issues of spatial, taxonomic and temporal scale in delineating links between mangrove diversity and ecosystem function. Glob. Ecol. Biogeogr. Lett. 7, 15–25.

Fenchel, T., 1996. Worm burrows and oxic microniches in marine sediments .2. Distribution patterns of ciliated protozoa. Mar. Biol. 127, 297–301.

Field, C.B., Osborn, J.G., Hoffmann, L.L., Polsenberg, J.F., Ackerly, D.D., Berry, J.A., Bjorkman, O., Held, Z., Matson, P.A., Mooney, H.A., 1998. Mangrove biodiversity and ecosystem function. Glob. Ecol. Biogeogr. Lett. 7, 3–14.

Fratini, S., Vigiani, V., Vannini, M., Cannicci, S., 2004. *Terebralia palustris* (Gastropoda; Potamididae) in a Kenyan mangal: Size structure, distribution and impact on the consumption of leaf litter. Mar. Biol. 144, 1173–1182.

Fromard, F., Puig, H., Mougin, E., Marty, G., Betoulle, J.L., Cadamuro, L., 1998. Structure, above-ground biomass and dynamics of mangrove ecosystems: new data from French Guiana. Oecologia 115, 39–53.

Frusher, S.D., Giddins, R.L., Smith, T.J., 1994. Distribution and abundance of grapsid crabs (Grapsidae) in a mangrove estuary-effects of sediment characteristics, salinity tolerances, and osmoregulatory ability. Estuaries 17, 647–654.

Gillikin, D.P., De Grave, S., Tack, J.F., 2001. The occurrence of the semi-terrestrial shrimp Merguia oligodon (de man, 1888) in Neosarmatium smithi h. Milne Edwards, 1853 burrows in Kenyan mangroves. Crustaceana 74, 505–507.

Gwyther, J., 2003. Nematode assemblages from *Avicennia marina* leaf litter in a temperate mangrove forest in south-eastern Australia. Mar. Biol. 142, 289–297.

Gwyther, J., Fairweather, P.G., 2005. Meiofaunal recruitment to mimic pneumatophores in a cool-temperate mangrove forest: Spatial context and biofilm effects. J. Exp. Mar. Biol. Ecol. 317, 69–85.

Hall, D., Lee, S.Y., Meziane, T., 2006. Fatty acids as trophic tracers in an experimental estuarine food chain: Tracer transfer. J. Exp. Mar. Biol. Ecol. 336, 42–53.

Hector, A., 1998. The effect of diversity on productivity: Detecting the role of species complementarity. Oikos 82, 597–599.

Hindell, J.S., Jenkins, G.P., 2004. Spatial and temporal variability in the assemblage structure of fishes associated with mangroves (*Avicennia marina*) and intertidal mudflats in temperate Australian embayments. Mar. Biol. 144, 385–395.

Hixon, M.A., Beets, J.P., 1989. Shelter characteristics and Caribbean fish assemblages- experiments with artificial reefs. Bull. Mar. Sci. 44, 666–680.

Hixon, M.A., Beets, J.P., 1993. Predation, prey refuges, and the structure of coral-reef fish assemblages. Ecol. Monogr. 63, 77–101.

Hollingsworth, A., Connolly, R.M., 2006. Feeding by fish visiting inundated subtropical saltmarsh. J. Exp. Mar. Biol. Ecol. 336, 88–98.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setala, H., Symstad, A.J., Vandermeer, J., Wardle, D.A., 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. Ecol. Monogr. 75, 3–35.

Hopkinson, C.S., Giblin, A.E., Garritt, R.H., Tucker, J., Hullar, M.A.J., 1998. Influence of the benthos on growth of planktonic estuarine bacteria. Aquat. Microb. Ecol. 16, 109–118.

Inglis, G.J., Kross, J.E., 2000. Evidence for systemic changes in the benthic fauna of tropical estuaries as a result of urbanization. Mar. Pollut. Bull. 41, 367–376.

Jones, C.G., Lawton, J.H., Shachak, M., 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78, 1946–1957.

Kelehar, B.P., Underwood, A.J., Chapman, M.G., 1998. Effect of boardwalks on the semaphore crab *Heloecius cordiformis* in temperate urban mangrove forests. J. Exp. Mar. Biol. Ecol. 227, 281–300.

Kneib, R.T., 1997. The role of tidal marshes in the ecology of estuarine nekton. Oceanogr. Mar. Biol. Ann. Rev. 35, 163–220.

Kneib, R.T., Lee, S.Y., Kneib, J.P., 1999. Adult-juvenile interactions in the crabs *Sesarma* (*Perisesarma*) *bidens* and S. (*Holometopus*) *dehaani* (Decapoda : Grapsidae) from intertidal mangrove habitats in Hong Kong. J. Exp. Mar. Biol. Ecol. 234, 255–273.

Knops, J.M.H., Tilman, D., Haddad, N.M., Naeem, S., Mitchell, C.E., Haarstad, J., Ritchie, M.E., Howe, K.M., Reich, P.B., Siemann, E., Groth, J., 1999. Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. Ecol. Lett. 2, 286–293.

Koch, V., Wolff, M., 2002. Energy budget and ecological role of mangrove epibenthos in the Caete estuary, north Brazil. Mar. Ecol. Prog. Ser. 228, 119–130.

Kristensen, E., Alongi, D.M., 2006. Control by fiddler crabs (*Uca vocans*) and plant roots (*Avicennia marina*) on carbon, iron, and sulfur biogeochemistry in mangrove sediment. Limnol. Oceanogr. 51, 1557–1571.

Laegdsgaard, P., Johnson, C., 2001. Why do juvenile fish utilise mangrove habitats? J. Exp. Mar. Biol. Ecol. 257, 229–253.

Lee, S.Y., 1997. Potential trophic importance of the faecal material of the mangrove sesarmine crab *Sesarma messa*. Mar. Ecol. Prog. Ser. 159, 275–284.

Lee, S.Y., 1998. Ecological role of grapsid crabs in mangrove ecosystems: A review. Mar. Freshw. Res. 49, 335–343.

Lee, S.Y., 2004. Relationship between mangrove abundance and tropical prawn production: A re-evaluation. Mar. Biol. 145, 943–949.

Lee, S.Y., 2005. Exchange of organic matter and nutrients between mangroves and estuaries: Myths, methodological issues and missing links. Int. J. Ecol. Environ. Sci. 31, 163–175.

Lee, S.Y., Kneib, R.T., 1994. Effects of biogenic structure on prey consumption by the xanthid crabs *Eurytium limosum* and *Panopeus herbstii* in a salt-marsh. Mar. Ecol. Prog. Ser. 104, 39–47.

Lee, S.Y., Kwok, P.W., 2002. The importance of mangrove species association to the population biology of two sesarmine crabs, *Perisesarma bidens* and *Parasesarma affinis*. Wetlands Ecol. Manag. 10, 215–226.

Lee, S.Y., Leung, V., 1999. The brachyuran fauna of the Mai Po marshes nature reserve and Deep Bay, Hong Kong. In: Lee, S.Y. (Ed.), The Mangrove Ecosystem of Deep Bay and the Mai Po marshes, Hong Kong. Hong Kong University Press, Hong Kong, pp. 57–82.

Levin, L.A., Boesch, D.F., Covich, A., Dahm, C., Erseus, C., Ewel, K.C., Kneib, R.T., Moldenke, A., Palmer, M.A., Snelgrove, P., Strayer, D., Weslawski, J.M., 2001. The function of marine critical transition zones and the importance of sediment biodiversity. Ecosystems 4, 430–451.

Lindegarth, M., Hoskin, M., 2001. Patterns of distribution of macrofauna in different types of estuarine, soft sediment habitats adjacent to urban and non-urban areas. Estuar. Coast. Shelf Sci. 52, 363–373.

Lugo, A.E., Cintron, G., 1975. The mangrove forests of Puerto Rico and their management. In: Walsh, G., Snedaker, S.C., Teas, H. (Eds.), Proc. Int. Symp. Biology and Management of Mangroves. Institute of Food and Agricultural Sciences, Gainsville, pp. 825–846.

Lui, T.H., Lee, S.Y., Sadovy, Y., 2002. Macrobenthos of a tidal impoundment at the Mai Po marshes nature reserve, Hong Kong. Hydrobiologia 468, 193–212.

Macintosh, D., 1984. Ecology and productivity of Malaysian mangrove crab populations (Decapoda: Brachyura). In: Soepadmo, E., Rao, A.N., Macintosh, D. (Eds.), Proc. Asian Symp. Mangrove Environment: Research and Management. University of Malaya and Unesco, Kuala Lumpur, pp. 354–377.

Macnae, W., 1968. A general account of the fauna and flora of mangrove swamps and forests in the Indo-west-Pacific region. Adv. Mar. Biol. 6, 73–270.

Manson, F.J., Loneragan, N.R., Skilleter, G.A., Phinn, S.R., 2005. An evaluation of the evidence for linkages between mangroves and fisheries: A synthesis of the literature and identification of research directions. Oceanogr. Mar. Biol. Ann. Rev. 43, 483–513.

Martinetto, P., Iribarne, O., Palomo, G., 2005. Effect of fish predation on intertidal benthic fauna is modified by crab bioturbation. J. Exp. Mar. Biol. Ecol. 318, 71–84.

McCoy, E.D., Bell, S.S., 1991. Habitat structure: The evolution and diversification of a complex topic. In: Bell, S.S., McCoy, E.D., Mushinsky, H.R. (Eds.), Habitat Structure: The Physical Arrangement of Objects in Space. Chapman and Hall, London, pp. 3–28.

McGuinness, K.A., 1997. Seed predation in a tropical mangrove forest: A test of the dominance-predation model in northern Australia. J. Trop. Ecol. 13, 293–302.

McIvor, C.C., Smith, T.J., 1995. Differences in the crab fauna of mangrove areas at a southwest Florida and a northeast Australia location-implications for leaf-litter processing. Estuaries 18, 591–597.

McKee, K.L., 1995. Mangrove species distribution and propagule predation in Belize- an exception to the dominance predation hypothesis. Biotropica 27, 334–345.

Meager, J.J., Williamson, I., Loneragan, N.R., Vance, D.J., 2005. Habitat selection of juvenile banana prawns, *Penaeus merguiensis* de Man: Testing the roles of habitat structure, predators, light phase and prawn size. J. Exp. Mar. Biol. Ecol. 324, 89–98.

Meynecke, J.-O., Lee, S.Y., Duke, N.C., Warnken, J., 2007. Relationships between estuarine habitats and coastal fisheries in Queensland. Australia. Bull. Mar. Sci. 80.

Moore, T.N., Fairweather, P.G., 2006. Decay of multiple species of seagrass detritus is dominated by species identity, with an important influence of mixing litters. Oikos 114, 329–337.

Morrisey, D.J., Skilleter, G.A., Ellis, J.I., Burns, B.R., Kemp, C.E., Burt, K., 2003. Differences in benthic fauna and sediment among mangrove (*Avicennia marina var. australasica*) stands of different ages in New Zealand. Estuar. Coast. Shelf Sci. 56, 581–592.

Morton, B., 1976. Biology, ecology and functional aspects of organs of feeding and digestion of southeast-Asian mangrove bivalve, *Enigmonia aenigmatica* (Mollusca- Anomiacea). J. Zool. 179, 437–466.

Naeem, S., 2006. Expanding scales in biodiversity-based research: Challenges and solutions for marine systems. Mar. Ecol. Prog. Ser. 311, 273–283.

Neilson, M.J., Richards, G.N., 1989. Chemical-composition of degrading mangrove leaf litter and changes produced after consumption by mangrove crab *Neosarmatium smithi* (Crustacea, Decapoda, Sesarmidae). J. Chem. Ecol. 15, 1267–1283.

Neilson, M.J., Giddins, R.L., Richards, G.N., 1986. Effect of tannins on the palatability of mangrove leaves to the tropical sesarminid crab *Neosarmatium smithi*. Mar. Ecol. Prog. Ser. 34, 185–186.

Nobbs, M., McGuinness, K.A., 1999. Developing methods for quantifying the apparent abundance of fiddler crabs (Ocypodidae : *Uca*) in mangrove habitats. Aust. J. Ecol. 24, 43–49.

Osborne, K., Smith, T.J., 1990. Differential predation on mangrove propagules in open and closed canopy forest habitats. Vegetatio 89, 1–6.

Palomo, G., Botto, F., Navarro, D., Escapa, M., Iribarne, O., 2003. Does the presence of the SW Atlantic burrowing crab *Chasmagnathus granulatus* Dana affect predator-prey interactions between shorebirds and polychaetes? J. Exp. Mar. Biol. Ecol. 290, 211–228.

Perry, D.M., 1988. Effects of associated fauna on growth and productivity in the red mangrove. Ecology 69, 1064–1075.

Pinheiro, M.A.A., Baveloni, M.D., Terceiro, O.D.L., 2003. Fecundity of the mangrove crab *Ucides cordatus* (Linnaeus, 1763) (Brachyura, Ocypodidae). Invertebr. Reprod. Dev. 43, 19–26.

Proches, S., Marshall, D.J., Ugrasen, K., Ramcharan, A., 2001. Mangrove pneumatophore arthropod assemblages and temporal patterns. J. Mar. Biol. Assoc. UK 81, 545–552.

Proffitt, C.E., Devlin, D.J., 2005. Grazing by the intertidal gastropod *Melampus coffeus* greatly increases mangrove leaf litter degradation rates. Mar. Ecol. Prog. Ser. 296, 209–218.

Queiroga, H., Almeida, M.J., Alpuim, T., Flores, A.A.V., Francisco, S., Gonzalez-Gordillo, I., Miranda, A.I., Silva, I., Paula, J., 2006. Tide and wind control of megalopal supply to estuarine crab populations on the Portugese west coast. Mar. Ecol. Prog. Ser. 307, 21–36.

Reise, K., 2002. Sediment mediated species interactions in coastal waters. J. Sea Res. 48, 127–141.

Ridd, P.V., 1996. Flow through animal burrows in mangrove creeks. Estuar. Coast. Shelf Sci. 43, 617–625.

Robertson, A.I., 1986. Leaf-burying crabs- their influence on energy-flow and export from mixed mangrove forests (*Rhizophora* spp.) in northeastern Australia. J. Exp. Mar. Biol. Ecol. 102, 237–248.

Robertson, A.I., 1991. Plant animal interactions and the structure and function of mangrove forest ecosystems. Aust. J. Ecol. 16, 433–443.

Robertson, A.I., Duke, N.C., 1990. Mangrove fish communities in tropical Australia: Spatial and temporal patterns in densities, biomass and community structure. Mar. Biol. 104, 369–379.

Robertson, A.I., Alongi, D.M., Boto, K.G., 1992. Food chains and carbon fluxes. In: Robertson, A.I., Alongi, D.M. (Eds.), Tropical Mangrove Ecosystems. American Geophysical Union, New York, pp. 293–326.

Rosenberg, R., Ringdahl, K., 2005. Quantification of biogenic 3-d structures in marine sediments. J. Exp. Mar. Biol. Ecol. 326, 67–76.

Ross, P.M., 2001. Larval supply, settlement and survival of barnacles in a temperate mangrove forest. Mar. Ecol. Prog. Ser. 215, 237–249.

Sasekumar, A., 1974. Distribution of macrofauna on a Malayan mangrove shore. J. Anim. Ecol. 43, 51–69.

Sasekumar, A., Chong, V.C., 1998. Faunal diversity in Malaysian mangroves. Glob. Ecol. Biogeogr. Lett. 7, 57–60.

Satumanatpan, S., Keough, M.J., 2001. Roles of larval supply and behavior in determining settlement of barnacles in a temperate mangrove forest. J. Exp. Mar. Biol. Ecol. 260, 133–153.

Satumanatpan, S., Keough, M.J., Watson, G.F., 1999. Role of settlement in determining the distribution and abundance of barnacles in a temperate mangrove forest. J. Exp. Mar. Biol. Ecol. 241, 45–66.

Schrijvers, J., Okondo, J., Steyaert, M., Vincx, M., 1995. Influence of epibenthos on meiobenthos of the *Ceriops tagal* mangrove sediment at Gazi bay, Kenya. Mar. Ecol. Prog. Ser. 128, 247–259.

Schrijvers, J., Camargo, M.G., Pratiwi, R., Vincx, M., 1998. The infaunal macrobenthos under east African *Ceriops tagal* mangroves impacted by epibenthos. J. Exp. Mar. Biol. Ecol. 222, 175–193.

Schwamborn, R., Ekau, W., Silva, A.P., Silva, T.A., Saint-Paul, U., 1999. The contribution of estuarine decapod larvae to marine zooplankton communities in north-east Brazil. Arch. Fish. Mar. Res. 47, 167–182.

Sheaves, M., Molony, B., 2000. Short-circuit in the mangrove food chain. Mar. Ecol. Prog. Ser. 199, 97–109.

Sivasothi, N., 2000. Niche preferences of tree-climbing crabs in Singapore mangroves. Crustaceana 73, 25–38.

Skilleter, G.A., Warren, S., 2000. Effects of habitat modification in mangroves on the structure of mollusc and crab assemblages. J. Exp. Mar. Biol. Ecol. 244, 107–129.

Skov, M.W., Hartnoll, R.G., 2001. Comparative suitability of binocular observation, burrow counting and excavation for the quantification of the mangrove fiddler crab *Uca annulipes* (H. Milne Edwards). Hydrobiologia 449, 201–212.

Skov, M.W., Hartnoll, R.G., 2002. Paradoxical selective feeding on a low-nutrient diet: Why do mangrove crabs eat leaves? Oecologia 131, 1–7.

Skov, M.W., Vannini, M., Shunula, J.P., Hartnoll, R.G., Cannicci, S., 2002. Quantifying the density of mangrove crabs: Ocypodidae and Grapsidae. Mar. Biol. 141, 725–732.

Slim, F.J., Hemminga, M.A., Ochieng, C., Jannink, N.T., delaMoriniere, E.C., vanderVelde, G., 1997. Leaf litter removal by the snail Terebralia palustris (Linnaeus) and sesarmid crabs in an east African mangrove forest (Gazi bay, Kenya). J. Exp. Mar. Biol. Ecol. 215, 35–48.

Smith, T.J., 1987. Seed predation in relation to tree dominance and distribution in mangrove forests. Ecology 68, 266–273.

Smith, T.J., Chan, H.T., Mcivor, C.C., Robblee, M.B., 1989. Comparisons of seed predation in tropical, tidal forests from 3 continents. Ecology 70, 146–151.

Smith, T.J., Boto, K.G., Frusher, S.D., Giddins, R.L., 1991. Keystone species and mangrove forest dynamics- the influence of burrowing by crabs on soil nutrient status and forest productivity. Estuar. Coast. Shelf Sci. 33, 419–432.

Sousa, W.P., Mitchell, B.J., 1999. The effect of seed predators on plant distributions: Is there a general pattern in mangroves? Oikos 86, 55–66.

Steinke, T.D., Rajh, A., Holland, A.J., 1993. The feeding-behavior of the red mangrove crab *Sesarma meinerti* de Man, 1887 (Crustacea, Decapoda, Grapsidae) and its effect on the degradation of mangrove leaf-litter. S.A. J. Mar. Sci. 13, 151–160.

Stieglitz, T., Ridd, P., Muller, P., 2000. Passive irrigation and functional morphology of crustacean burrows in a tropical mangrove swamp. Hydrobiologia 421, 69–76.

Svavarsson, J., Osore, M.K.W., Olafsson, E., 2002. Does the wood-borer *Sphaeroma terebrans* (Crustacea) shape the distribution of the mangrove *Rhizophora mucronata*? Ambio 31, 574–579.

Thomas, B.E., Connolly, R.M., 2001. Fish use of subtropical saltmarshes in Queensland, Australia: Relationships with vegetation, water depth and distance onto the marsh. Mar. Ecol. Prog. Ser. 209, 275–288.

Thongtham, N., Kristensen, E., 2005. Carbon and nitrogen balance of leaf-eating sesarmid crabs (*Neoepisesarma versicolor*) offered different food sources. Estuar. Coast. Shelf Sci. 65, 213–222.

Tomlinson, P.B., 1986. The Botany of Mangroves. Cambridge University Press, Cambridge.

Vannini, M., Ruwa, R.K., 1994. Vertical migrations in the tree crab *Sesarma leptosoma* (Decapoda, Grapsidae). Mar. Biol. 118, 271–278.

Vannini, M., Cannicci, S., Ruwa, K., 1995. Effect of light-intensity on vertical migrations of the tree crab, *Sesarma leptosoma* Hilgendorf (Decapoda, Grapsidae). J. Exp. Mar. Biol. Ecol. 185, 181–189.

Warren, J.H., 1990. The use of open burrows to estimate abundances of intertidal estuarine crabs. Aust. J. Ecol. 15, 277–280.

Warren, J.H., Underwood, A.J., 1986. Effects of burrowing crabs on the topography of mangrove swamps in New South Wales. J. Exp. Mar. Biol. Ecol. 102, 223–235.

Werry, J., Lee, S.Y., 2005. Grapsid crabs mediate link between mangrove litter production and estuarine planktonic food chains. Mar. Ecol. Prog. Ser. 293, 165–176.

Williamson, R.B., Wilcock, R.J., Wise, B.E., Pickmere, S.E., 1999. Effect of burrowing by the crab Helice crassa on chemistry of intertidal muddy sediments. Environ. Toxicol. Chem. 18, 2078–2086.

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Mangrove crabs as ecosystem engineers; with emphasis on sediment processes

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Abstract

The benthic fauna in mangrove forests is usually dominated by burrowing sesarmid (Grapsidae) and fiddler crabs (Ocypodidae). They are herbivores that retain, bury, macerate and ingest litter and microalgal mats. Most species within these two groups actively dig and maintain burrows in the sediment as a refuge from predation and environmental extremes. Based on the current knowledge on the biology and ecology of these crabs, it seems obvious that their activities have considerable impact on ecosystem functioning. However, no convincing conceptual framework has yet been defined into which the role of these crabs can be identified and characterized. The attributes by which these abundant animals affect the microbial and biogeochemical functional diversity fit well into the concept of ecosystem engineering. The conceptualization of mangrove benthic communities within this framework is distinguished and documented by examples provided from the most recent literature on mangrove ecosystem functioning. It appears that the features and processes driving the engineering effects on distribution and activity of associated organisms operate differently for sesarmid and fiddler crabs. The most obvious and well-documented difference between engineering effects of the two types of crab seems to be associated with foraging. More attention must be devoted in the future to elucidate engineering aspects related to crab burrows in mangrove environments. Particularly comparative work on the burrow-dwelling life styles of the two types of crab is needed.

Keywords: Ecosystem engineering; Mangrove; Sesarmid; Fiddler crab; Sediment biogeochemistry

1. Introduction

The mangrove ecosystem dominates along most tropical and subtropical coastlines (Por, 1984; Alongi, 2002). It is characterized as a forest growing in seawater at the interface between land and sea, particularly in sheltered areas with large tidal excursions. Mangrove forests are highly productive and support abundant planktonic and benthic communities, as well as high rates of microbial decomposition (Christensen, 1978; Alongi et al., 1999). The structuring feature of mangrove forests is tree species adapted to growth in anoxic intertidal sediment saturated with seawater. Among their adaptations are special structures such as pneumatophores (e.g. *Avicennia* spp.) and prop roots (e.g. *Rhizophora* spp.) that supply the roots with oxygen from the air and provide physical support for growth in soft mud (Kitaya et al., 2002). Salt from the seawater is either excluded at the roots (e.g. *Rhizophora* spp.) or excreted by glands on the leaves (e.g. *Avicennia* spp.) (Passioura et al., 1992; Clarke and Allaway, 1993).

The benthic fauna associated with mangrove forests is typically dominated by various burrowing decapods, such as sesarmid crabs and fiddler crabs. They are

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herbivores that retain, bury, macerate and ingest litter and microalgal mats (Emmerson and McGwynne, 1992; Lee, 1997; Kristensen and Alongi, 2006). By doing so, they prevent loss of nutrients and promote decomposition processes. In addition, most sesarmid and fiddler crabs actively dig and maintain burrows in the sediment. These structures function as a refuge from predation and environmental extremes, and may in some cases provide for food storage (Giddins et al., 1986; Warren, 1990; Dittmann, 1996). The burrows affect sediment topography and biogeochemistry by modifying particle size distribution, drainage, redox conditions and organic matter as well as nutrient availability (Mouton and Felder, 1996; Botto and Iribarne, 2000).

Many studies have dealt with the role of benthic fauna in mangrove ecosystem functioning, and the ecological importance of crabs seems well recognized (Smith et al., 1991; Thongtham and Kristensen, 2003). However, no convincing conceptual framework has yet been defined to identify and characterize these features. Most ecosystem effects of crabs are caused by non-trophic activities and fit well into the concept of ecosystem engineering. They modify physical structures, transport conditions and substance chemistry, and by doing so change the availability of resources for the associated microbial, fauna and plant communities.

This contribution will identify and describe the engineering attributes by which crab species primarily belonging to the decapod subfamily Sesarminae (family Grapsidae) and fiddler crabs (genus *Uca*; family Ocypodidae) affect the availability of resources for other biological assemblages in mangrove systems. In the present context, these assemblages refer primarily to microbial communities that mediate biogeochemical reactions. The conceptualization of mangrove benthic communities within the framework of ecosystem engineering will be distinguished and documented from examples provided from the most recent literature on mangrove ecosystem functioning.

2. What are ecosystem engineers?

The concept of ecosystem engineering was introduced about a decade ago by Jones et al. (1994, 1997). They defined organisms as ecosystem engineers when they 'directly or indirectly modulate the availability of resources (other than themselves) to other species, by causing physical state changes in biotic or abiotic materials. In so doing they modify, maintain and/or create habitats'. Direct transfer of resources by an organism to other species in the form of living or dead tissues is not engineering, but rather trophic interactions. Thus, a critical characteristic of ecosystem engineers is that they must change the quality, quantity and distribution of resources utilized by other species, excluding the engineer itself as a resource. Two major types of ecosystem engineers can be defined dependent on the mechanisms by which they change the environment (Jones et al., 1994): autogenic engineers change the environment via their own physical structures (i.e. living and dead tissues), while allogenic engineers change the environment by transforming living or non-living materials from one physical state to another via mechanical or other actions.

Ecosystem engineering is not synonymous with the concept of 'keystone species'. Keystone species control community structure (Paine, 1969; Krebs, 2001), and removal of keystone species causes massive changes in species composition and ecosystem functioning. The action of keystone species is usually regarded as trophic, but critical effects frequently involve engineering, for example via physical disturbance (Smith et al., 1991; Reise, 2002). It is as yet not fully clear whether the impact of many previously defined keystone species actually is due to engineering and not trophic effects.

Recently, Gutiérrez and Jones (2006) broadened the concept of ecosystem engineering to include organisms as agents of biogeochemical heterogeneity. These organisms can 'affect biogeochemical reactions by changing the availability of resources for microbes (e.g. carbon and nutrients) or by changing abiotic conditions affecting microbial reaction rates (e.g. redox and temperature)'. Due to the nature of microorganisms, the engineering effects primarily occur at scales of millimetres, but may in many cases be extrapolated and averaged to ecosystem scale. In contrast to the 'classic' concept of ecosystem engineering (Jones et al., 1994, 1997), where the impact of engineering largely is related to species diversity changes within biotic communities, the biogeochemical approach also considers the functional diversity of microbial communities. While species diversity is an important determinant of ecological changes at the population and community level, functional diversity is essential for understanding changes with respect to element cycling at the ecosystem level. Gutiérrez and Jones (2006) argued that biogeochemical heterogeneity develops as a consequence of variations in either abiotic conditions or the availability of microbial resources. The heterogeneity and activity of microbial reactions in any patch are therefore controlled by processes that changes the physical environment (physical structure), transport conditions (physical transport), availability of materials (substances) and any combination of these (Fig. 1). The activity of allogenic ecosystem engineers can alter the characteristics of patches by forming structures (such as

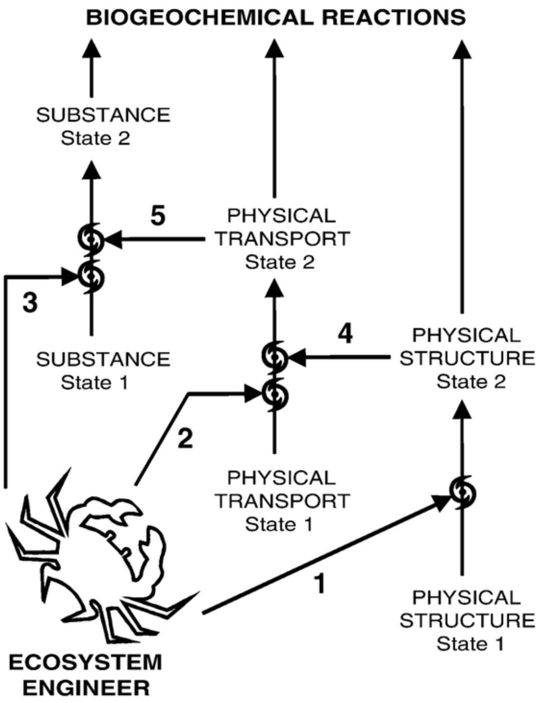

Fig. 1. Flow diagram showing the features by which ecosystem engineers affect biogeochemical activity and heterogeneity in sediment environments. The first feature includes modification of physical structures (for example burrows). The state change of the physical structure is driven by processes such as the burrowing and maintenance activity of the engineer (process 1). The second feature is related to physical transport (such as material, fluid and gas). Transport state changes means that the engineer redistributes materials by reworking within the sediment or actively pump fluid and gas in and out of the sediment via burrows (process 2). The physical structure itself can also passively mediate transport by processes such as collapsing burrows, passive fluid transport and diffusive gas transport (process 4). The third feature is associated with changes in the chemical properties of substances (for example, degradability and redox conditions). The engineer will typically handle or ingest potential food sources (substances) and by doing so modify and change the state of the substance (process 3). The modified substance (e.g. faeces) may become more or less available for other organisms, e.g. detritivores and decomposers. The physical transport will also potentially affect the state of substances by changing factors such as the redox conditions via removal of toxic metabolites and introduction of oxygen deep into sediments (process 5) (inspired by Gutiérrez and Jones, 2006).

burrows) that act as conduits or barriers for transport of organic matter, nutrients and redox active compounds (process 1, Fig. 1). The ecosystem engineer and the physical structures it forms can also affect the transport of substances to and from microbial communities by active transport of solids or fluids (processes 2 and 4, Fig. 1). Finally, the engineer can modify substances directly through e.g. handling (maceration), gut passage (enzymatic action) and burial by which the availability of these substances to microbial communities is augmented or hampered (processes 3 and 5, Fig. 1).

Even before Jones et al. (1994) introduced the concept, many studies have shown excellent examples of ecosystem engineering related to sediment biogeochemistry. For example, the activities of large burrowing invertebrates in marine benthic environments have long been known to affect the physical and chemical structure of sediments, altering abiotic conditions and nutrient availability for biogeochemical processes (e.g. Aller, 1982; Berner and Westrich, 1985). Instead of allogenic ecosystem engineering, these features have been labelled by the broader and not particularly well-defined concept of bioturbation. In its strict sense, bioturbation refers to the physical displacement of particles and water caused by macrofaunal activities in sediments, but it does not directly refer to the associated impact on microbial drivers of biogeochemistry. The conceptual framework of ecosystem engineering, on the other hand, elegantly emphasizes the coupling between bioturbation and sediment biogeochemistry.

Although the ecological consequences of ecosystem engineering in many cases may be trivial or difficult to identify, it is of fundamental interest to identify the types of environments where ecosystem engineering play the most important role. Among such environments, the relatively unexplored mangrove ecosystem is an obvious candidate for future studies. The diversity of plants and animals in mangrove forests is generally low, but they all play important roles for ecosystem functioning. Trees are the key engineers that form the unique mangrove environment, but the crab fauna are responsible engineers that drive efficient element transfers by maintaining high functional diversity and biogeochemical heterogeneity in sediments.

3. Mangrove functional diversity and biogeochemical heterogeneity

Before focusing on the engineering impacts of crabs, the involved functional dynamics of microbial communities and biogeochemical reactions in mangrove sediments must be identified. Mangrove sediments are usually composed of fine-grained mud with up to about 80% of particles < 63 μm and an organic carbon content ranging from 1 to 6 mmol g^{-1}. The main source of organic matter in mangrove environments is surface-deposited litter from trees (leaves, propagules and twigs) and subsurface root growth (Alongi, 1998). The contribution of detritus from macroalgae, benthic microalgae, phytoplankton and epiphytes is generally low (i.e. $< 14\%$ of the total primary production, Alongi, 1998) in most mangrove forests due to light limitation under the canopy. However, the >10× higher nitrogen content of algae (C:N ~ 7−10) compared with mangrove litter (C:N ~ 100) implies that algae contribute with a large fraction of the organic nitrogen input to mangrove food webs. Stable isotopes have indicated that mangrove-derived detritus (tree litter) is an important food source for select groups of invertebrates, while other species primarily feed on algae (Newell et al., 1995; Bouillon et al., 2008-this issue).

Microbial decomposition is generally slow in mangrove sediments because most of the detritus is of poor nutritious value and contains high levels of retarding compounds. The detritus is rich in tannins, lignin and structural carbohydrates (cellulose), which inhibits microbial degradation (Lee et al., 1990; Benner et al., 1990; Marchand et al., 2005). While cellulose and lignin can readily be degraded in oxic environments, these compounds are only degraded slowly under anoxic conditions. Lignin, for example, has a half-life of >150 y in anoxic mangrove sediment (Dittmar and Lara, 2001). The formation of old and refractory material in mangrove sediments can be observed visually as lignified and humified (spongy) litter fragments. Accordingly, Dittmar and Lara (2001) estimated that the average age of organic carbon in the upper 1.5 m of the sediment in a Brazilian mangrove forest is between 400 and 770 y.

The decay of mangrove litter in sediments begins with leaching of soluble organic substances. Newly fallen litter loses 20–40% of the organic carbon by leaching when submerged in seawater (Camilleri and Ribi, 1986; Twilley et al., 1997). Much of the leached DOM is labile and rapidly consumed by the benthic microbial community (Kristensen and Pilgaard, 2001), while some is exported to the mangrove waterways. Further decomposition of the remaining particulate material occurs by extracellular enzymatic hydrolysis mediated by bacteria and mycelial decomposers followed by assimilation of the solubilized compounds. In contrast to other marine ecosystems where bacteria dominate degradation processes, marine mycelial decomposers belonging to eumycotes (Fungi) and oomycotes (Protoctista) are highly adapted for the capture of cellulose-rich vascular plant litter in mangrove ecosystems (Newell, 1996).

Rates of microbial carbon oxidation in mangrove sediments typically range from 20 to 60 mmol m^{-2} d^{-1} (Kristensen et al., 2000; Alongi et al., 2001). Aerobic respiration occurs near the sediment surface, around crab burrows and along oxic root surfaces. The consumption of O_2 at these interfaces is usually so rapid that O_2 rarely penetrates >1 mm into the sediment (Kristensen et al., 1994). A wide variety of anaerobic microorganisms mediate most carbon oxidation below the oxic zone. Anaerobic sulfate reduction has long been considered the most important respiration processes in mangrove sediments (Alongi, 1998), with a share of up to 50% of the total carbon oxidation. Consequently, most mangrove sediments contain high levels of reduced inorganic sulfur primarily in the form of pyrite (Holmer et al., 1994). Recent evidence suggests, however, that the role of iron respiration for organic carbon mineralization may be comparable to or higher than that of sulfate reduction in iron-rich mangrove environments (Kristensen et al., 2000; Kristensen and Alongi, 2006). As sulfate reduction usually is hampered in the presence of more potent electron acceptors (e.g. O_2 and Fe^{3+}; Canfield et al., 1993), this process becomes inferior to iron respiration when oxidizing roots and infaunal burrows increase the Fe^{3+} content deep in mangrove sediments (Nielsen et al., 2003). However, the role of each pathway varies considerably within and between mangrove environments, depending on several interrelated factors, including sediment composition, bioturbation, tidal inundation frequency, sediment composition as well as sulfate, iron and organic carbon availability (Table 1).

Sedimentary organic matter in mangrove environments is richer in nitrogen (molar C:N ratio of 20–30) than fresh litter (Kristensen et al., 1995). A rapid initial release of carbon and retention or enrichment of nitrogen must therefore occur during early degradation of mangrove litter (Twilley et al., 1997; Wafar et al., 1997). As microorganisms generally need substrates with an elemental C:N ratio < 10 for maintenance and growth, mangrove litter is a highly insufficient substrate, even after burial into the sediment. Thus, a respiratory

Table 1
Percentage partitioning of electron acceptors for the terminal oxidation of carbon in mangrove environments

Location	e–acceptor				
	O_2	NO_3^-	Mn^{4+}	Fe^{3+}	SO_4^{2-}
Thailand (+sesarmid)[1]	3	1	~0	78	18
Thailand (+fiddler)[1]	56	~0	~0	33	12
Australia (+fiddler)[2]	2	~0	~0	62	36
Tanzania (+mix)[3]	14	~0	~0	77	9
Skidaway (+fiddler)	*~0*	*~0*	*~0*	*95*	*5*
Skidaway (−crabs)[4]	*~0*	*~0*	*~0*	*~0*	*100*

The presence and absence of sesarmid and fiddler crabs are indicated. The Skidaway saltmarsh data (*italics*) are included to emphasize the dramatic shift in microbial metabolism due to the presence of crabs. No similar type of study has been conducted in mangrove environments.
[1]Kristensen et al. (2000); [2]Kristensen and Alongi (2006); [3]Kristensen et al. (unpubl. data) [4]Kostka et al. (2002).

loss of ~ 75% of carbon from fresh litter is necessary to reach the observed sedimentary C:N ratio if other sources and sinks of carbon and nitrogen are excluded (Dittmar and Lara, 2001). Mangrove environments are therefore depleted in dissolved inorganic nitrogen (DIN) and the sediments generally act as sinks of DIN from the surroundings (Alongi, 1996; Rivera–Monroy and Twilley, 1996). Accordingly, the cycling of inorganic nitrogen must be rapid and efficient (i.e. tight) to support microbial growth in mangrove sediments.

4. Engineering effects of sesarmid and fiddler crabs on mangrove biogeochemistry

4.1. Burrow construction and maintenance

Most sesarmid and fiddler crabs construct and maintain burrow structures in mangrove sediment with significant engineering effect (processes 1, 2 and 4, Fig. 1) on the distribution and activity of associated organisms. The burrows are used by the crabs as a retreat or refuge when environmental conditions at the sediment surface are intolerable, for example during high tide or when conditions are too dry and hot (De la Iglesia et al., 1994; Botto and Iribarne, 2000; Thongtham and Kristensen, 2003). The two groups of crab generally occupy different habitats within the mangrove environment. Sesarmids are most abundant under tree canopies where their food source, leaf litter, is abundant, while the network of pneumatophores and cable roots provide protection against predators and extreme temperatures (Thongtham and Kristensen, 2003). Fiddler crabs, on the other hand, prefer open areas, particularly near creek banks, where strong sunlight stimulates growth of microphytobenthos, which is a primary food source for these crabs (Nobbs, 2003). Furthermore, they avoid any harassment and predation by sesarmids in these areas. Both types of crab clearly modify their habitat and create much of the visible topographic structures, e.g. mounds and depressions that are typical for mangrove sediments (Warren and Underwood, 1986).

The morphology of fiddler crab burrows is quite simple and similar among species, and it usually consists of a more or less permanent vertical shaft extending 10 to 40 cm into the sediment (Fig. 2A). Often, the burrows are bent into a J– or L-shape ending with a chamber (Koretsky et al., 2002; Lim, 2006). The burrows are continuously constructed, maintained and abandoned. The amount of sediment excavated during burrow construction and maintenance is considerable. Thus, McCraith et al. (2003) estimated that a population of *Uca pugnax* (40–300 burrows m^{-2}) in a North American saltmarsh excavated 120–160 cm^3 of sediment m^{-2} d^{-1} and continually mixed the upper 8–15 cm of the sediment. However, the excavated sediment must be counteracted by infilling of abandoned burrows and collapse of burrow walls. As a result, fiddler crabs alter the quality of organic matter on the sediment surface by replacing surface derived reactive material (e.g. fresh microphytobenthos) with much less reactive and partly degraded material from depth in the sediment (Gutiérrez et al., 2006).

Burrows of sesarmid crabs vary considerable in morphology and some species do not construct burrows, but utilize crevices or abandoned burrows of other species (Gillikin and Kamanu, 2005). Burrows of *Neoepisesarma versicolor* in Thailand, for example, range from very simple, straight burrows with few branches to complex, labyrinthine structures with up to 5 openings (Fig. 2B) (Thongtham and Kristensen, 2003).

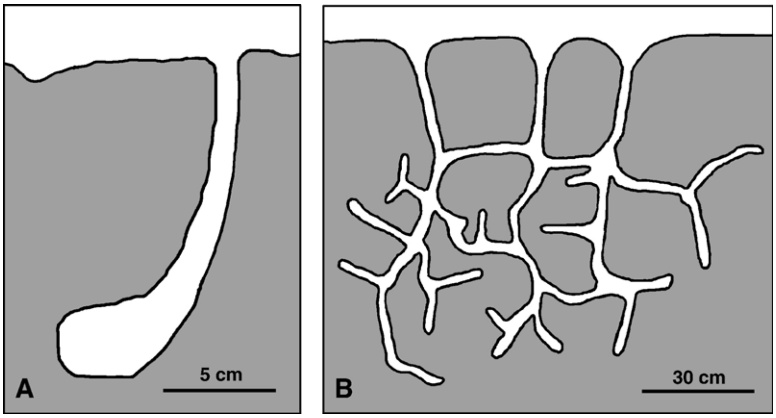

Fig. 2. Schematic drawings showing (A) the typical shape and dimensions of fiddler crab burrows, and (B) sesarmid crab burrows (modified from Kristensen and Kostka, 2005).

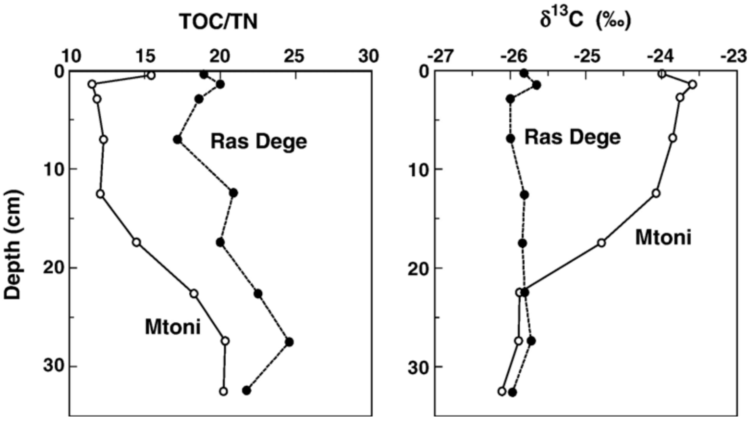

Fig. 3. Vertical profiles of TOC/TN ratio and $\delta^{13}C$ in the *Ulva lactuca* impacted Mtoni mangrove forest and the pristine Ras Dege mangrove forest. The data were obtained during the dry season in September (Bouillon and Kristensen, unpubl. data).

The surface opening of *N. versicolor* burrows is always associated with a more or less vertically oriented shaft. The length of the shaft varies from 5 to 25 cm with small burrows belonging to an associated fauna of small crustaceans and juvenile sesarmids protruding as side branches. The deeper part of *N. versicolor* burrows usually comprises smooth walled horizontal tunnels with several dead-ends and small chambers in an unpredictable pattern. The depth of burrows varies from ~ 55 to 110 cm. Crab burrow morphology is affected by factors such as sediment characteristics and age of burrows as well as type and abundance of associated fauna. Sesarmid crab burrows are long-lived and particularly the deeper parts are expected to last for a very long time. The complex structure of these deeper parts may actually be the result of continued construction by several generations of occupants. Because of frequent collapse of the near-surface parts of burrows, the crabs must continually maintain, rearrange and often reposition entrances (Micheli et al., 1991). Although the abundance of sesarmid crabs is low (1–5 ind m^{-2}) compared with fiddler crabs, these larger crabs excavate an equivalent amount of sediment (80–210 $cm^3\ m^{-2}\ d^{-1}$) and probably affect the organic matter composition at the sediment surface to at least the same extent.

In contrast to fiddler crabs, many sesarmid crabs tend to bury leaf litter and detritus during burrow construction and maintenance. The litter is frequently pulled directly into the burrows (Robertson, 1986; Ashton, 2002; Skov et al., 2002). The extent by which sesarmid crabs translocate deposited litter is clearly evident from the results of a recent study near Dar es Salaam, Tanzania (Bouillon and Kristensen, unpublished; see also Bouillon et al., 2008-this issue). The eutrophic Mtoni mangrove area receives masses of drifting macroalgae (e.g. *Ulva* sp.) via tidal action, particularly during spring tides in the dry season. Algae deposited at the sediment surface are handled, ingested and ultimately buried by sesarmid crabs. No such algal deposition occurs in the nearby oligotrophic Ras Dege mangrove area, where crabs primarily handle mangrove litter. The chemical composition of macroalgal detritus differs from mangrove litter with respect to TOC/TN ratios and $\delta^{13}C$ signatures (macroalgae: TOC/TN ~ 7–15, $\delta^{13}C$ ~ –15 ‰; mangrove litter: TOC/TN ~ 50–100, $\delta^{13}C$ ~ –30 ‰). The intensive subduction of macroalgal detritus by sesarmid crabs at Mtoni is clearly evident as lower TOC/TN ratio and enriched $\delta^{13}C$ signals of the bulk organic matter in the sediment down to 20–30 cm compared with Ras Dege, where leaf litter is a more important organic source (Fig. 3).

Except for occasional litter plastering by sesarmid crabs, neither of the two groups of crab directly stimulate

Table 2
Abundance and basic dimensions of various sesarmid and fiddler crab burrows

Species	Abundance	Depth	Surface area	Reference
	ind. m^{-2}	cm	m^2/m^2	
Uca pugilator	52 ± 10	15 ± 10	0.46	1
Uca pugnax	13 ± 4	20 ± 3	0.15	1
Uca vocans	12	10 ± 3	0.08	2
Uca annulipes	12	10 ± 3	0.07	2
Neoepisesarma versicolor	0.2	84 ± 7	0.33	3
Sesarma messa/ Alpheus cf. macklay	1.7	120	6.46	4

The inner burrow wall surface area (m^2) is given per m^2 sediment surface for the entire population.
1: Koretsky et al., 2002; 2: Lim, 2006; 3: Thongtham and Kristensen, 2003; 4: Stieglitz et al., 2000.

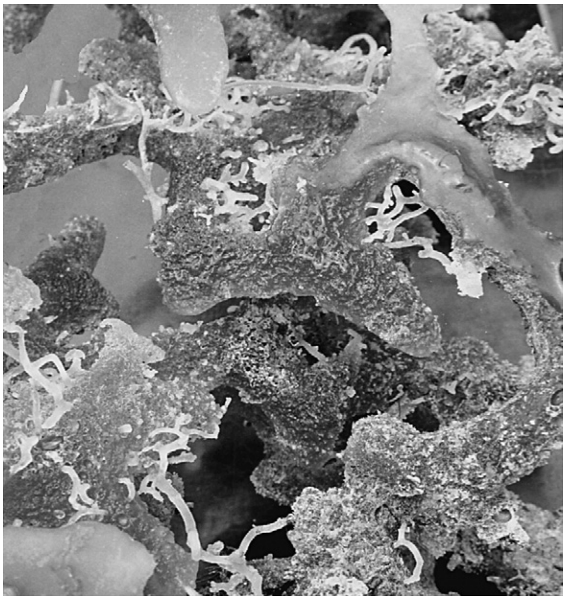

Fig. 4. Close–up photo of burrow resin cast of the sesarmid crab *Neoepisesarma versicolor* from the Bangrong mangrove forest, Phuket, Thailand. The numerous small burrows of the associated fauna are clearly visible as fine protrusions along the main burrow shaft (Thongtham and Kristensen, unpubl. data).

microbial activity along burrow walls by secreting reactive mucus (Kristensen and Kostka, 2005). Their burrowing activities nevertheless increase the potential for biological and chemical exchange simply by increasing the interface between sediment and water/air. According to the data available (Table 2), each fiddler crab burrow increases the interface area by ~ 1%, while the increase per sesarmid crab burrow is 150–380%. If the up to two orders of magnitude differences in abundance between the two groups are considered (fiddler crabs: 10–500 m^{-2}; sesarmid crabs: 0.2–10 m^{-2}), the increase in interface area under natural conditions is considerable and comparable for both (Hartnoll et al., 2002; Skov et al., 2002; Thongtham and Kristensen, 2003).

The gas and solute exchange across the walls of the numerous burrows can only be rectified if there is access to transport via air or water phases. In contrast to the engineering effect of many subtidal polychaetes, as pointed out by Gutiérrez and Jones (2006), no mangrove crabs actively ventilate their burrows. Only their sporadic crawling movements into and out of as well as inside burrows may mediate some transport. In fact, many fiddler crabs even prevent transport by plugging their burrow entrances during tidal inundation because it allows them access to trapped air suitable for respiratory needs and prevents burrow collapse (De la Iglesia et al., 1994). Both sesarmid and fiddler crab burrows are nevertheless dependent on passive irrigation via tidal action, but the mechanism by which water and air are transported and thus the functionality of burrows depends strongly on the sediment characteristics and burrow structure. Burrows in permeable sandy sediments are usually flushed with water and air through tidal-driven percolation within the sand, while deep burrows in cohesive sediments are flooded from above during high tide and drain through deep cracks or by pressure differences between multiple openings (Thongtham and Kristensen, 2003). Stieglitz et al. (2000) found that the total flow through large burrows of *Sesarma messa* in northern Australia is up to 100 L m^{-2} $tide^{-1}$, which is equivalent to 30% of the tidal water entering that particular mangrove area. Along with the water drainage during low tide, oxygen is introduced deep (i.e. > 1 m) into the sediment via air intrusion causing cascading redox effects on metal and sulfur cycling.

The engineering impacts of burrows as physical structures and associated physical transport on small fauna and microorganisms in the sediment are numerous and widespread. It may, however, at times be difficult to discriminate the effects of the structures themselves from those mediated by transport. The association of small burrowing fauna (juvenile crabs, callianassids, polychaetes and gastropods) within burrows of adult sesarmid crabs (Thongtham and Kristensen, 2003) is a clear example of ecosystem engineering caused by physical structures (i.e. burrows) (Fig. 4). The adult crabs modify the environment by burrow construction (process 1, Fig. 1) favouring the occupation of new ecological niches where small fauna have access to constant environmental conditions, ample food supplies and protection from predators. No such association has been recorded for the relatively short-lived fiddler crab burrows, whereas it frequently occurs in e.g. thalassinid burrows (Kinoshita, 2002; De Gibert et al., 2006). It is likely that meiofaunal abundance and community structure also is altered along burrow walls of both sesarmid and fiddler crab burrows as reported for polychaete

Table 3
Fluxes (mmol m^{-2} d^{-1}) across the sediment-water/air interface of CO_2, NH_4^+ and NO_3^- in the Mtoni and Ras Dege mangrove forests, Tanzania (Kristensen, unpubl. data)

Compound	Mtoni	Ras Dege
CO_2	106.3 ± 18.3	78.1 ± 7.2
NH_4^+	2.03 ± 0.20	−0.91 ± 0.29
NO_3^-	1.12 ± 0.59	−0.29 ± 0.02

Results are given as mean ± SE (n = 3). Negative values indicate uptake by the sediment.

burrows in temperate areas (Reise, 1981), but no reports are yet available to confirm this proposition for mangrove environments.

The most obvious engineering impact caused by crab-mediated physical transport (process 2, Fig. 1) is the downward translocation of fresh litter detritus and the associated influence on heterotrophic microbial communities within the sediment. It has been argued that the relocation of microphytobenthic and macrophyte detritus by the excavation activities of crabs or litter directly pulled into burrows enhances the heterogeneity and thereby the efficiency of microbial decomposition in subsurface mangrove sediments (Emmerson and McGwynne, 1992; Micheli, 1993; Botto and Iribarne, 2000). The study from Tanzania mentioned above, where a massive input of *Ulva* sp. is buried by sesarmid crabs in the Mtoni mangrove forests, clearly shows a subsequent impact of detritus burial on bulk sediment carbon and nitrogen cycling (Table 3). The labile and nitrogen-rich *Ulva* detritus in Mtoni mediates rapid carbon and nitrogen mineralization within the sediment that result in large efflux of CO_2 and dissolved inorganic nitrogen (NH_4^+ and NO_3^-). Conversely, at Ras Dege where the sediment is supplied with more refractory and nitrogen-poor leaf litter, the lower efflux of CO_2 suggests an overall modest microbial activity. Furthermore, the uptake of dissolved inorganic nitrogen by this sediment complies with the general notion of nitrogen limitation in mangrove sediments when leaf litter is the primary source of organic matter (Alongi, 1996; Kristensen, unpubl. data).

Another important engineering effect of sesarmid and fiddler crab burrows is related to the biogeochemistry of redox-sensitive and largely microbially-driven processes involving iron and sulfur. A number of studies have in recent years suggested that macrofauna substantially affect the geochemical cycles of S and Fe in marine sediments (e.g. Kostka et al., 2002; Gribsholt et al., 2003; Nielsen et al., 2003). In the case of mangrove crabs, formation of burrow structures (process 1, Fig. 1) and the largely passive transport of water and air channelled by these (process 4, Fig. 1) are involved mutually. The driving factor is the intrusion of oxygen that enhances aerobic decomposition (Kristensen and Holmer, 2001), increases the volume of oxidized Fe^{3+}-containing sediment, and neutralizes toxic metabolites from anaerobic processes (e.g. sulfide). Crab burrows may therefore affect the partitioning between electron acceptors (e.g. SO_4^{2-} versus Fe^{3+}) used by anaerobic bacteria in the terminal oxidation of organic carbon (Table 1). The key to maintaining a delicate redox balance is availability of a sufficiently large reactive iron pool within the sediment. Radial profiling of crab burrows in iron-rich mangrove sediments has confirmed an increased supply of reactive Fe^{3+} along the walls, which causes Fe^{3+} reduction to out-compete sulfate reduction (Fig. 5). Thus, crab burrows (and plant roots) maintain sufficiently high redox conditions to prevent excessive rates of sulfate reduction and associated accumulation of toxic sulfide in mangrove sediment. The sulfide produced under these conditions is largely precipitated

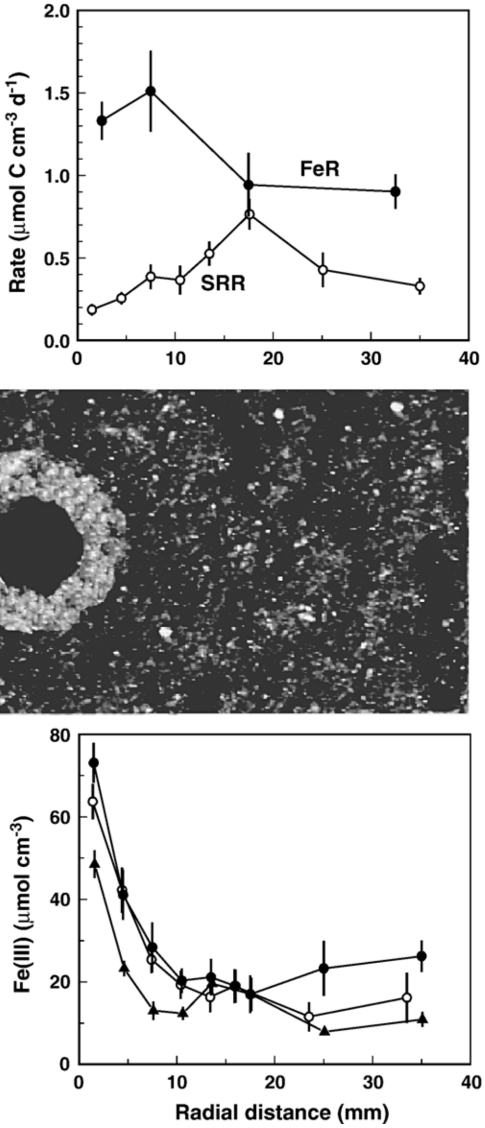

Fig. 5. Radial profiles around a fiddler crab burrow of: Upper panel, dissimilatory iron reduction (FeR) and sulfate reduction (SRR), and lower panel, oxidized iron (Fe^{3+}). The middle photograph shows the radial colour changes around the burrow. The light oxidized zone extends 5–10 mm away from the burrow lumen and into the surrounding sediment. Further away, black mackinawite (FeS) dominates the coloration of the sediment (modified from Gribsholt et al., 2003).

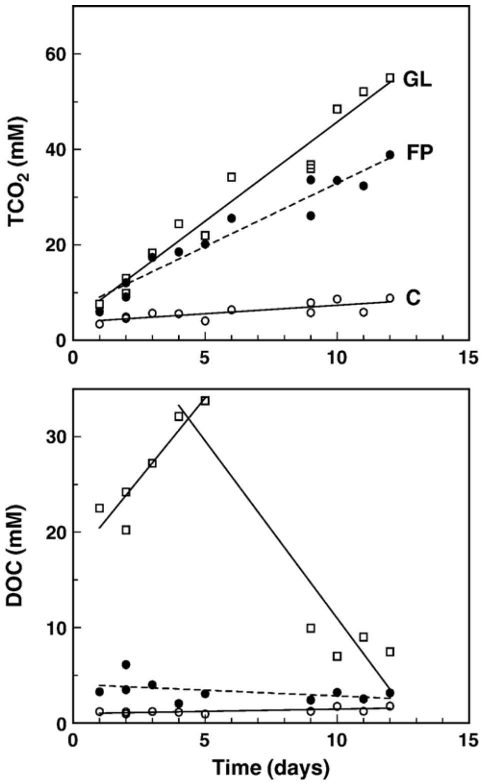

Fig. 6. Temporal pattern of TCO_2 and DOC concentrations in anoxic sediment incubations amended with green *Rhizophora apiculata* leaves (GL), faecal pellets from the sesarmid crab *Neoepisesarma versicolor* after feeding on green *Rhizophora apiculata* leaves (FP). The control sediment (C) was kept unamended (modified from Kristensen and Pilgaard, 2001).

as relatively inert pyrite (Holmer et al., 1999), which is harmless to plants and animals.

4.2. Sesarmid crabs and the fate of ingested plant litter

Burrow construction and maintenance is not the only engineering effect of mangrove crabs. Also the handling and ingestion of food substances (processes 3 and 5, Fig. 1) has substantial effects on other organisms in the environment. Many sesarmid crab species are remarkable in their ability to consume mangrove litter (Dye and Lasiak, 1987; Robertson et al., 1992). Studies from a variety of mangrove environments have shown that litter consumption and burial by sesarmid crabs may remove 30–90% of the annual litterfall (e.g. Robertson, 1986; Micheli, 1993; Slim et al., 1997). It appears that the senescence and degradation stage of leaves is important to their palatability to crabs. Thus, Thongtham and Kristensen (2005) showed that *Neoepisesarma versicolor* consumes fresh green and scenescent yellow *Rhizophora apiculata* leaves at a considerably lower rate than partly degraded brown leaves. This observation is consistent with those of Giddins et al. (1986) for *Neosarmatium smithii* and Micheli (1993) for *Sesarma messa* and *N. smithii*. The higher palatability of brown leaves compared with green and, in particular, yellow leaves probably results from improved nutritional value and removal of inhibitory compounds by the aging process (Poovachiranon and Tantichodok, 1991).

In general, sesarmid crabs consume about half of the handled litter immediately, while the remainder is pulled into burrows to promote microbial colonization and leaching of tannins. The litter stored in burrows may later be consumed by the crabs or is left for further microbial degradation. After shredding and maceration followed by passage through the crabs intestinal system, much of the litter is returned to the sediment environment in the form of partly digested faeces. The assimilation efficiency of carbon by sesarmid crabs feeding on a leaf diet ranges from 40 to 70% (Lee, 1997; Thongtham and Kristensen, 2005), which means that about half of the ingested litter subsequently becomes available for decomposer or detritus food webs. It is noteworthy that the C:N ratio of faeces is lower than in the eaten leaf litter (Lee, 1997; Thongtham and Kristensen, 2005), probably due to bacterial growth and nitrogen retaining within the intestinal system.

Kristensen and Pilgaard (2001) provided evidence for the engineering effect of deposited faecal pellets from *N. versicolor* fed green *R. apiculata* leaves on the heterogeneity of anaerobic microbial activity in sediment. They compared the fate of carbon in chopped green leaves (less than 3 by 3 mm) with that of freshly collected faecal material after the detritus was buried in anoxic mangrove sediment. Anaerobic microbial decay determined as TCO_2 production was 11.7× higher for sediment amended with green leaf detritus than without any organic matter addition, while the stimulation in sediment amended with faecal material only was 7.5 times (Fig. 6).

Table 4
Rates of anaerobic carbon transformations (nmol cm^{-3} d^{-1}) in mangrove sediment after homogeneous mixing with 0.5% (dw) green leaf detritus (GL) of *Rhizophora apiculata* or 0.5% (dw) faecal pellets (FP) of *Neoepisesarma versicolor* after feeding on green *Rhizophora apiculata* leaves

	TCO_2 prod	DOC prod	Net C prod
C	277±66	37±13	314
GL	3243±215	−2899±464	344
FP	2068±169	−95±67	1973

The control sediment (C) was handled similarly, except for the addition of organic matter. Values are given as mean±SE as obtained from Fig. 6 of Kristensen and Pilgaard (2001).

At first glance, it appears that the uneaten leaf detritus sustained highest microbial activity, but a closer look at the data reveals that excessive leaching of labile DOC from the fresh leaf detritus material (up to 30 mM in the porewater) supported most of the excess microbial activity in this treatment. Thus, after correction for the differential contribution of DOC to the microbial carbon oxidation, it turned out that the solid faecal material supported 55× faster microbial decay than the solid leaf material (Table 4). Lee (1997) similarly showed that faecal material from *S. messa* feeding on *R. stylosa* is a profitable food source for the detritus-feeding amphipod *Parhyalella* sp. Individuals of *Parhyalella* sp. fed with detritus containing crab faeces attained significantly higher moulting frequency and lower mortality than those fed a diet of leaf detritus alone.

4.3. Fiddler crab forcing of the microbial distribution and activity in sediment

The engineering effects of fiddler crab foraging are generally confined to the upper few millimetres of the sediment (Dye and Lasiak, 1986). They feed on fine particles by picking sediment from the surface using the minor chelae and placing it in the mouth cavity. Here the edible particles including microalgal cells, nematodes, and bacteria are sorted and ingested. The non-edible particles are shaped into small irregular balls that are deposited at the sediment surface at regular intervals by the minor chelae (France, 1998). There has been some controversy in the literature about the food selectivity of fiddler crabs. Some authors argue that *Uca* species primarily select bacteria (Dye and Lasiak, 1986), while others claim that the major food source is microphytobenthos (France, 1998; Reinsel, 2004). There is obviously different selectivity among species and the outcome strongly depends on environmental conditions (Meziane et al., 2002). For example, Kristensen and Alongi (2006) found that grazing by the fiddler crab, *Uca vocans*, maintained near-surface microalgal abundance (Chl-a) 64% lower and bacterial abundance 23% lower than in defaunated control sediment (Table 5). While most species of fiddler crabs clearly ingest both benthic microalgae and bacteria (France, 1998; Bouillon et al., 2002), it is less clear how they handle meiobenthos and small macrobenthos (Reinsel, 2004). The commonly observed reduction of meiofaunal density and diversity by fiddler crabs (Schrijvers et al., 1995; Olafsson and Ndaro, 1997) can be a direct effect through predation or an indirect effect through disturbance or competition for food (Reinsel, 2004; Weis and Weis, 2004).

While effects of fiddler crab feeding are largely confined to the sediment surface, their activities may affect redox sensitive elements (e.g. Fe) as well as engineering effects of microbial distribution and activity down to at least 2 cm depth. The 35–230% higher content of Fe^{3+} and 50–90% lower content of Fe^{2+} found by Kristensen and Alongi (2006) in the upper 2 cm of the sediment when *Uca vocans* is present (Table 5) must be caused by continuous mixing and oxidation of surface sediment by the intense activities of the crabs. Mixing occurs not only during feeding but also when the dactyls of the legs sink into the sediment during crawling. Deposition at the surface of feeding balls and subsurface sediment during burrow

Table 5
Vertical distribution of organic carbon content (POC), microphytobenthos (Chl–a), bacteria, reactive Fe^{3+} (Fe(III)), reactive Fe^{2+} (Fe(II)), total carbon oxidation (C–ox), dissimilatory iron reduction (FeR) and dissimilatory sulfate reduction (SRR) in *Avicennia marina* vegetated mangrove sediment in the presence (+C) and absence (−C) of the fiddler crab, *Uca vocans*

	0–1 cm		**1–2 cm**		**6–8 cm**	
	+C	**−C**	**+C**	**−C**	**+C**	**−C**
POC (mmol g^{-1})	1.51±0.05	1.83±0.12	1.52±0.03	1.68±0.03	1.40±0.27	1.58±0.01
Chl–a (μg g^{-1})	2.9±0.5	8.0±0.6	2.4±0.2	3.7±0.8	2.3±0.4	2.0±0.3
Bacteria (10^9 cm^{-3})	6.1±0.5	7.9±0.7	5.5±0.3	6.3±0.9	4.2±0.9	4.2±0.2
Fe(III) (μmol cm^{-3})	115±4	85±5	75±16	23±3	12±5	9±1
Fe(II) (μmol cm^{-3})	2±0	20±1	45±15	94±5	124±9	132±8
	0–2 cm				**6–8 cm**	
	+C	**−C**			**+C**	**−C**
C–ox (μmol cm^{-3} d^{-1})	0.29±0.00	1.43±0.00			0.34±0.13	0.43±0.12
FeR (μmol cm^{-3} d^{-1})	0.43±0.16	6.56±1.25			0.41±0.63	0.14±0.63
SRR (nmol cm^{-3} d^{-1})	8±2	32±7			111±32	82±30

Values are given as mean±SE (n=3) (data from Kristensen and Alongi, 2006).

construction and maintenance, combined with the smoothening and oxidation effect of crawling crabs, augments the effective mixing depth. The low rates of carbon oxidation in near-surface sediment inhabited by *U. vocans* (Kristensen and Alongi, 2006; Table 5) is caused by lack of reactive organic carbon and not availability of electron acceptors (O_2, Fe^{3+} or SO_4^{2-}). This is substantiated by the 15 x higher dissimilatory iron reduction (FeR) in the surface of ungrazed mesocosms that are poorer in Fe^{3+} but much richer in labile microalgal organic carbon. The parallel, but much less dramatic, pattern with 4 x higher sulfate reduction (SRR) near the sediment surface in ungrazed mesocosms compared with grazed mesocosms is probably also caused by the higher organic matter availability.

5. Conclusions: Are mangrove crabs really ecosystem engineers?

The answer to this question must be a clear and unambiguous, yes! While this is said, it must be emphasized that the features and processes driving engineering effects on the distribution and activity of associated organisms in general are operating differently for sesarmid and fiddler crabs (Table 6). This is not surprising considering the divergent biology of the two types of crab with respect to factors such as preferred habitats, complexity and size of burrow morphologies, and food preferences.

It is well documented that burial of plant detritus by the excavation activities of sesarmid crabs or litter directly pulled into their burrows enhance the heterogeneity and thereby the efficiency of microbial decomposition in subsurface mangrove sediments. No such information is yet available for fiddler crabs. Also the passive irrigation of both sesarmid and fiddler crabs with water and air that introduces oxygen deep into the sediment enhances aerobic decomposition as well as modifies the partitioning between electron acceptors in the terminal oxidation of organic carbon. The intensity and depth distribution by which these engineering effects operate may vary considerably between the two types of crab. Burrow construction may also favour the occupation of new ecological niches, where small fauna (juvenile macrofauna and meiofaunal) have access to constant environmental conditions, ample food supplies and protection from predators. This engineering effect is well known for other burrowing marine invertebrates, but has only been proved sporadically for sesarmid crabs and not at all for fiddler crabs. More attention must certainly be devoted in the future to fully elucidate the engineering aspects related to crab burrows in mangrove environments. Particularly comparative work on the burrow-dwelling life styles of sesarmid and fiddler crabs is needed.

The most obvious and well-documented difference between engineering effects of the two crab groups seems to be associated with foraging. The litter handling and ingestion by sesarmid crabs form finely fragmented organic material that is an ideal substrate for and stimulate both microbial colonization and macrofaunal detritivores. Conversely, the surface-feeding activities of fiddler crabs efficiently remove reactive organic carbon (e.g. microphytobenthos and bacteria) and thereby diminish the biological activity in surface sediment by ingesting and competitively starving decomposers and other organisms involved in the detritus food web.

Table 6
Overview of ecosystem engineering attributes of sesarmid and fiddler crabs and their effect on the associated biological assemblages

Feature and state change	**Biological/biogeochemical effect**	**Crab responsible**
Burrow construction and maintenance	Creates ecological niches for small fauna	Sesarmid (and fiddler)
Redistribution of organic matter and burial of litter	Enhanced heterotrophic microbial activity in sediment Increased microbial heterogeneity Nutrient conservation	Sesarmid (and fiddler)
Exchange between sediment and water/air by: Passive irrigation Diffusive gas exchange	Changed subsurface sediment redox conditions Enhanced subsurface microbial iron reduction Lowered microbial sulfate reduction	Sesarmid and fiddler
Litter feeding and egestion	Enhanced heterotrophic microbial activity in sediment Nutrient conservation Improved nutrition for detritivores	Sesarmid
Surface feeding and mixing	Changed near-surface redox conditions Increased availability of oxidized iron Lowered microbial biomass Lowered near-surface heterotrophic microbial activity Enhanced subsurface microbial iron reduction	Fiddler

Parentheses indicate that effects are likely for fiddler crabs, but that no evidence currently exists.

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References

Aller, R.C., 1982. The effects of macrobenthos on chemical properties of marine sediment and overlying water. In: McCall, P.L., Tevesz, P.J.S. (Eds.), Animal-Sediment Relations. Plenum, New York, pp. 53–102.

Alongi, D.M., 1996. The dynamics of benthic nutrient pools and fluxes in tropical mangrove forests. J. Mar. Res. 54, 123–148.

Alongi, D.M., 1998. Coastal Ecosystem Processes. CRC Press, Boca Raton.

Alongi, D.M., 2002. Present state and future of the world's mangrove forests. Environ. Conserv. 29, 331–349.

Alongi, D.M., Tirendi, F., Dixon, P., Trott, L.A., Brunskill, G.J., 1999. Mineralization of organic matter in intertidal sediments of a tropical semi-enclosed delta. Estuar. Coast. Shelf Sci. 48, 451–467.

Alongi, D.M., Wattayakorn, G., Pfitzner, J., Tirendi, F., Zagorskis, I., Brunskill, G.J., Davidson, A., Clough, B.F., 2001. Organic carbon accumulation and metabolic pathways in sediments of mangrove forests in southern Thailand. Mar. Geol. 179, 85–103.

Ashton, E.C., 2002. Mangrove sesarmid crab feeding experiments in Peninsular Malaysia. J. Exp. Mar. Biol. Ecol. 273, 97–119.

Benner, R., Hatcher, P.G., Hedges, J.I., 1990. Early diagenesis of mangrove leaves in a tropical estuary: Bulk chemical characterization using solid-state ^{13}C NMR and elemental analysis. Geochim. Cosmochim. Acta 54, 2003–2013.

Berner, R.A., Westrich, J.T., 1985. Bioturbation and the early diagenesis of carbon and sulfur. Am. J. Sci. 285, 193–206.

Botto, F., Iribarne, O., 2000. Contrasting effect of two burrowing carbs (Chasmagnathus granulata and Uca uruguayensis) on sediment composition and transport in estuarine environments. Estuar. Coast. Shelf Sci. 51, 141–151.

Bouillon, S., Connolly, R.M., Lee, S.Y. 2008. Organic matter exchange and cycling in mangrove ecosystems: recent insights from stable isotope studies. J. Sea Res. 59, 44–58 (this issue).

Camilleri, J.C., Ribi, G., 1986. Leaching of dissolved organic carbon (DOC) from dead leaves, formation of flakes from DOC, and feeding on flakes by crustaceans in mangroves. Mar. Biol. 91, 337–344.

Canfield, D.E., Jørgensen, B.B., Fossing, H., Glud, R., Gundersen, J., Ramsing, N.B., Thamdrup, B., Hansen, J.W., Nielsen, L.P., Hall, P.O.J., 1993. Pathways of organic carbon oxidation in three continental margin sediments. Mar. Geol. 113, 27–40.

Christensen, B., 1978. Biomass and primary production of Rhizophora apiculata Bl. in a mangrove in southern Thailand. Aquat. Bot. 4, 43–52.

Clarke, P.J., Allaway, W.G., 1993. The regeneration niche of the gray mangrove (Avicennia marina) - effects of salinity, light and sediment factors on establishment, growth and survival in the field. Oecologia 93, 548–556.

De Gibert, J.M., Netto, R.G., Tognoli, F.M.W., Grangeiro, M.E., 2006. Commensal worm traces and possible juvenile thalassinidean burrows associated with Ophiomorpha nodosa, Pleistocene, southern Brazil. Palaeogeogr. Palaeoclimat. Palaeoecol. 230, 70–84.

De la Iglesia, H.O., Rodriquez, E.M., Dezi, R.E., 1994. Burrow plugging in the crab Uca uruguayensis and its synchronization with photoperiod and tides. Physiol. Behav. 55, 913–919.

Dittmann, S., 1996. Effects of macrobenthic burrows on infaunal communities in tropical tidal flats. Mar. Ecol., Prog. Ser. 134, 119–130.

Dittmar, T., Lara, R.J., 2001. Molecular evidence for lignin degradation in sulfate-reducing mangrove sediments (Amazonia, Brazil). Geochim. Cosmochim. Acta 65, 1417–1428.

Dye, A.H., Lasiak, T.A., 1986. Microbenthos, meiobenthos and fiddler crabs: trophic interactions in a tropical mangrove sediment. Mar. Ecol., Prog. Ser. 32, 259–264.

Dye, A.H., Lasiak, T.A., 1987. Assimilation efficiency of fiddler crabs and deposit-feeding gastropods from tropical mangrove sediments. Comp. Biochem. Physiol. 87A, 341–344.

Emmerson, W.D., McGwynne, L.E., 1992. Feeding and assimilation of mangrove leaves by the crab Sesarma meinerti Deman in relation to leaf-litter production in Mgazana, a warm temperate southern African mangrove swamp. J. Exp. Mar. Biol. Ecol. 157, 41–53.

France, R., 1998. Estimating the assimilation of mangrove detritus by fiddler crabs in Laguna Joyuda, Puerto Rico, using dual stable isotopes. J. Trop. Ecol. 14, 413–425.

Giddins, R.L., Lucas, J.S., Neilson, M.J., Richards, G.N., 1986. Feeding ecology of the mangrove crab Neosarmatium smithi (Crustacea, Decapoda, Sesarmidae). Mar. Ecol., Prog. Ser. 33, 147–155.

Gillikin, D.P., Kamanu, C.P., 2005. Burrowing in the East African mangrove crab, *Chiromantes ortmanni* (Crosnier, 1965) (Decapoda, Brachyura, Sesarmidae). Crustaceana 78, 1273–1275.

Gribsholt, B., Kostka, J.E., Kristensen, E., 2003. Impact of fiddler crabs and plant roots on sediment biogeochemistry in a Georgia salt marsh. Mar. Ecol., Prog. Ser. 259, 237–251.

Gutiérrez, J.L., Jones, C.G., 2006. Physical ecosystem engineers as agents of biogeochemical heterogeneity. BioScience 56, 227–236.

Gutiérrez, J.L., Jones, C.G., Groffman, P.M., Findlay, S.E.G., Iribarne, O.O., Ribeiro, P.D., Bruschetti, C.M., 2006. The contribution of crab burrow excavation to carbon availability in surficial salt-marsh sediments. Ecosystems 9, 647–658.

Hartnoll, R.G., Cannicci, S., Emmerson, W.D., Fratini, S., Macia, A., Mgaya, Y., Porri, F., Ruwa, R.K., Shunula, J.P., Skov, M.W., Vannini, M., 2002. Geographic trends in mangrove crab abundance in East Africa. Wetlands Ecol. Manag. 10, 203–213.

Holmer, M., Kristensen, E., Banta, G.T., Hansen, K., Jensen, M.H., Bussarawit, N., 1994. Biogeochemical cycling of sulfur and iron in sediments of a south-east Asian mangrove, Phuket Island, Thailand. Biogeochemistry 26, 145–161.

Holmer, M., Andersen, F.Ø., Holmboe, N., Kristensen, E., Thongtham, N., 1999. Transformation and exchange processes in the Bangrong mangrove forest-seagrass bed system, Thailand. Seasonal and spatial variations in benthic metabolism and sulfur biogeochemistry. Aquat. Microb. Ecol. 20, 203–212.

Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. Oikos 69, 373–386.

Jones, C.G., Lawton, J.H., Shachak, M., 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78, 1946–1957.

Kinoshita, K.Y., 2002. Burrow structure of the mud shrimp Upogebia major (Decapoda: Thalassinidea: Upogebiidae). J. Crustac. Biol. 22, 474–480.

Kitaya, Y., Yabuki, K., Kiyota, M., Tani, A., Hirano, T., Aiga, I., 2002. Gas exchange and oxygen concentration in pneumatophores and prop roots of four mangrove species. Trees 16, 155–158.

Koretsky, C.M., Meile, C., Van Cappellen, P., 2002. Quantifying bioirrigation using ecological parameters. Geochem. Trans. 3, 17–30.

Kostka, J.E., Gribsholt, B., Petrie, E., Dalton, D., Skelton, H., Kristensen, E., 2002. The rates and pathways of carbon oxidation in bioturbated saltmarsh sediments. Limnol. Oceanogr. 47, 230–240.

Krebs, C.J., 2001. Ecology: The Experimental Analysis of Distribution and Abundance, 5th ed. Benjamin Cummings, San Francisco.

Kristensen, E., Alongi, D.M., 2006. Control by fiddler crabs (Uca vocans) and plant roots (Avicennia marina) on carbon, iron and sulfur biogeochemistry in mangrove sediment. Limnol. Oceanogr. 51, 1557–1571.

Kristensen, E., Holmer, M., 2001. Decomposition of plant materials in marine sediment exposed to different electron acceptors (O2, NO3– and SO42–), with emphasis on substrate origin, degradation kinetics and the role of bioturbation. Geochim. Cosmochim. Acta 65, 419–434.

Kristensen, E., Kostka, J.E., 2005. Macrofaunal burrows and irrigation in marine sediment: microbiological and biogeochemical interactions. In: Kristensen, E., Haese, R.R., Kostka, J.E. (Eds.), Interactions between Macro– and Microorganisms in Marine Sediments. American Geophysical Union, Washington, DC, pp. 125–158.

Kristensen, E., Pilgaard, R., 2001. The role of fecal pellet deposition by leaf-eating sesarmid crabs on litter decomposition in a mangrove sediment (Phuket, Thailand). In: Aller, J.Y., Woodin, S.A., Aller, R.C. (Eds.), Organism-Sediment Interactions. Univ. S. Carolina Press, Columbia, pp. 369–384.

Kristensen, E., King, G.M., Holmer, M., Banta, G.T., Jensen, M.H., Hansen, K., Bussarawit, N., 1994. Sulfate reduction, acetate turnover and carbon metabolism of the Ao Nam Bor mangrove, Phuket, Thailand. Mar. Ecol., Prog. Ser. 109, 245–255.

Kristensen, E., Holmer, M., Banta, G.T., Jensen, M.H., Hansen, K., 1995. Carbon, nitrogen and sulfur cycling in sediments of the Ao Nam Bor mangrove forest, Phuket, Thailand: A review. Phuket Mar. Biol. Cent. Res. Bull. 60, 37–64.

Kristensen, E., Andersen, F.Ø., Holmboe, N., Holmer, M., Thongtham, N., 2000. Carbon and nitrogen mineralization in sediments of the Bangrong mangrove area, Phuket, Thailand. Aquat. Microb. Ecol. 22, 199–213.

Lee, K.–H., Moran, M.A., Benner, R., Hodson, R.E., 1990. Influence of soluble components of red mangrove (*Rhizophora mangle*) leaves on microbial decomposition of structural (lignocellulosic) leaf components in seawater. Bull. Mar. Sci. 46, 374–386.

Lee, S.Y., 1997. Potential trophic importance of the faecal material of the mangrove sesarmine crab Sesarma messa. Mar. Ecol., Prog. Ser. 159, 275–284.

Lim, S.S.L., 2006. Fiddler crab burrow morphology: how do burrow dimensions and bioturbative activities compare in sympatric populations of *Uca vocans* (Linnaeus, 1758) and *U.annulipes* (H. Milne Edwards, 1837)? Crustaceana 79, 525–540.

Marchand, C., Disnar, J.–R., Lallier–Verges, E., Lottier, N., 2005. Early diagenesis of carbohydrates and lignin in mangrove sediments subject to variable redox conditions (French Guiana). Geochim. Cosmochim. Acta 69, 131–142.

McCraith, B.J., Gardner, L.R., Wethey, D.S., Moore, W.S., 2003. The effect of fiddler crab burrowing on sediment mixing and radionuclide profiles along a topographic gradient in a southeastern salt marsh. J. Mar. Res. 61, 359–390.

Meziane, T., Sanabe, M.C., Tsuchiya, M., 2002. Role of fiddler crabs of a tropical intertidal flat on the fate of sedimentary fatty acids. J. Exp. Mar. Biol. Ecol. 270, 191–201.

Micheli, F., 1993. Feeding ecology of mangrove crabs in North Eastern Australia: mangrove litter consumption by Sesarma messa and Sesarma smithii. J. Exp. Mar. Biol. Ecol. 171, 165–186.

Micheli, F., Gherardi, F., Vannini, M., 1991. Feeding and burrowing ecology of two East African mangrove crabs. Mar. Biol. 111, 247–254.

Mouton, E.C., Felder, D.L., 1996. Burrow distributions and population estimates for the fiddler crabs Uca spinicarpa and Uca longisignalis in a Gulf of Mexico salt marsh. Estuaries 19, 51–61.

Newell, R.I.E., Marshall, N., Sasekumar, A., Chong, V.C., 1995. Relative importance of benthic microalgae, phytoplankton, and mangroves as sources of nutrition for penaid prawns and other coastal invertebrates from Malaysia. Mar. Biol. 123, 595–606.

Newell, S.Y., 1996. Established and potential impacts of eukaryotic mycelial decomposers in marine/terrestrial ecotones. J. Exp. Mar. Biol. Ecol. 200, 187–206.

Nielsen, O.I., Kristensen, E., Macintosh, D.J., 2003. Impact of fiddler crabs (Uca spp.) on rates and pathways of benthic mineralization in deposited mangrove shrimp pond waste. J. Exp. Mar. Biol. Ecol. 289, 59–81.

Nobbs, M., 2003. Effects of vegetation differ among three species of fiddler crabs (Uca spp.). J. Exp. Mar. Biol. Ecol. 284, 41–50.

Olafsson, E., Ndaro, S.G.M., 1997. Impact of mangrove cras Uca annulipes and Dotilla fenestrate on meiobenthos. Mar. Ecol., Prog. Ser. 158, 225–231.

Paine, R.T., 1969. A note on trophic complexity and community stability. Am. Nat. 103, 91–93.

Passioura, J.B., Ball, M.C., Knight, J.H., 1992. Mangroves may salinize the soil and in so doing limit their transpiration rate. Funct. Ecol. 6, 476–481.

Por, F.D., 1984. The ecosystem of the mangal: General considerations. In: Por, F.D., Dor, I. (Eds.), Hydrobiology of the Mangal. W. Junk Publishers, The Hague, pp. 1–14.

Poovachiranon, S., Tantichodok, P., 1991. The role of sesarmid crabs in the mineralization of leaf litter of Rhizophora apiculata in a mangrove, southern Thailand. Phuket Mar Biol. Cent. Res. Bull. 56, 63–74.

Reinsel, K.A., 2004. Impact of fiddler crab foraging and tidal inundation on an intertidal sandflat: season–dependent effects in one tidal cycle. J. Exp. Mar. Biol. Ecol. 313, 1–17.

Reise, K., 1981. High abundance of small zoobenthos around biogenic structures in tidal sediments of the Wadden Sea. Helgol. Meeresunters. 34, 413–425.

Reise, K., 2002. Sediment mediated species interactions in coastal waters. J. Sea Res. 48, 127–141.

Rivera–Monroy, V.H., Twilley, R.R., 1996. The relative role of denitrification and immobilization in the fate of inorganic nitrogen in mangrove sediments (Terminos Lagoon, Mexico). Limnol. Oceanogr. 41, 284–296.

Robertson, A.I., 1986. Leaf–burying crabs: Their influence on energy flow and export from mixed mangrove forests (Rhizophora spp.) in north eastern Australia. J. Exp. Mar. Biol. Ecol. 102, 237–248.

Robertson, A.I., Alongi, D.M., Boto, K.G., 1992. Foods chains and carbon fluxes. In: Robertson, A.I., Alongi, D.M. (Eds.), Tropical Mangrove Ecosystems. Coastal and Estuarine Studies 41. American Geophysical Union, Washington, DC, pp. 293–326.

Schrijvers, J., Okondo, J., Steyaert, M., Vincx, M., 1995. Influence of epibenthos on meiobenthos of the Ceriops tagal mangrove sediment at Gazi Bay Kenya. Mar. Ecol., Prog. Ser. 128, 247–259.

Skov, M.W., Vannini, M., Shunula, J.P., Hartnoll, R.G., Cannicci, S., 2002. Quantifying the density of mangrove crabs: Ocypodidae and Grapsidae. Mar. Biol. 141, 725–732.

Slim, F.J., Hemminga, M.A., Ochieng, C., Jannink, N.T., Cocheret de la Moriniere, E., Van der Velde, G., 1997. Leaf litter removal by the snail Terebralia palustris (Linnaeus) and sesarmid crabs in an east African mangrove forest (Gazi Bay, Kenya). J. Exp. Mar. Biol. Ecol. 215, 35–48.

Smith, T.J., Boto, K.G., Frusher, S.D., Giddins, R.L., 1991. Keystone species and mangrove forest dynamics – the influence of burrowing by crabs on soil nutrient status and forest productivity. Estuar. Coast. Shelf Sci. 33, 419–432.

Stieglitz, T., Ridd, P., Müller, P., 2000. Passive irrigation and functional morphology of crustacean burrows in a tropical mangrove swamp. Hydrobiologia 421, 69–76.

Thongtham, N., Kristensen, E., 2003. Physical and chemical characteristics of mangrove crab (Neoepisesarma versicolor) burrows in the Bangrong mangrove forest, Phuket, Thailand; with emphasis on behavioural response to changing environmental conditions. Vie Milieu 53, 141–151.

Thongtham, N., Kristensen, E., 2005. Carbon and nitrogen balance of leaf-eating sesarmid crabs (Neoepisesarma versicolor) offered different food sources. Estuar. Coast. Shelf Sci. 65, 213–222.

Twilley, R.R., Pozo, M., Garcia, V.H., Rivera–Monroy, V.H., Zambrano, R., Bodero, A., 1997. Litter dynamics in riverine mangrove forests in the Guayas River estuary, Ecuador. Oecologia 111, 109–122.

Wafar, S., Untawale, A.G., Wafar, M., 1997. Litter fall and energy flux in a mangrove ecosystem. Estuar. Coast. Shelf Sci. 44, 111–124.

Warren, J.H., 1990. The use of open burrows to estimate abundances of intertidal estuarine crabs. Aust. J. Ecol. 15, 277–280.

Warren, J.H., Underwood, A.J., 1986. Effects of crabs on the topography of mangrove swamps in New South Wales. J. Exp. Mar. Biol. Ecol. 102, 223–235.

Weis, J.S., Weis, P., 2004. Behavior of four species of fiddler crabs, genus Uca, in southeast Sulawesi, Indonesia. Hydrobiologia 523, 47–58.

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Organic matter exchange and cycling in mangrove ecosystems: Recent insights from stable isotope studies

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Abstract

Mangrove ecosystems are highly productive tropical coastal ecosystems which have a potentially high impact on the carbon budget of the tropical and global coastal zone. The carbon dynamics in mangrove ecosystems has been the subject of numerous studies during the past decades, but we are still far from having an integrated view of the overall ecosystem functioning in terms of organic matter processing. The application of recent analytical techniques has produced a wealth of new information but has also indicated the gaps in our knowledge on organic matter cycling in these ecosystems. This paper provides an overview of our current understanding of organic matter dynamics in mangrove ecosystems, and reviews data based on stable isotope analyses, on (i) the delineation of carbon sources in different organic matter pools, (ii) utilization patterns of organic carbon by microbial and faunal communities, and (iii) organic matter exchange between mangroves and adjacent ecosystems. Although the use of stable isotopes has a number of limitations and has not always been able to unambiguously assess source contributions, it has been invaluable in refuting some long-standing paradwigms, and has shown that source characterization is crucial in order to better estimate organic matter budgets in these dynamic ecosystems. Future studies on process rates or flux measurements should therefore ideally be combined with a variety of chemical tracers to determine the source of the organic matter considered.

Keywords: Mangrove; Carbon; Nitrogen; Outwelling; Foodwebs; Stable isotopes

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1. Introduction

Mangrove forests have long been proposed to play an important role in the carbon balance of tropical coastal ecosystems. Jennerjahn and Ittekkot (2002) have estimated that inputs from mangrove forests could account for 11% of the total input of terrestrial carbon into the ocean and 15% of the total carbon accumulating in modern marine sediments. Similarly, Dittmar et al. (2006) estimated that mangroves contribute ∼10% of the terrestrial dissolved organic carbon (DOC) exported to the ocean globally, despite their small area relative to other habitats. Recent upscaling of water-air CO_2 fluxes measured in (a limited number of) surface waters adjacent to mangroves suggests that mineralization of organic matter and subsequent CO_2 emission from the water column could also represent a significant source

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of CO_2 in the overall oceanic CO_2 budget (Borges et al., 2005). Despite the expected uncertainties associated with such global estimates, at the very least these numbers indicate a potentially large role of mangrove carbon in the coastal zone, and highlight the importance of understanding mangrove ecosystem C dynamics to better constrain global oceanic C budgets.

Mangrove ecosystems can attain high levels of primary production. Odum and Heald (1975) first proposed that mangrove litterfall provides a trophic subsidy in adjacent coastal waters (the 'outwelling hypothesis'), via a detritus–based foodweb whereby mangrove litter is converted into more palatable microbial biomass, which in turn acts as the dominant food source for higher trophic levels. In view of the economic importance of fisheries in mangrove systems and adjacent waters, such a trophic dependency is a much–publicised function of mangrove systems and an important argument for their conservation. The majority of studies, however, have found that mangrove organic matter is exported and incorporated into coastal foodwebs only to a very limited extent (Lee, 1995). A small number of studies have reported more extensive export and use of mangrove carbon and other nutrients in particular locations (e.g. Dittmar et al., 2001). The variability in findings is highlighted by stable isotope evidence for a very limited contribution of mangrove carbon to penaeid prawns in northern Australia (Loneragan et al., 1997), but a much greater apparent contribution in Malaysia (Chong et al., 2001).

Existing estimates of net primary productivity and mineralization in mangrove systems are probably underestimates due to methodological problems or uncertainties (Alongi, 2005). Recent direct measurements of rates of photosynthesis suggest that previous estimates of net primary production (based mostly on litter fall rates) might be significantly underestimated (Clough et al., 1997), with litterfall representing an average of ~30% of net canopy production (Alongi et al., 2005). Similarly, care should be taken when upscaling mineralization data. Carbon dioxide release from sediments, a common proxy for mineralization, is significantly lower than depth–integrated rates of mineralization, suggesting that part of the CO_2 produced may be released by porewater drainage (Alongi, 2005; Bouillon et al., 2007a).

Clearly, there remains a large degree of uncertainty about the overall fate of mangrove production, its importance in the oceanic C budget, and the role of allochthonous organic matter. In order to better constrain estimates on the role of mangroves, we need to critically review available data and take into account the uncertainties associated with many components of organic matter cycling in mangrove systems. Novel analytical techniques and approaches applied in mangrove–related studies in recent years have exposed some of the knowledge gaps. In this review, we first introduce some theoretical aspects underlying the application of stable isotope analysis in mangrove systems and summarise the variability in isotope signatures in mangrove tissues and other relevant primary producers. The remainder of the review synthesises the new insights on organic matter cycling in mangrove ecosystems based on stable isotope analyses, focussing on (i) utilization of organic matter by faunal communities, (ii) exchange of organic matter between mangroves and adjacent habitats, and (iii) the fate of exported mangrove–derived organic matter.

2. Applying stable isotope techniques in mangrove systems

Analysis of natural abundance isotope ratios as indicators of the origin of organic matter and of trophic interactions is based upon three important assumptions:

1. differences (may) exist in the stable isotope signatures of different primary producers;
2. these differences are maintained or altered in a sufficiently predictable way during degradation processes; and
3. consistent and predictable changes in the isotopic signatures occur during transfer to higher trophic levels.

2.1. Variability in isotope ratios in mangroves and other primary producers

$\delta^{13}C$ values can be used to distinguish among photosynthetic pathway types (e.g. O'Leary, 1981), with terrestrial C_3 and C_4 plants showing non–overlapping $\delta^{13}C$ distributions, and plants using the CAM (Crassulacean Acid Metabolism) pathway showing intermediate $\delta^{13}C$ signatures which may overlap with those of C_3 or C_4 plants. In C_3 plants (such as mangroves) the major components of the overall fractionation are (1) the differential diffusion rates of CO_2 through the stomata, and (2) the fractionation by ribulose biphosphate carboxylase/oxygenase (Rubisco), the initial enzyme of C_3–photosynthesis. According to Farquhar et al. (1989), overall discrimination in C_3 plants can be described by:

$$\Delta = a + (b - a)^* \left(\frac{c_i}{c_a}\right) \tag{1}$$

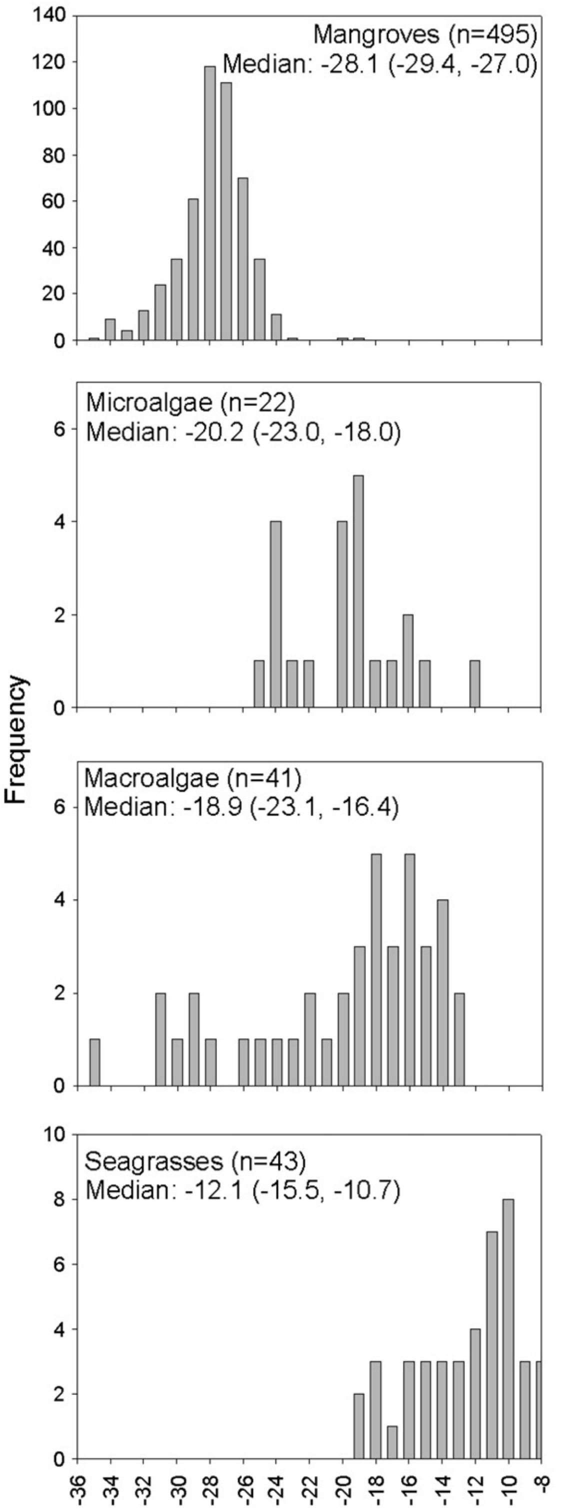

Fig. 1. Compilation of literature $\delta^{13}C$ data on mangrove leaves, micro-and macroalgae, and seagrasses from seagrass beds adjacent to mangrove forests. Median $\delta^{13}C$ values are given on each plot. Values between brackets are the 25th and 75th percentiles. Data sources available on request.

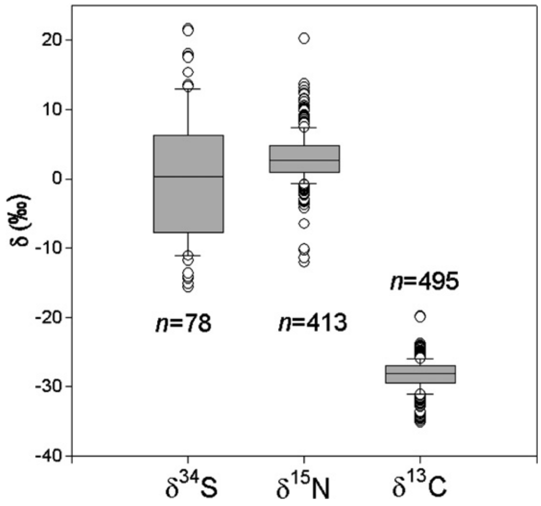

Fig. 2. Boxplot of a compilation of literature $\delta^{34}S$, $\delta^{15}N$ and $\delta^{13}C$ data on mangrove leaf tissues, illustrating the relative variability of the three isotope tracers. Data sources available on request.

where Δ is the overall carbon isotope discrimination by the leaf (in ‰), a: the fractionation due to diffusion across the stomata (~4.4‰, constant), b: the net fractionation caused by carboxylation (~27‰, constant); and c_i and c_a are the internal (intercellular) and external (ambient) partial pressure of CO_2, respectively. If the leaf stomata are relatively closed, then c_i tends towards zero and Δ therefore tends towards 4.4‰ (=a). If, on the other extreme, stomatal limitations are minimal, c_i=c_a and Δ approaches 27‰ (=b). As c_i/c_a values are typically between 0.4 and 0.8, the Δ range is about 13–22‰, and assuming a $\delta^{13}C$ of atmospheric CO_2 of −7.8‰, this leads to typical $\delta^{13}C$ values for C_3 plants ranging between −24 and −30‰. Leaf $\delta^{13}C$ values thus reflect the long–term physiological activity of the leaf, and show a rather wide range for mangroves (between −35.1 and −21.9‰, Figs. 1 and 2). Several studies have examined the effect of environmental conditions such as salinity, nutrient status, growth form, and humidity on mangrove $\delta^{13}C$ values, both in the natural environment (e.g., Kao and Chang, 1998; McKee et al., 2002) and under culture conditions (e.g., Farquhar et al., 1982; Ish-Shalom-Gordon et al., 1992; Lin and Sternberg, 1992a; Kao et al., 2001). The possible role of variations in source (i.e. CO_2) $\delta^{13}C$ values has not been examined, although it is plausible that such variations occur in certain dense mangrove stands. Several laboratory and field studies have reported that increased salinity decreases stomatal conductance and thus leads to a more enriched $\delta^{13}C$ (e.g., Medina and Francisco, 1997; Lin and Sternberg, 1992b; Kao et al., 2001), but the relationship is not necessarily linear (Ish-

Shalom-Gordon et al., 1992). Due to salinity stress and/or nutrient limitation effects, dwarf or stunted forms of mangroves typically show distinctly more enriched $\delta^{13}C$ values relative to their tall conspecifics (e.g., Lin and Sternberg, 1992b; McKee et al., 2002). The relationship between stable isotope signatures of mangroves and environmental factors is clearly quite complex but nevertheless holds potential for inferring longer-term changes in environmental conditions recorded in mangrove tree rings (e.g., Verheyden et al., 2004) or in the sedimentary record (e.g., Smallwood et al., 2003; Wooller et al., 2003a).

$\delta^{13}C$ values can vary among mangrove tissue types, but as yet no consistent patterns in variation have emerged. Ellison et al. (1996) found no significant differences between leaves, branches, and twigs of *Rhizophora mangle*, but cable roots and small rootlets were all significantly enriched in ^{13}C relative to leaf material. Ish-Shalom-Gordon et al. (1992) found little or no consistent difference in $\delta^{13}C$ of leaves and stems in their experimental study for *Avicennia germinans*, and Boon et al. (1997) also found no significant differences between *Avicennia marina* leaves and branches, while pneumatophores were on some occasions significantly depleted in ^{13}C relative to leaves (by up to 3.1‰). Lee et al. (2001) found twigs and bark tissue of *Kandelia candel* and *Aegiceras corniculatum* to be slightly depleted (by <2‰) relative to leaf tissues. Similarly, Muzuka and Shunula (2005) found no consistent patterns in $\delta^{13}C$ and $\delta^{15}N$ differences between roots, leaves, flowers and fruits of various mangroves.

Isotope analysis of food webs often uses isotopes of nitrogen and/or sulfur along with carbon. Variability in mangrove $\delta^{15}N$ and, particularly, $\delta^{34}S$ values is more pronounced than for $\delta^{13}C$ (Fig. 2). This variability in $\delta^{15}N$ and $\delta^{34}S$ often occurs over short distances, with differences of up to 10‰ for N (e.g., Fry et al., 2000) and 29‰ for S (e.g., Okada and Sasaki, 1998) occurring among sites within a single estuary. Such differences may result from variation in the source values and/or in differences in fractionation during uptake (Fry et al., 2000). One of the important drivers of source variability for N is pollution from urban sewage or agriculture, and $\delta^{15}N$ values for mangroves have been used to map the extent of influence of sewage N (McClelland and Valiela, 1998; Fry et al., 2000; Costanzo et al., 2001; Jones et al., 2001, see also Wooller et al., 2003b). For $\delta^{34}S$, technical difficulties have led to low replication in earlier studies, reducing the rigour of conclusions (e.g., Newell et al., 1995; Loneragan et al., 1997; Wiedemeyer, 1997). Improved survey designs providing a better measure of spatial variability in S isotopes of mangroves have increased the usefulness of $\delta^{34}S$ (e.g., Hsieh et al., 2002; Benstead et al., 2006). In general, the typically large differences in average sulfur isotope signatures between mangroves and other primary producers in estuaries mean that they will prove useful in distinguishing the importance of different primary producers to food webs, despite the relatively high variability (Connolly et al., 2004).

In the aquatic environment, the substrate for algal photosynthesis is dissolved carbon dioxide or bicarbonate. $\delta^{13}C$ values for DIC ($=CO_2+H_2CO_3+HCO_3^-+CO_3^{2-}$) approach 0‰ if there is an equilibrium with CO_2 from the atmosphere (e.g. in an open ocean environment), but several processes may alter the $\delta^{13}C$ of the DIC pool: (1) autotrophic production in the water column causes the residual DIC pool to become enriched in ^{13}C, due to the preferential fixation of ^{12}C during photosynthesis; (2) the diffusive efflux of CO_2 to the atmosphere causes the residual DIC pool to be enriched in ^{13}C, as 'lighter' CO_2 diffuses at a faster rate; (3) the dissolution or precipitation of $CaCO_3$ influences the overall $\delta^{13}C$ DIC, as carbonates usually have enriched $\delta^{13}C$ values compared to the DIC pool; and (4) mineralization processes result in the addition of ^{13}C–depleted CO_2 as the $\delta^{13}C$ of respired CO_2 will be similar to that of the organic substrate. Besides these variations in the $\delta^{13}C$ composition of the substrate for photosynthesis, a variety of factors influence the degree of fractionation between the substrate and the biomass formed, including the availability of DIC, growth rate limiting factors such as nutrients or light, temperature, species, and the size and dimensions of the cells. Thus, the carbon stable isotope composition of algae can show large variations, being generally in the range of −17 to −23‰ for marine phytoplankton, but significantly more ^{13}C–depleted in estuarine and freshwater environments. Benthic microalgae in marine waters are typically enriched in ^{13}C relative to phytoplankton by an average of ~5‰ (France, 1995). This difference is thought to be a result of the thicker boundary layer experienced by benthic algae (MacLeod and Barton, 1998), causing more diffusion–limitation of CO_2 and thus a decrease in overall fractionation. Our compilation of $\delta^{13}C$ values for benthic algae include epiphytic and edaphic algae, and shows that the algae generally are enriched relative to mangroves (Fig. 1). Cyanobacteria data are pooled with those for benthic microalgae, but the few available data suggest that cyanobacteria typically show the most enriched $\delta^{13}C$ values (e.g., Al-Zaidan et al., 2006). The amount of $\delta^{15}N$ data on algae is more limited, and there is no indication that values are sufficiently different to be of general use as an additional source indicator. In some cases, however, epiphytes show markedly depleted $\delta^{15}N$ (e.g. −8 to −6‰, Bouillon et al., 2004c), and these can be reflected in consumer $\delta^{15}N$ as was suggested for *Onchidium* sp. and various species of *Littoraria* (Christensen et al., 2001; Bouillon et al., 2004c).

Seagrasses adjacent to mangroves can be imported into tidal creeks and into the intertidal forest, and thus represent another potential source of carbon in mangroves. Seagrass $\delta^{13}C$ values vary considerably but are typically enriched relative to other estuarine producers, with most values between −16 and −12‰ (Hemminga and Mateo, 1996). Seagrasses adjacent to mangrove forests show remarkable variability in $\delta^{13}C$ over short distances (Fig. 1), with more depleted values close to the mangroves, steadily becoming more enriched with distance towards the sea (e.g. a range of almost 10‰ over <4 km distance found by Hemminga et al. (1994) and Marguillier et al. (1997), see also Lin et al. (1991) and France and Holmquist (1997)). This trend probably reflects parallel changes in the $\delta^{13}C$ of the DIC pool, being more negative close to mangroves where mineralization supplements the DIC pool with ^{13}C-depleted CO_2. As discussed later, such a trend is also expected for phytoplankton and benthic microalgae, although no direct measurements on microalgae have been made because of the difficulties in obtaining pure samples for analysis.

2.2. Changes in stable isotope signatures during senescence and degradation

Relatively few data are available on the effects of senescence and degradation on the $\delta^{13}C$ signature of mangrove tissues. Rao et al. (1994) noted little difference (<1‰) between fresh and senescent leaves for five species of Kenyan mangroves, but for four other species, senescent leaves were markedly depleted (by 1.3– 2.6‰) relative to fresh ones. No marked differences were observed between green and senescent leaves by Schwamborn et al. (2002) and Kieckbusch et al. (2004), and the direction and magnitude of the difference between green and yellow leaves for two species in the study of Lee (2000) was opposite. Kao et al. (2002) and Wooller et al. (2003a) demonstrated that $\delta^{13}C$ of *K. candel* and *R. mangle* were not significantly altered during senescence. Several degradation experiments have demonstrated that changes in the $\delta^{13}C$ signatures during decomposition are either insignificant (Zieman et al., 1984; Dehairs et al., 2000; Wooller et al., 2003a; Werry and Lee, 2005) or very small, i.e. typically < ~1.5‰ (Primavera, 1996; France, 1998; Fourqurean and Schrlau, 2003). From the few data available, there are no indications that floating leaves collected in creeks or offshore are different from fresh leaves (Rodelli et al., 1984; Schwamborn et al., 2002). This lack of effect of decomposition on mangrove isotopes is consistent with results from decomposition studies of other producers (Ehleringer et al., 2000). Nevertheless, even in sites where litter is expected to be the sole input, the sediment organic matter pool in mangrove forests is consistently enriched in ^{13}C relative to the litter (e.g., Lallier-Verges et al., 1998), probably because of an increase in microbial and fungal residues (Ehleringer et al., 2000).

Shifts in the isotopic signature of decomposing mangrove litter are probably dependent on the type, diversity and abundance of microbial decomposers colonising the organic matter.

Similarly, experimental work has indicated that changes in $\delta^{15}N$ are either small (e.g., Fourqurean and Schrlau, 2003; Wooller et al., 2003a; Werry and Lee, 2005), or insignificant (e.g., Dehairs et al., 2000). Werry and Lee (2005) noted, however, much more significant depletion of ^{15}N of shredded mangrove leaf litter material in the faeces of the sesarmine crab *Parasesarma erythrodactyla*, and attributed this change to the higher density of colonising microbes compared to whole leaf litter. Since changes in $\delta^{15}N$ are mainly due to the microbial immobilization or new N (Caraco et al., 1998), the magnitude and direction of $\delta^{15}N$ changes will depend on a range of factors such as the inorganic N-substrate, the importance of N_2 fixation (e.g., Woitchik et al., 1997), the $\delta^{15}N$ of the added N, and the degree of fractionation during immobilization. Changes in the stable isotopic signature of mangrove litter through macrofaunal processing and microbial decomposition, if significant, will have strong implications for using these signatures as tracers for energy flow.

2.3. Changes in stable isotope signatures during assimilation

Fractionation during assimilation by consumers typically enriches $\delta^{13}C$ values by 0–1‰, although the full range of enrichment values found in aquatic systems may vary between −2.1 and +2.8‰ (Vander Zanden and Rasmussen, 2001; McCutchan et al., 2003). Fractionation for $\delta^{15}N$ is larger, with enrichment often around 2.7 to 3.4‰ but with a full range between −0.7 and +9.2‰. Sulfur fractionation is smaller even than for C (McCutchan et al., 2003). In aquatic ecosystems, the degree of fractionation for C and N appears to be more variable for invertebrates than for fish, laboratory results are more variable than field estimates, and trophic fractionation in herbivores is more variable than in carnivores (Vander Zanden and Rasmussen, 2001). Caution is therefore required when using average literature values for fractionation to calculate the trophic position of consumers or to adjust mean consumer values in preparation for analysis with mixing models. Rigorous tests on how natural (e.g. salinity) and anthropogenic (e.g. pollution) environmental variations may affect fractionation in consumers are needed to validate the application of stable isotope analysis in particular environmental settings.

2.4. Analysis of isotope data using mixing models

Stable isotope data are often used to determine the contribution of different primary sources to consumers in a food web. Two-source mixing models have been frequently used in the form:

$$\delta^{13}C_{consumer} = (X_{A}.\delta^{13}C_{A} + X_{B}.\delta^{13}C_{B}) + \Delta \tag{2}$$

where $\delta^{13}C_A$ and $\delta^{13}C_B$ are the carbon isotope composition of dietary source A and B, respectively, X_A and X_B are the proportion of source A and B to the consumers diet ($0<X_A$, $X_B<1$), and Δ is the fractionation associated with a trophic level transfer. The application of such a model becomes problematic when the isotopic difference between the two sources is small or when the variability in $\delta^{13}C$ values of a single source is high (Lee, 2005), even where models incorporating variance are used (Phillips and Gregg, 2001). Moreover, it is essential that correct $\delta^{13}C$ values are assigned to each source, which has not been the case in many mangrove studies (see below). When multiple stable isotope ratios are analysed (e.g. $\delta^{13}C$ and $\delta^{15}N$, or $\delta^{13}C$ and $\delta^{34}S$), it is possible to use this additional information to derive the contribution of three different food sources to a consumer's diet. Theoretically speaking, the number of producer sources that can be resolved in a multiple isotope ratio analysis deploying n elements is n+1. $\delta^{34}S$ is more useful as a second element than $\delta^{15}N$, because of the large degree of fractionation of ^{15}N during trophic transfer, the sensitivity of $\delta^{15}N$ to local conditions (such as urban pollutants), and the small differences among producers in their $\delta^{15}N$ signatures (Connolly et al., 2004). A problem with 3-source mixing models using multiple elements is that they provide unreliable estimates of contributions where food sources contain different proportions of the elements. In mangrove systems, for example, consumers can be expected to assimilate a higher proportion of N (and S) from animal than from plant sources. This is illustrated in Fig. 3, where the relative contributions of three hypothetical sources (using realistic input values of mangroves, sediment organic matter, and benthic microalgae) for a given consumer are shown as 0, 25, 50, 75, and 100% isolines - the effect of differences in the C and N content of the different sources is that the isolines are curvilinear rather than straight, and hence, that not taking these differences into account result in a severe bias in the estimated source contributions (Phillips and Koch, 2001).

Another approach that has recently gained popularity is the IsoSource model (Phillips and Gregg, 2003), a technique that constrains the possible contribution by different sources when the number of sources is too large to find a unique solution (see also Phillips et al., 2005). IsoSource has proven informative in studies of mangrove contributions to food webs (Melville and Connolly, 2005; Benstead et al., 2006), but the approach still suffers from a number of limitations. For example, variability in the degree of trophic fractionation is not taken into account, and the concentration-dependent adjustment in the two-source model (Phillips and Koch, 2001) is not available in IsoSource. These shortcomings would normally result in a range of solutions that is conservative (i.e. too narrow), and biased towards those sources with low concentrations of N (or S).

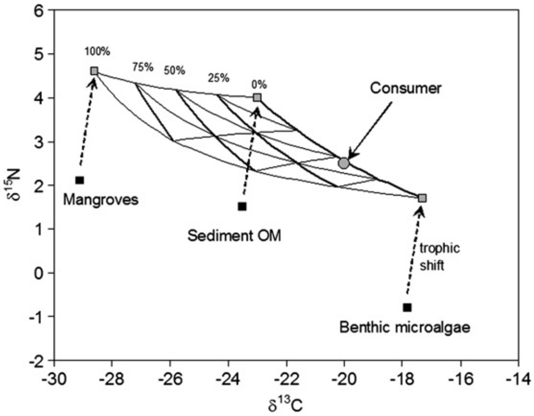

Fig. 3. Contribution of thre different sources (representative data given for mangroves, sediment organic matter, and microphytobenthos) to the diet of a consumer (represented by the grey circle), using a concentration−dependent 3−source mixing model (Phillips and Koch, 2001). The original $\delta^{13}C$ and $\delta^{15}N$ signatures for the sources (black squares) have been corrected for fractionation associated with a trophic shift (grey squares). Isolines represent the relative contribution (in steps of 25%) of the three sources to a consumers' diet. In the example consumer, the contribution of mangroves, sediment organic matter and microphytbenthos are 2, 42, and 56%, respectively.

3. Cycling within the mangrove forest: role of benthic fauna

Whereas a large number of studies have dealt with the trophic subsidy for consumers in aquatic environments adjacent to mangrove systems, less attention has been paid to foodweb structure in intertidal mangrove faunal communities, and their potential importance as prey items for mobile fauna (see Sheaves and Molony, 2000). Despite the fact that these communities have more direct access to mangroves as a food source, a number of recent studies have indicated that mangrove invertebrates show a much more diverse pattern of resource utilization than previously expected (e.g., Thimdee et al., 2001, 2004; Bouillon et al., 2002b). The degree to which they rely on mangrove-derived C also varies across mangrove systems, with a higher reliance in ‘closed’ systems where more of the mangrove production is retained and where there is less exchange of material with adjacent systems (Bouillon et al., 2002a, 2004c). A number of stable isotope studies have focussed on specific species or groups of fauna, and are largely consistent with these conclusions (e.g. *Uca* spp.: France, 1998; *Littoraria* spp.: Christensen et al., 2001; Lee et al., 2001; *Terebralia palustris*: Slim et al., 1997; *Aratus pisonii*: Lacerda et al., 1991). Despite the potentially large-scale movement of organic matter, evidence is emerging that many invertebrates have a small home-range and derive most of their diet from locally available food sources (Guest et al., 2006). This has been illustrated by the small-scale changes in stable isotope signatures (and hence, carbon sources used by invertebrates) in the vicinity of habitat boundaries (Guest and Connolly, 2004; Guest et al., 2004).

Allochthonous carbon and local production by benthic microalgae appear to be important food sources for a wide variety of invertebrate species, including those typically considered as important in leaf litter processing. Very few mangrove animal species have been examined for their overall food resources, and our knowledge is biased by the neglect of whole groups of fauna, in particular most groups of infauna and meiofauna. The diversity in resource utilization for the entire community is almost certainly underestimated, and the overall role of consumers in the processing of different organic matter sources is still far from clear.

An example of the complexities of carbon cycling is provided by a sacoglossan, *Elysia* sp. nov., common in shallow tidal pools under *Avicennia* spp. in Andhra Pradesh, India. Sacoglossans are herbivorous marine opisthobranchs (sea slugs) which feed mainly on green or red algae, but an often-encountered phenomenon in this group is the occurrence of kleptoplasty, i.e. the intercellular retention of chloroplasts obtained from the algae. These chloroplasts often remain functional for prolonged periods (up to 10 months, Rumpho et al., 2000) and presumably provide part of the carbon requirements of the host. Our data on *Elysia* sp. nov. show unusually depleted δ^{13}C signatures (between −43.3 and −35.2 ‰ in different seasons and sites, Fig. 4) previously unrecorded in any kleptoplastidic or other algae-invertebrate symbiosis (see Raven et al., 2001). We hypothesize that strong internal recycling of CO_2, i.e. the fixation of host-respired CO_2 by the functional kleptoplastids, in combination with a ^{13}C-depleted external DIC pool, could be responsible for the observed δ^{13}C values. Although these appear to be the first isotope data on sacoglossans with kleptoplasty from mangroves, other species are known to occur in these systems, e.g. *E. bangtawaensis* from Thailand (Swennen, 1997) and *E. australis* in Moreton Bay, eastern Australia (Davie, 1998).

Such highly specialized symbiotic relationships are probably more widespread than is often assumed. Lucinid bivalves are known to host sulfur-oxidizing bacteria, have been found in a number of reducing environments such as mangrove sediments (Lebata and Primavera, 2001), and show δ^{13}C signatures around −32 to −28‰ and δ^{15}N values ranging between −11 and +4‰ (Fig. 4), which is consistent with a strong contribution by their symbionts. The significance of such trophic interactions in tropical mangrove sediments

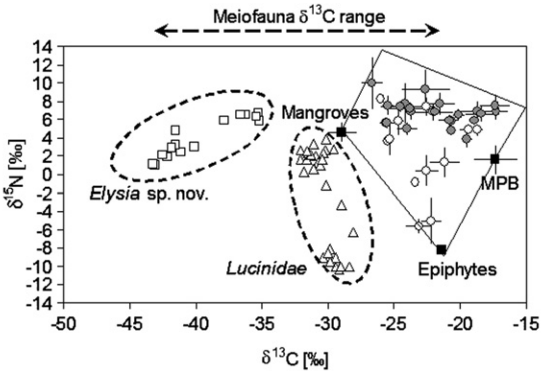

Fig. 4. Plot of δ^{13}C and δ^{15}N signatures for typical mangrove primary producers (black squares), macro−epifauna (grey circles: brachyuran crabs, open circles: molluscs), *Elysia* sp. nov. (open squares), the lucinid bivalves *Anodontia edulenta* and *Austriella corrugata* (open triangles; S. Bouillon and J.H. Primavera, unpubl. data) and preliminary range of meiofauna δ^{13}C (T. Moens and S. Bouillon, unpubl. data). Data for primary producers and macro−epifauna were taken from Bouillon et al. (2002a).

should not be underestimated, as some lucinids are known to occur at very high local density (e.g. *Austriella* cf. *plicifera* in Moreton Bay, Queensland, Australia; S.Y. Lee, unpubl. data). Symbiotic relationships have been documented in meiofaunal taxa from a variety of coastal habitats, and mouthless species have recently been reported from mangrove systems (Kito and Aryuthaka, 2006). Some of these taxa collected from mangroves in Kenya have highly depleted δ^{13}C signatures, with values as low as −43‰ (T. Moens and S. Bouillon, unpubl. data). It thus appears that not only do many mangrove invertebrates rely extensively on algal sources rather than on mangrove litter, but that a wide range of organisms may show very specialized pathways of carbon and nitrogen acquisition through symbiotic relationships. To date, however, there are no data that give any indication of the importance of such trophic interactions. Given that isotope signatures of such symbioses can be quite distinct (Fig. 4), isotope approaches should be useful in revealing the importance of symbiotic relationships in mangrove systems. The trophic dependency of other mangrove macrofauna on these symbiotic species is largely unknown.

The unexpected diversity in patterns of resource utilization in mangrove systems can be considered a form of niche segregation: mangrove systems represent complex and highly dynamic environmental conditions, where faunal assemblages typically show distinct horizontal or vertical zonation, or where different species forage at different times (low/high tide, day/night). The ability of closely related species to use different food resources therefore likely represents an additional strategy to optimally exploit this environment.

Despite stable isotope evidence that macrofauna often utilize carbon from sources other than mangroves, other evidence demonstrates that removal and consumption of mangrove litter can represent a significant fraction of the overall litterfall, and thus an important trophic link. Key species involved in litter processing include sesarmid crabs (e.g., Lee, 1998), the ocypodid *Ucides cordatus* (up to ~80% of annual litterfall, Nordhaus et al., 2006), and the molluscs *Terebralia palustris* (Slim et al., 1997) and *Melampus coffeus* (Proffitt and Devlin, 2005).

The apparently contradictory aspects of macrofauna trophodynamics are best understood by considering densities and carbon requirements of macrofauna. Even where algae are important and only a portion of the carbon requirements of macrofauna is derived from mangroves, the high consumer densities and rates of consumption mean that most or all of the leaf litter is turned over (Bouillon et al., 2004c). Furthermore, most emphasis in carbon budgets has to date been on conspicuous macrofauna such as crabs. If the entire community of epifauna and infauna is considered, the impact on organic matter cycling and litter dynamics could be overwhelming. In order to obtain a realistic estimate of this community role, data on faunal assemblage structure and secondary production coupled to information on resource utilization would be required - data that are entirely lacking for any mangrove system. Although the impact of fauna in current mangrove C budgets is often considered only in terms of direct herbivory or invoked to estimate the proportion of leaf litter retained within the system due to burial and/or consumption by sesarmid crabs, it is clear that future ecosystem budgets should attempt to re-evaluate the potential role of other resident, less conspicuous, fauna (e.g., in- and meiofauna).

4. Isotopes as tracers of movement of organic matter - import and export

Stable isotope ratios have been used in a large number of studies to infer the contribution of mangrove carbon and other potential sources to the sedimentary or suspended organic matter pool (e.g., Lacerda et al., 1986, 1995; Machiwa, 2000; Kuramoto and Minagawa, 2001; Thimdee et al., 2003). A major shortcoming of some studies is that variations in $\delta^{13}C_{POC}$ values have been related to the admixture of mangrove-derived carbon and ‘marine’ phytoplankton, whereby the latter is characterized by typical δ^{13}C values of ~−20 to −18‰ (e.g., Rezende et al., 1990; Chong et al., 2001). This approach is an oversimplification since it assumes that phytoplankton within estuaries or mangrove creeks has a δ^{13}C signature similar to that of marine phytoplankton. This is unlikely, however, since mangrove creeks and estuaries typically have δ^{13}C signatures for DIC which are distinctly depleted in ^{13}C by 6–8‰ (Fig. 5), with a clear gradient towards the marine environment (Fig. 6). Primary producers in the water column can therefore be expected to show a similar depletion in ^{13}C relative to DIC as those in open marine environments, where $\delta^{13}C_{DIC}$ is typically around 0‰, as described for seagrasses in Section 2.1. (see also Fig. 6). The cause of the ^{13}C-depletion in the DIC pool in the water column may be dilution by a freshwater source (e.g. in estuaries) and/or the inputs of DIC from mineralization in the water column or in the intertidal sediments, whereby the excess DIC shows a strongly negative δ^{13}C signature, similar to that of its source (e.g. Bouillon et al., 2007b).

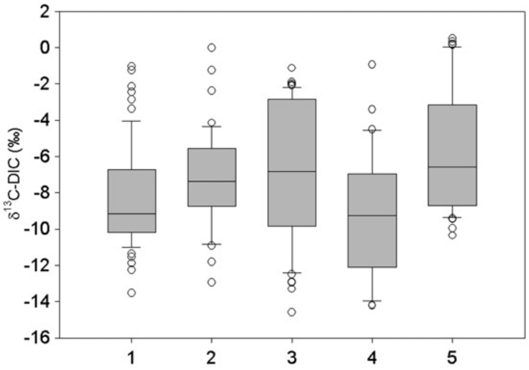

Fig. 5. Boxplot compilation of data on the δ^{13}C composition of dissolved inorganic carbon (δ^{13}C−DIC) from a number of mangrove creeks. (1): Coringa Wildlife Sanctuary, India (Bouillon et al., 2003b and unpubl. data); (2): Tana delta, Kenya (Bouillon et al., 2007a); (3) mangrove creeks in Ca Mau, Vietnam (S. Bouillon and A.V. Borges, unpubl. data); (4) Gazi Bay, Kenya (Bouillon et al., 2007b); (5) Ras Dege, Tanzania (Bouillon et al., 2007c).

Although δ^{13}C alone is thus often not sufficient to unambiguously estimate the contribution of various sources to the POC pool, its potential is much enhanced when used in combination with other tracers such as POC/PN ratios (Hemminga et al., 1994; Cifuentes et al., 1996; Bouillon and Dehairs, 2000; Gonneea et al., 2004), δ^{15}N (e.g., Cifuentes et al., 1996), POC/Chl-a ratios (Cifuentes et al., 1996) or biochemical tracers such as lignin-derived phenols (Dittmar et al., 2001). Nevertheless, considering that a multitude of sources with different signatures may be present and that other tracers such as POC/PN ratios and δ^{15}N may change substantially during degradation and microbial reworking, the power of stable isotopes in delineating sources comes from being able to constrain the contribution of different sources (i.e. define upper and lower possible contributions), rather than enabling an exact quantification of the various inputs.

It has become clear that both local and imported sources can contribute to the sediment organic matter pool in intertidal mangrove sediments, and elemental and δ^{13}C data are generally consistent with a simple two-source mixing model whereby mangrove litter and suspended matter are taken as end-members (Bouillon et al., 2003a; see also Kristensen et al., submitted for publication ms). Riverine input of terrestrial carbon to mangrove systems is another aspect of carbon budgets yet to be adequately addressed. Recent results on the isotope composition of organic matter in mangrove systems with catchments supporting significant amounts of C4 vegetation highlight the potential importance of riverine-transported terrestrial material. In the Tana estuary and delta (northern Kenya), Bouillon et al. (2007a) found an important contribution of C4 material to riverine particulate and dissolved organic carbon (POC and DOC), as well as in intertidal sediments below the mangrove canopy. In contrast, porewater DOC from the same sampling locations had much more depleted δ^{13}C signatures reflecting a predominantly mangrove origin (Fig. 7). δ^{13}C data on bacterial markers from these samples (Bouillon and Boschker, 2006), however, indicate that bacteria derive their C from both C3 (i.e. mangrove) and C4 material in almost the same proportion as found in the sediment TOC pool. In the Betsiboka estuary (Madagascar), a similar high contribution of C4 material has been observed in both the water column POC and DOC, and in the intertidal

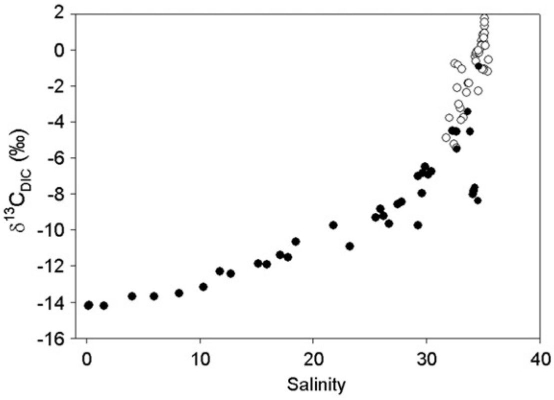

Fig. 6. Gradient of $\delta^{13}C_{\mathbf{DIC}}$ along the salinity gradient in the Gazi Bay mangrove–seagrass ecosystem (data from Bouillon et al. (2007b)). Filled circles represents samples collected in the tidal mangrove creeks, open circles represent data from the seagrass beds.

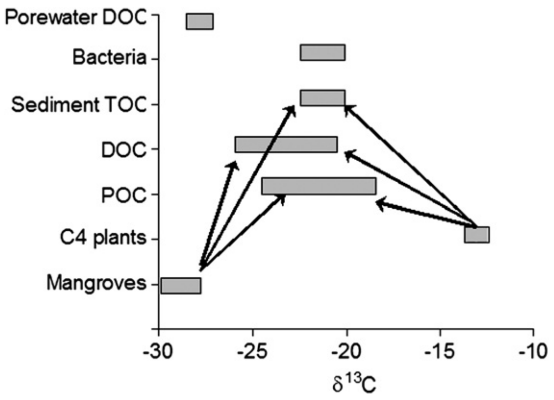

Fig. 7. Range of δ^{13}C values found in different compartments in the Tana estuary and delta (data from Bouillon and Boschker (2006), Bouillon et al. (2007a)).

mangrove sediments (O. Ralison and S. Bouillon, unpubl. data). The importance of terrestrial matter from catchments dominated by C3 plants has not been revealed by C isotopes, since imported terrestrial material and local mangrove inputs are indistinguishable based on their δ^{13}C signatures. The highly efficient trapping of suspended matter in mangroves (e.g., Victor et al., 2004), and the evidence from C4 catchments, suggest that terrestrial material might also be an important C input in these systems, but complementary (molecular and isotopic) approaches will be needed to evaluate this. Dittmar et al. (2001), for example, used a combination of δ^{13}C and lignin-derived phenol signatures to estimate the contribution of terrestrial, marine, and mangrove-derived organic matter to the POC and DOC pool in a Brazilian mangrove estuary. Their data suggested high terrestrial contributions in the upper parts of the estuary, but a predominance of mangrove and marine organic matter in the creek water column. Another isotopic approach has been recommended by Raymond and Bauer (2001), who report that paired ^{14}C and ^{13}C measurements can potentially separate riverine and marine allochthonous sources of POC and DOC. Further development and application of such approaches in a range of systems will be required to obtain a more general view on the contribution and fate of different organic matter sources in mangrove systems. For example, recent data on the stable isotope composition of DOC in mangrove systems (see Bouillon et al., 2006, 2007c) indicate that the origin of DOC can be highly variable and quite distinct from that of POC. Given the high productivity of mangroves, their potential importance in the C budget of the coastal zone is high (Jennerjahn and Ittekkot, 2002; Dittmar et al., 2006), but our ability to quantify this role is currently limited.

In conclusion, the original focus on outwelling of mangrove carbon towards adjacent habitats has now been redirected, and recent results emphasize the role of imported organic matter in the intertidal zone (Bouillon et al., 2003a; Kennedy et al., 2004). This raises additional questions about the fate of the imported material, and a number of studies have already indicated that they contribute both to sustaining intertidal invertebrate communities (Bouillon et al., 2004c; Connolly et al., 2005) and to mineralization by sedimentary bacteria (Bouillon et al., 2004b, 2004d; Bouillon and Boschker, 2006). Stable isotopes are likely to play an important role in future studies of carbon sources and fluxes, but a number of alternative or complementary molecular approaches have recently been applied in mangrove systems: viz. lignin-derived phenols (Moran et al., 1991; Dittmar and Lara, 2001), carbohydrate composition (Marchand et al., 2005), amino acid and hexosamine profiles (Jennerjahn and Ittekkot, 1997), and biomarkers such as n-alkanes (Mead et al., 2005), triterpenols and sterols (Koch et al., 2003, 2005; Versteegh et al., 2004; Kim et al., 2005; Jaffé et al., 2006).

5. Fate of exported mangrove C: importance in adjacent foodwebs

Since the hypothesis that mangroves (partially) sustained aquatic foodwebs was first postulated, there have been numerous stable isotope studies (~ 40) of foodweb dynamics in and around mangroves. The original approach of Rodelli et al. (1984), of analysing carbon isotopes of consumers along a gradient from tidal mangrove creeks towards open marine waters, has been adopted in several later studies (e.g., Fleming et al., 1990; Newell et al., 1995; Lee, 2000; Chong et al., 2001; Bouillon et al., 2000, 2002b, 2004a). Rodelli et al. (1984) found a distinct gradient in consumer δ^{13}C values, with generally depleted δ^{13}C values in mangrove creek consumers, more enriched values offshore, and intermediate values in coastal inlets. End-members considered were mangroves (δ^{13}C ~−27‰), marine phytoplankton (−22 to −20‰) and a variety of other algae (−22.5 to −14.8‰). Subsequent studies in other sites, however, detected only very limited contributions of mangrove carbon to offshore foodwebs (e.g., Loneragan et al., 1997; Lee, 2000; Macia, 2004).

Technical difficulties meant that these studies lacked measurements of phytoplankton δ^{13}C or $\delta^{13}C_{DIC}$. As mentioned above, the gradient in consumer isotope values is likely to be confounded with an expected gradient in microalgal δ^{13}C from depleted in mangroves to enriched offshore, preventing these studies from quantifying mangrove contributions. In a study on the carbon sources for penaeid prawns, Chong et al. (2001), citing Hayase et al. (1999), actually provided some indirect evidence for the existence of ^{13}C-depleted phytoplankton in mangrove creeks. They noted that δ^{13}C values of total suspended organic matter showed a large spatial gradient between the mangrove creeks and the marine environment (−25.6 to −17.9‰, i.e. more than 8‰), whereas the estimated contribution of phytoplankton to the POC pool (based on Chl-a measurements) changed very little over the same gradient (from 17 to 25%), a discrepancy strongly indicating that phytoplankton in the creeks was significantly depleted in ^{13}C. The high estimate of mangrove contribution to some species of penaeids by Chong et al. (2001) should therefore be reconsidered.

A number of approaches have been proposed to take the spatial variation in autotroph stable isotope signatures into account and to improve the utility of stable isotopes to assess the relative contribution of various sources. First, Fry and Smith (2002) proposed a mixing model to determine the relative contribution of mangroves and phytoplankton to filter-feeding barnacles along an estuarine gradient, and measured $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ of both mangroves and barnacles along the entire gradient. Since the resolving power of $\delta^{15}N$ is limited and $\delta^{13}C$ signatures of both primary sources overlap (i.e. along some parts of the gradient, $\delta^{13}C$ signatures for phytoplankton are expected to be similar), $\delta^{34}S$ was selected to calculate the contribution of both sources to the barnacle diet, based on a simple two-end mixing model. Although we commend their approach, Fry and Smith (2002) would have overestimated mangrove contributions by not accounting for the higher S content in phytoplankton than mangroves (see Section 2.4.). Using indicative values of 1.05% and 0.31% for the S content of phytoplankton and mangroves (data from Ho et al. (2003) and Fry and Smith (2002), respectively), a re-evaluation of the data presented in Fry and Smith (2002) suggests that the estimated contribution by mangroves ranges between 9 and 17%, rather than between 30 and 58% as originally estimated. If such concentration effects can be taken into account, however, this sampling strategy offers a spatially-explicit approach to estimating the contribution of different sources along landscape gradients, and thus holds the potential to infer the effect of spatially varying environments on the resources that sustain faunal communities.

A second approach is to exploit the observed variation in stable isotope signatures of consumers and potential carbon sources rather than the absolute values. This approach assesses the degree of selectivity with which consumers exploit carbon sources, and eliminates the need for assumptions about isotope fractionation. Examples have been described in Bouillon et al. (2000, 2004a) to estimate the degree of selectivity of zooplankton and benthic invertebrates, respectively, based on the spatial and seasonal variations of $\delta^{13}C$ signatures of consumers, POC, and DIC. The approach has its own assumptions, most importantly that selectivity is similar either seasonally or spatially (see Bouillon et al., 2004a). Spatial analysis of variation in carbon and nitrogen isotopes has been further refined by Melville and Connolly (2003), who developed a two-element correlation test between consumer and source signatures, and used it to indicate important sources for fish in a mangrove-lined bay.

Since most studies have potentially confounded a gradient in consumer $\delta^{13}C$ with a (usually unmeasured) gradient in phytoplankton $\delta^{13}C$, there is in our opinion currently no unambiguous evidence that mangrove carbon contributes substantially to faunal communities, either in tidal mangrove creeks or adjacent waters (see also Fry and Ewel, 2003). This does not imply that such a contribution is absent, but merely that existing data either suggest only a minimal role and a clear selectivity for alternative sources, or do not allow any unambiguous conclusions to be drawn. Future studies on these aspects are likely to benefit from careful sampling of all necessary components (i.e. including data on algal sources at varying spatial scales), and the incorporation of complementary tracers such as fatty acid markers (e.g., Alfaro et al., 2006; Hall et al., 2006).

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References

Alfaro, A.C., Thomas, F., Sergent, L., Duxbury, M., 2006. Identification of trophic interactions within an estuarine food web (northern New Zealand) using fatty acid biomarkers and stable isotopes. Estuar. Coast. Shelf Sci. 10, 271–286.

Alongi, D.M., 2005. Mangrove-microbe-soil relations. In: Kristensen, E., Haesse, R.R., Kostka, J.E. (Eds.), Interactions between Macro- and Microorganisms in Marine Sediments. Coastal and Estuarine Studies, vol. 60. American Geophysical Union, Washington DC, pp. 85–103.

Alongi, D.M., Clough, B.F., Robertson, A.I., 2005. Nutrient-use efficiency in arid-zone forests of the mangroves *Rhizophora stylosa* and *Avicennia marina*. Aquat. Bot. 82, 121–131.

Al-Zaidan, A.S.Y., Kennedy, H., Jones, D.A., Al-Mohanna, S.Y., 2006. Role of microbial mats in Sulaibikhat Bay (Kuwait) mudflat food webs: evidence from $\delta^{13}C$ analysis. Mar. Ecol. Prog. Ser. 308, 27–36.

Benstead, J.P., March, J.G., Fry, B., Ewel, K.C., Pringle, C.M., 2006. Testing IsoSource: stable isotope analysis of a tropical fishery with diverse organic matter sources. Ecology 87, 326–333.

Boon, P.I., Bird, F.L., Bunn, S.E., 1997. Diet of the intertidal callianassid shrimps *Biffarius arenosus* and *Trypea australiensis* (Decapoda : Thalassinidae) in Western Port (southern Australia), determined with multiple stable-isotope analyses. Mar. Freshw. Res. 48, 503–511.

Borges, A.V., Delille, B., Frankignoulle, M., 2005. Budgeting sinks and sources of CO_2 in the coastal ocean: Diversity of ecosystems counts. Geophys. Res. Lett. 32, L14601. doi:10.1029/2005GL023053.

Bouillon, S., Boschker, H.T.S., 2006. Bacterial carbon sources in coastal sediments: a cross-system analysis based on stable isotope data of biomarkers. Biogeosciences 3, 175–185.

Bouillon, S., Dehairs, F., 2000. Estimating spatial and seasonal phytoplankton $\delta^{13}C$ variations in an estuarine mangrove ecosystem. Isot. Environ. Health Stud. 36, 273–284.

Bouillon, S., Chandra Mohan, P., Sreenivas, N., Dehairs, F., 2000. Sources of suspended matter and selective feeding by zooplankton in an estuarine mangrove ecosystem, as traced by stable isotopes. Mar. Ecol. Prog. Ser. 208, 79–92.

Bouillon, S., Koedam, N., Raman, A.V., Dehairs, F., 2002a. Primary producers sustaining macro-invertebrate communities in intertidal mangrove forests. Oecologia 130, 441–448.

Bouillon, S., Raman, A.V., Dauby, P., Dehairs, F., 2002b. Carbon and nitrogen stable isotope ratios of subtidal benthic invertebrates in an estuarine mangrove ecosystem (Andhra Pradesh, India). Estuar. Coast. Shelf Sci. 54, 901–913.

Bouillon, S., Dahdouh-Guebas, F., Rao, A.V.V.S., Koedam, N., Dehairs, F., 2003a. Sources of organic carbon in mangrove sediments: variability and possible implications for ecosystem functioning. Hydrobiologia 495, 33–39.

Bouillon, S., Frankignoulle, M., Dehairs, F., Velimirov, B., Eiler, A., Etcheber, H., Abril, G., Borges, A.V., 2003b. Inorganic and organic carbon biogeochemistry in the Gautami Godavari estuary (Andhra Pradesh, India) during pre-monsoon: the local impact of extensive mangrove forests. Glob. Biogeochem. Cycles 17, 1114. doi:10.1029/2002GB002026.

Bouillon, S., Koedam, N., Baeyens, W., Satyanarayana, B., Dehairs, F., 2004a. Selectivity of subtidal benthic invertebrate communities for local microalgal production in an estuarine mangrove ecosystem during the post-monsoon period. J. Sea Res. 51, 133–144.

Bouillon, S., Moens, T., Koedam, N., Dahdouh-Guebas, F., Baeyens, W., Dehairs, F., 2004b. Variability in the origin of carbon substrates for bacterial communities in mangrove sediments. FEMS Microbiol. Ecol. 49, 171–179.

Bouillon, S., Moens, T., Overmeer, I., Koedam, N., Dehairs, F., 2004c. Resource utilization patterns of epifauna from mangrove forests with contrasting inputs of local versus imported organic matter. Mar. Ecol. Prog. Ser. 278, 77–88.

Bouillon, S., Moens, T., Dehairs, F., 2004d. Carbon sources sustaining benthic mineralization in mangrove and adjacent seagrass sediments (Gazi bay, Kenya). Biogeosciences 1, 71–78.

Bouillon, S., Korntheuer, M., Baeyens, W., Dehairs, F., 2006. A new automated setup for stable isotope analysis of dissolved organic carbon. Limnol. Oceanogr. Methods 4, 216–226.

Bouillon, S., Dehairs, F., Schiettecatte, L.S., Borges, A.V., 2007a. Biogeochemistry of the Tana estuary and delta (northern Kenya). Limnol. Oceanogr. 52, 46–59.

Bouillon, S., Dehairs, F., Velimirov, B., Abril, G., Borges, A.V., 2007b. Dynamics of organic and inorganic carbon across contiguous mangrove and seagrass systems (Gazi bay, Kenya). J. Geophys. Res. 112, G02018. doi:10.1029/2006JG000325.

Bouillon, S., Middelburg, J.J., Dehairs, F., Borges, A.V., Abril, G., Flindt, M.R., Ulomi, S., Kristensen, E., 2007c. Importance of intertidal sediment processes and porewater exchange on the water column biogeochemistry in a pristine mangrove creek (Ras Dege, Tanzania). Biogeosciences 4, 311–322.

Caraco, N.F., Lampman, G., Cole, J.J., Limburg, K.E., Pace, M.L., Fisher, D., 1998. Microbial assimilation of DIN in a nitrogen rich estuary: implications for food quality and isotope studies. Mar. Ecol. Prog. Ser. 167, 59–71.

Chong, V.C., Low, C.B., Ichikawa, T., 2001. Contribution of mangrove detritus to juvenile prawn nutrition: a dual stable isotope study in a Malaysian mangrove forest. Mar. Biol. 138, 77–86.

Christensen, J.T., Sauriau, P.G., Richard, P., Jensen, P.D., 2001. Diet in mangrove snails: preliminary data on gut contents and stable isotope analysis. J. Shellfish Res. 20, 423–426.

Cifuentes, L.A., Coffin, R.B., Solorzano, L., Cardenas, W., Espinoza, J., Twilley, R.R., 1996. Isotopic and elemental variations of carbon and nitrogen in a mangrove estuary. Estuar. Coast. Shelf Sci. 43, 781–800.

Clough, B.F., Ong, J.E., Gong, W.K., 1997. Estimating leaf area index and photosynthetic production in canopies of the mangrove *Rhizophora apiculata*. Mar. Ecol. Prog. Ser. 159, 285–292.

Connolly, R.M., Guest, M.A., Melville, A.J., Oakes, J.M., 2004. Sulfur stable isotopes separate producers in marine food-web analysis. Oecologia 138, 161–167.

Connolly, R.M., Gorman, D., Guest, M.A., 2005. Movement of carbon among estuarine habitats and its assimilation by invertebrates. Oecologia 144, 684–691.

Costanzo, S.D., O'Donohue, M.J., Dennison, W.C., Loneragan, N.R., Thomas, M., 2001. A new approach for detecting and mapping sewage impacts. Mar. Pollut. Bull. 42, 149–156.

Davie, P.J.F., 1998. Wild Guide to Moreton Bay. Queensland Museum, Brisbane. 408 pp.

Dehairs, F., Rao, R.G., Chandra Mohan, P., Raman, V., Marguillier, S., Hellings, L., 2000. Tracing mangrove carbon in suspended matter and aquatic fauna of the Gautami-Godavari Delta, Bay of Bengal (India). Hydrobiologia 431, 225–241.

Dittmar, T., Lara, R.J., 2001. Molecular evidence for lignin degradation in sulphate-reducing mangrove sediments (Amazonia, Brazil). Geochim. Cosmochim. Acta 65, 1417–1428.

Dittmar, T., Lara, R.J., Kattner, G., 2001. River or mangrove? Tracing major organic matter sources in tropical Brazilian coastal waters. Mar. Chem. 73, 253–271.

Dittmar, T., Hertkorn, N., Kattner, G., Lara, R.J., 2006. Mangroves, a major source of dissolved organic carbon to the oceans. Glob. Biogeochem. Cycles 20, GB1012. doi:10.1029/2005GB002570.

Ehleringer, J.R., Buchmann, N., Flanagan, L.B., 2000. Carbon isotope ratios in belowground carbon cycle processes. Ecol. Appl. 10, 412–422.

Ellison, A.M., Farnsworth, E.J., Twilley, R.R., 1996. Facultative mutualism between red mangroves and root-fouling sponges in Belizean mangal. Ecology 77, 2431–2444.

Farquhar, G.D., Ball, M.C., Van Caemmerer, S., Roksandic, Z., 1982. Effect of salinity and humidity on $\delta^{13}C$ value of halophytes - evidence for diffusional isotope fractionation determined by the ratio of intercellular/atmospheric partial pressure of CO_2 under different environmental conditions. Oecologia 52, 121–124.

Farquhar, G.D., Ehleringer, J.R., Hubick, K.T., 1989. Carbon isotope discrimination and photosynthesis. Annu. Rev. Plant Phys. 40, 503–537.

Fleming, M., Lin, G., Sternberg, L.D.S.L., 1990. Influence of mangrove detritus in an estuarine ecosystem. Bull. Mar. Sci. 47, 663–669.

Fourqurean, J.W., Schrlau, J.E., 2003. Changes in nutrient content and stable isotope ratios of C and N during decomposition of seagrasses and mangrove leaves along a nutrient availability gradient in Florida Bay, USA. Chem. Ecol. 19, 373–390.

France, R.L., 1995. Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications. Mar. Ecol. Prog. Ser. 124, 307–312.

France, R., 1998. Estimation the assimilation of mangrove detritus by fiddler crabs in Laguna Joyuda, Puerto Rico, using dual stable isotopes. J. Trop. Ecol. 14, 413–425.

France, R.L., Holmquist, J.G., 1997. δ^{13}C variability of macroalgae: effects of water motion via baffling by seagrasses and mangroves. Mar. Ecol. Prog. Ser. 149, 305–308.

Fry, B., Ewel, K.C., 2003. Using stable isotopes in mangrove fisheries research: a review and outlook. Isot. Environ. Health Stud. 39, 191–196.

Fry, B., Smith, T.J., 2002. Stable isotope studies of red mangroves and filter feeders from the Shark River estuary, Florida. Bull. Mar. Sci. 70, 871–890.

Fry, B., Bern, A.L., Ross, M.S., Meeder, J.F., 2000. δ^{15}N studies of nitrogen use by the Red Mangrove, *Rhizophora mangle* L. in South Florida. Estuar. Coast. Shelf Sci. 50, 291–296.

Gonneea, M.E., Paytan, A., Herrera-Silveira, J.A., 2004. Tracing organic matter sources and carbon burial in mangrove sediments over the past 160 years. Estuar. Coast. Shelf Sci. 61, 211–227.

Guest, M.A., Connolly, R.M., 2004. Fine-scale movement and assimilation of carbon in saltmarsh and mangrove habitat. Aquat. Ecol. 38, 599–609.

Guest, M.A., Connolly, R.M., Loneragan, N.R., 2004. Carbon movement and assimilation by invertebrates in estuarine habitats occurring at a scale of metres. Mar. Ecol. Prog. Ser. 278, 27–34.

Guest, M.A., Connolly, R.M., Lee, S.Y., Loneragan, N.R., Breitfuss, M.J., 2006. Mechanism for the small-scale movement of carbon among estuarine habitats: organic matter transfer not crab movement. Oecologia 148, 88–96.

Hall, D., Lee, S.Y., Meziane, T., 2006. Fatty acids as trophic tracers in an experimental estuarine food chain: tracer transfer. J. Exp. Mar. Biol. Ecol. 336, 42–53.

Hayase, S., Ichikawa, T., Tanaka, K., 1999. Preliminary report on stable isotope ratio analysis for samples from Matang mangrove brackish water ecosystems. Jpn. Agric. Res. Q. 33, 215–221.

Hemminga, M.A., Mateo, M.A., 1996. Stable carbon isotopes in seagrasses: variability in ratios and use in ecological studies. Mar. Ecol. Prog. Ser. 140, 285–298.

Hemminga, M.A., Slim, F.J., Kazungu, J., Ganssen, G.M., Nieuwenhuize, J., Kruyt, N.M., 1994. Carbon outwelling from a mangrove forest with adjacent seagrass beds and coral reefs (Gazi Bay, Kenya). Mar. Ecol. Prog. Ser. 106, 291–301.

Ho, T.Y., Quigg, A., Finkel, Z.V., Milligan, A.J., Wyman, K., Falkowski, P.G., Morel, F.M.M., 2003. The elemental composition of some marine phytoplankton. J. Phycol. 39, 1145–1159.

Hsieh, H.L., Chen, C.P., Chen, Y.G., Yang, H.H., 2002. Diversity of benthic organic matter flows through polychaetes and crabs in a mangrove estuary: δ^{13}C and δ^{34}S signals. Mar. Ecol. Prog. Ser. 227, 145–155.

Ish-Shalom-Gordon, N., Lin, G., Sternberg, L.D.S.L., 1992. Isotopic fractionation during cellulose synthesis in two mangrove species: salinity effects. Phytochemistry 31, 2623–2626.

Jaffé, R., Rushdi, A.I., Medeiros, P.M., Simoneit, B.R.T., 2006. Natural product biomarkers as indicators of sources and transport of sedimentary organic matter in a subtropical river. Chemosphere 64, 1870–1884.

Jennerjahn, T.C., Ittekkot, V., 1997. Organic matter in sediments in the mangrove areas and adjacent continental margins of Brazil: I. Amino acids and hexosamines. Oceanol. Acta 20, 359–369.

Jennerjahn, T.C., Ittekkot, V., 2002. Relevance of mangroves for the production and deposition of organic matter along tropical continental margins. Naturwissenschaften 89, 23–30.

Jones, A.B., O'Donohue, M.J.O., Udy, J., Dennison, W.C., 2001. Assessing ecological impacts of shrimp and sewage effluent: biological indicators with standard water quality analyses. Estuar. Coast. Shelf Sci. 52, 91–109.

Kao, W.Y., Chang, K.W., 1998. Stable carbon isotope ratio and nutrient content of the *Kandelia candel* mangrove populations of different growth forms. Bot. Bull. Acad. Sin. 39, 39–45.

Kao, W.Y., Tsai, H.C., Tsai, T.T., 2001. Effect of NaCl and nitrogen availability on growth and photosynthesis of seedlings of a mangrove species, *Kandelia candel* (L.) Druce. J. Plant Physiol. 158, 841–846.

Kao, W.Y., Tsai, H.C., Shih, C.N., Tsai, T.T., Handley, L.L., 2002. Nutrient contents, δ^{13}C and δ^{15}N during leaf senescence in the mangrove, *Kandelia candel* (L.) Druce. Bot. Bull. Acad. Sin. 43, 277–282.

Kennedy, H., Gacia, E., Kennedy, D.P., Papadimitriou, S., Duarte, C.M., 2004. Organic carbon sources to SE Asian coastal sediments. Estuar. Coast. Shelf. Sci. 60, 59–68.

Kieckbusch, D.K., Koch, M.S., Serafy, J.E., Anderson, W.T., 2004. Trophic linkages among primary producers and consumers in fringing mangroves of subtropical lagoons. Bull. Mar. Sci. 74, 271–285.

Kim, J.H., Dupont, L., Behling, H., Versteegh, G.J.M., 2005. Impacts of rapid sea-level rise on mangrove deposit erosion: application of taraxerol and *Rhizophora* records. J. Quat. Sci. 20, 221–225.

Kito, K., Aryuthaka, C., 2006. New mouthless nematode of the genus Parastomonema Kito, 1989 (Nematoda: Siphonolaimidae) from a mangrove forest on the coast of Thailand, and erection of the new subfamily Astomonematinae within the Siphonolaimidae. Zootaxa 1177, 39–49.

Koch, B.P., Rullkötter, J., Lara, R.J., 2003. Evaluation of triterpenols and sterols as organic matter biomarkers in a mangrove ecosystem in Brazil. Wetl. Ecol. Manage. 11, 257–263.

Koch, B.P., Harder, J., Lara, R.J., Kattner, G., 2005. The effect of selective microbial degradation on the composition of mangrove derived pentacyclic triterpenols in surface sediments. Org. Geochem. 36, 273–285.

Kristensen, E., Bouillon, S., Dittmar, T., Marchand, C. submitted for publication. Organic matter dynamics in mangrove ecosystems. Aquatic Botany.

Kuramoto, T., Minagawa, M., 2001. Stable carbon and nitrogen isotopic characterization of organic matter in a mangrove ecosystem on the south-western coast of Thailand. J. Oceanogr. 57, 421–431.

Lacerda, L.D., Rezende, C.E., Martinelli, L.A., Ovalle, A.R.C., Mozeto, A., Nogueira, F., Victoria, R.L., Aragon, G.T., Da Cunha, C.T., Souza, C.A.R., 1986. Composição isotópica de carbono em componentes de um ecossistema manguezal na Baía de Sepetiba, Rio de Janeiro. Ciênc. Cult. 38, 1714–1717.

Lacerda, L.D., Silva, S.A.R., Rezende, C.E., Martinelli, L.A., 1991. Food sources for the mangrove tree crab *Aratus pisonii*: a carbon stable isotopic study. Rev. Bras. Biol. 51, 685–687.

Lacerda, L.D., Ittekkot, V., Patchineelam, S.R., 1995. Biogeochemistry of mangrove soil organic matter: a comparison between *Rhizophora* and *Avicennia* soils in south-eastern Brazil. Estuar. Coast. Shelf. Sci. 40, 713–720.

Lallier-Verges, E., Perrussel, B.P., Disnar, J.-R., Baltzer, F., 1998. Relationships between environmental conditions and the diagenetic evolution of organic matter derived from higher plants in a modern mangrove swamp system (Guadeloupe, French West Indies). Org. Geochem. 29, 1663–1686.

Lebata, M.J.H.L., Primavera, J.H., 2001. Gill structure, anatomy and habitat of *Anodontia edulenta*: evidence of endosymbiosis. J. Shellfish Res. 20, 1273–1278.

Lee, S.Y., 1995. Mangrove outwelling: a review. Hydrobiologia 295, 203–212.

Lee, S.Y., 1998. Ecological role of grapsid crabs in mangrove ecosystems: a review. Mar. Freshw. Res. 49, 335–343.

Lee, S.Y., 2000. Carbon dynamics of Deep Bay, eastern Pearl River estuary, China. II : Trophic relationship based on carbon and nitrogen stable isotopes. Mar. Ecol. Prog. Ser. 205, 1–10.

Lee, S.Y., 2005. Exchange of organic matter and nutrients between mangroves and estuaries: myths, methodological issues and missing links. Int. J. Ecol. Environ. Sci. 31, 163–176.

Lee, O.H.K., Williams, G.A., Hyde, K.D., 2001. The diets of *Littoraria ardouiniana* and *L. melanostoma* in Hong Kong mangroves. J. Mar. Biol. Assoc. U.K. 81, 967–973.

Lin, G., Sternberg, L.D.S.L., 1992a. Effect of growth form, salinity, nutrient and sulfide on photosynthesis, carbon isotope discrimination and growth of red mangrove (*Rhizophora mangle* L.). Aust. J. Plant Physiol. 19, 509–517.

Lin, G., Sternberg, L.D.S.L., 1992b. Differences in morphology, carbon isotope ratios, and photosynthesis between scrub and fringe mangroves in Florida, USA. Aquat. Bot. 42, 303–313.

Lin, G., Banks, T., Sternberg, L.O., 1991. Variation in δ^{13}C values for the seagrass *Thalassia testudinum* and its relations to mangrove carbon. Aquat. Bot. 40, 333–341.

Loneragan, N.R., Bunn, S.E., Kellaway, D.M., 1997. Are mangroves and seagrasses sources of organic carbon for penaeid prawns in a tropical Australian estuary? A multiple stable-isotope study. Mar. Biol. 130, 289–300.

Machiwa, J.F., 2000. 13C signatures of flora, macrofauna and sediment of a mangrove forest partly affected by sewage wastes. Tanzan. J. Sci. 26, 15–28.

Macia, A., 2004. Primary carbon sources for juvenile penaeid shrimps in a mangrove-fringed Bay of Inhaca Island, Mozambique: a dual carbon and nitrogen isotope analysis. W. Ind. Ocean J. Mar. Sci. 3, 151–161.

MacLeod, N.A., Barton, D.R., 1998. Effects of light intensity, water velocity, and species composition on carbon and nitrogen stable isotope ratios in periphyton. Can. J. Fish. Aquat. Sci. 55, 1919–1925.

Marchand, C., Disnar, J.R., Lallier-Verges, E., Lottier, N., 2005. Early diagenesis of carbohydrates and lignin in mangrove sediments subject to variable redox conditions (French Guiana). Geochim. Cosmochim. Acta 69, 131–142.

Marguillier, S., Van der Velde, G., Dehairs, F., Hemminga, M.A., Rajagopal, S., 1997. Trophic relationships in an interlinked mangrove-seagrass ecosystem as traced by δ^{13}C and δ^{15}N. Mar. Ecol. Prog. Ser. 151, 115–121.

McClelland, J.W., Valiela, I., 1998. Linking nitrogen in estuarine producers to land-derived sources. Limnol. Oceanogr. 43, 577–585.

McCutchan, J.H., Lewis, W.M., Kendall, C., McGrath, C.C., 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos 102, 378–390.

McKee, K.L., Feller, I.C., Popp, M., Wanek, W., 2002. Mangrove isotopic (δ^{15}N and δ^{13}C) fractionation across a nitrogen vs. phosphorus limitation gradient. Ecology 83, 1065–1075.

Mead, R., Xu, Y., Chong, J., Jaffé, R., 2005. Sediment and soil organic matter source assessment as revealed by the molecular distribution and carbon isotopic composition of n-alkanes. Org. Geochem. 36, 363–370.

Medina, E., Francisco, M., 1997. Osmolality and δ^{13}C of leaf tissues of mangrove species from environments of contrasting rainfall and salinity. Estuar. Coast. Shelf Sci. 45, 337–344.

Melville, A.J., Connolly, R.M., 2003. Spatial analysis of stable isotope data to determine primary sources of nutrition for fish. Oecologia 136, 499–507.

Melville, A.J., Connolly, R.M., 2005. Food webs supporting fish over subtropical mudflats are based on transported organic matter not in situ microalgae. Mar. Biol. 148, 363–371.

Moran, M.A., Wicks, R.J., Hodson, R.E., 1991. Export of dissolved organic-matter from a mangrove swamp ecosystem- evidence from natural fluorescence, dissolved lignin phenols, and bacterial secondary production. Mar. Ecol. Prog. Ser. 76, 175–184.

Muzuka, A.N.N., Shunula, J.P., 2005. Stable isotope compositions of organic carbon and nitrogen of two mangrove stands along the Tanzanian coastal zone. Estuar. Coast. Shelf Sci. 66, 447–458.

Newell, R.I.E., Marshall, N., Sasekumar, A., Chong, V.C., 1995. Relative importance of benthic microalgae, phytoplankton, and mangroves as sources of nutrition for penaeid prawns and other coastal invertebrates from Malaysia. Mar. Biol. 123, 595–606.

Nordhaus, I., Wolff, M., Diele, K., 2006. Litter processing and population food intake of the mangrove crab *Ucides cordatus* in a high intertidal forest in northern Brazil. Estuar. Coast. Shelf Sci. 67, 239–250.

Odum, W.E., Heald, E.J., 1975. The detritus-based food web of an estuarine mangrove community. In: Cronin, L.E. (Ed.), Estuarine Research. Academic Press, New York, pp. 265–286.

Okada, N., Sasaki, A., 1998. Sulfur isotopic composition of mangroves. Isot. Environ. Health Stud. 34, 61–65.

O'Leary, M.H., 1981. Carbon isotope fractionation in plants. Phytochemistry 20, 553–567.

Phillips, D.L., Gregg, J.W., 2001. Uncertainty in source partitioning using stable isotopes. Oecologia 127, 171–179.

Phillips, D.L., Gregg, J.W., 2003. Source partitioning using stable isotopes: coping with too many sources. Oecologia 136, 261–269.

Phillips, D.L., Koch, P.L., 2001. Incorporating concentration dependence in stable isotope mixing models. Oecologia 130, 114–125.

Phillips, D.L., Newsome, S.D., Gregg, J.W., 2005. Combining sources in stable isotope mixing models: alternative methods. Oecologia 144, 520–527.

Primavera, J.H., 1996. Stable carbon isotope ratios of penaeid juveniles and primary producers in a riverine mangrove in Guimeras, Phillipines. Bull. Mar. Sci. 58, 675–683.

Proffitt, C.E., Devlin, D.J., 2005. Grazing by the intertidal gastropod *Melampus coffeus* greatly increases mangrove litter degradation rates. Mar. Ecol. Prog. Ser. 296, 209–218.

Rao, R.G., Woitchik, A.F., Goeyens, L., Van Riet, A., Kazungu, J., Dehairs, F., 1994. Carbon, nitrogen contents and stable isotope abundance in mangrove leaves from an east African coastal lagoon (Kenya). Aquat. Bot. 47, 175–183.

Raven, J.A., Walker, D.I., Jensen, K.R., Handley, L.L., Scrimgeour, C.M., McInroy, S.G., 2001. What fraction of the organic carbon in sacoglossans is obtained from photosynthesis by kleptoplastids? An investigation using the natural abundance of stable carbon isotopes. Mar. Biol. 138, 537–545.

Raymond, P.A., Bauer, J.E., 2001. Use of ^{14}C and ^{13}C natural abundances or evaluating riverine, estuarine and coastal DOC and POC sources and cycling: a review and synthesis. Org. Geochem. 32, 469–485.

Rezende, C.E., Lacerda, L.D., Ovalle, A.R.C., Silva, C.A.R., Martinelli, L.A., 1990. Nature of POC transport in a mangrove ecosystem : a carbon stable isotopic study. Estuar. Coast. Shelf Sci. 30, 641–645.

Rodelli, M.R., Gearing, J.N., Gearing, P.J., Marshall, N., Sasekumar, A., 1984. Stable isotope ratios as a tracer of mangrove carbon in Malaysian ecosystems. Oecologia 61, 326–333.

Rumpho, M.E., Summer, E.J., Manhart, J.R., 2000. Solar-powered sea slugs. Mollusk/algal chloroplast symbiosis. Plant Physiol. 123, 29–38.

Schwamborn, R., Ekau, W., Voss, M., Saint-Paul, U., 2002. How important are mangroves as a carbon source for decapod crustacean larvae in a tropical estuary? Mar. Ecol. Prog. Ser. 229, 195–205.

Sheaves, M., Molony, B., 2000. Short-circuit in the mangrove food chain. Mar. Ecol. Prog. Ser. 199, 97–109.

Slim, F.J., Hemminga, M.A., Ochieng, C., Jannick, N.T., Cocheret de la Morinière, E., Van der Velde, G., 1997. Leaf litter removal by the snail *Terebralia palustris* (Linneaus) and sesarmid crabs in an East African mangrove forest (Gazi Bay, Kenia). J. Exp. Mar Biol. Ecol. 215, 35–48.

Smallwood, B.J., Wooller, M.J., Jacobson, M.E., Fogel, M.L., 2003. Isotopic and molecular distributions of biochemicals from fresh and buried *Rhizophora mangle* leaves. Geochem. Trans. 4, 38–46.

Swennen, C., 1997. Two new gastropods, *Elysia bangtawaensis* and *E. siamensis* from southern Thailand (Ophistobranchia, Sacoglossa, Elysiidae). Bull. Zool. Mus. Univ. Amsterdam 16, 33–39.

Thimdee, W., Deein, G., Sangrungruang, C., Matsunaga, K., 2001. Stable carbon and nitrogen isotopes of mangrove crabs and their food sources in a mangrove-fringed estuary in Thailand. Benthos Res. 56, 73–80.

Thimdee, W., Deein, G., Sangrungruang, C., Nishioka, J., Matsunaga, K., 2003. Sources and fate of organic matter in Khung Krabaen Bay (Thailand) as traced by ^{13}C and C/N atomic ratios. Wetlands 23, 729–738.

Thimdee, W., Deein, G., Sangrungruang, C., Matsunaga, K., 2004. Analysis of primary food sources and trophic relationships of aquatic animals in a mangrove-fringed estuary, Khung Krabaen Bay (Thailand) using dual stable isotope techniques. Wetl. Ecol. Manage. 12, 135–144.

Vander Zanden, M.J., Rasmussen, J.B., 2001. Variation in δ^{15}N and δ^{13}C trophic fractionation: implications for aquatic food web studies. Limnol. Oceanogr. 46, 2061–2066.

Verheyden, A., Helle, G., Schleser, G.H., Dehairs, F., Beeckman, H., Koedam, N., 2004. Annual cyclicity in high-resolution stable carbon and oxygen isotope ratios in the wood of the mangrove tree *Rhizophora mucronata*. Plant Cell Environ. 27, 1525–1536.

Versteegh, G., Schefuss, E., Dupont, L., Marret, F., Damsté, J.S., Jansen, J.H.F., 2004. Taraxerol and *Rhizophora* pollen as proxies for tracking past Mangrove ecosystems. Geochim. Cosmochim. Acta 68, 411–422.

Victor, S., Golbuu, Y., Wolanski, E., Richmond, R.H., 2004. Fine sediment trapping in two mangrove-fringed estuaries exposed to contrasting land-use intensity, Palau, Micronesia. Wetl. Ecol. Manage. 12, 277–283.

Werry, J., Lee, S.Y., 2005. Grapsid crabs mediate link between mangrove litter production and estuarine planktonic food chains. Mar. Ecol. Prog. Ser. 293, 165–176.

Wiedemeyer, W., 1997. Analysis of the benthic food web of a mangrove ecosystem at northeastern Brazil. Ph.D. Thesis, Christian Albrechts Universität, Kiel, Germany.

Woitchik, A.F., Ohowa, B., Kazungu, J.M., Rao, R.G., Goeyens, L., Dehairs, F., 1997. Nitrogen enrichment during decomposition of mangrove litter in an east African coastal lagoon (Kenya): relative importance of biological nitrogen fixation. Biogeochemistry 39, 15–35.

Wooller, M., Smallwood, B., Scharler, U., Jacobson, M., Fogel, M., 2003a. A taphonomic study of δ^{13}C and δ^{15}N values in Rhizophora *mangle* leaves for a multi-proxy approach to mangrove paleoecology. Org. Geochem. 34, 1259–1275.

Wooller, M., Smallwood, B., Jacobson, M., Fogel, M., 2003b. Carbon and nitrogen stable isotopic variation in *Laguncularia racemosa* (L.) (white mangrove) from Florida and Belize: implications for trophic level studies. Hydrobiologia 499, 13–23.

Zieman, J.C., Macko, S.A., Mills, L., 1984. Role of seagrasses and mangroves in estuarine food webs: temporal and spatial changes in stable isotope composition and amino acid content during decomposition. Bull. Mar. Sci. 35, 380–392.

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Selection of an omnivorous diet by the mangrove tree crab *Aratus pisonii* in laboratory experiments

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Abstract

Observational studies on leaf damage, gut content analyses, and crab behaviour have demonstrated that like numerous other mangrove and salt-marsh generalists, the mangrove tree crab *Aratus pisonii* feeds on a variety of food resources. This study is the first that experimentally tests feeding preferences of *A. pisonii*, as well as the first to test experimentally whether chemical composition of food resources is responsible for food selection. Feeding preferences were determined among a variety of plant, algal, and animal resources available in the field both in Florida and Belize, using multiple-choice feeding assays, where male and female crabs simultaneously were offered a variety of food items. To test whether chemistry of food resources was responsible for feeding preferences, chemical extracts of food resources were incorporated in an agar-based artificial food, and used in feeding assays. Results of feeding assays suggest that crabs prefer animal matter from ~ 2.5 to 13× more than other available resources, including leaves of the red mangrove *Rhizophora mangle*, which contribute the most to their natural diet. Artificial feeding assays also demonstrated that chemical cues were responsible for selection of animal matter, up to 25× more than other available resources. Non-polar extracts (derived from extraction in 1:1 ethyl actetate:methanol) stimulated feeding the most, suggesting that fatty acids, triglycerides, or sterols may be important for growth, reproduction, or survival. Results for both sexes were similar across most assays. While chemical composition of food resources appears to play some role in selection, this does not discount the potential role of other factors, such as resource availability, competition, predation, or reproductive requirements in influencing feeding preferences. Bioassay-guided fractionation of extracts should aid in determining chemical constituents that play the greatest role in determining feeding preferences.

Keywords: *Aratus pisonii*; Compensatory feeding; Feeding preference; Mangroves; Omnivores; *Rhizophora mangle*

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1. Introduction

While many mangrove and salt-marsh crabs consume significant amounts of plant material, evidence suggests that these organisms are more appropriately considered omnivores rather than herbivores (Malley, 1978; Giddins et al., 1986; Dahdouh-Guebas et al., 1997, 1999; Buck et al., 2003). Many of these crabs appear to be opportunistic feeders on animal matter, supplementing their nutritionally poor plant diet with live or dead animal matter, rich in nitrogen and protein. Some studies show a positive correlation between consumption or feeding preferences and marine plant/algal nutritional value (Camilleri, 1989; Barile et al., 2004); however, others

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demonstrate either no or negative relationships (Duffy and Hay, 1991; Micheli, 1993; Pennings et al., 1998; Cruz-Rivera and Hay, 2001), suggesting that nutrition may not necessarily be the driving factor that results in significant plant consumption. This raises two questions: (1) is significant consumption of plant matter merely compensatory feeding to fulfil caloric requirements until a more valuable food source becomes available; and (2) do these plants contain dietary requirements unrelated to nitrogen and protein content necessitating high feeding on plant matter? If the answer to these questions is yes, this suggests that eating a mixed diet would be more beneficial to the growth, survival, and fitness of mangrove and salt-marsh crabs.

One such crab, the tree crab *Aratus pisonii* is a key organism in the mangrove environment. It is one of the most abundant animals found in Florida and Caribbean mangroves, and it is the primary herbivore of the red mangrove (*Rhizophora mangle*) (Feller and Chamberlain, in review). *A. pisonii* is one of a few crabs in the world that actually feeds on live leaves, and it is able to access leaves all the way up to the top of the canopy (Erickson et al., 2003). Through feeding, mangrove crabs link primary production to higher trophic levels by serving as prey (Beever et al., 1979; Wilson, 1989; Olmos et al., 2001). They also link it to smaller organisms of the same trophic level, and the detrital pathway through leaf shredding and the production of faecal material (Camilleri, 1989; Emmerson and McGwynne, 1992; Steinke et al., 1993; Lee, 1997; Werry and Lee, 2005). Feeding by herbivores can cause premature abscission, elevate soil nutrients, hasten nutrient cycling, and retain nutrients within ecosystems (Risley and Crossley, 1988). Research is currently being conducted to examine how mangrove crabs influence the above parameters regarding nutrient cycling (Nordhaus et al., 2006; S. Chapman, pers. comm., 2005). As a fresh leaf feeder, *A. pisonii* can influence mangrove physiology, chemistry, reproduction, and evolutionary development (Onuf et al., 1977; M. Ball, pers. comm., 2003). Despite this crab feeding mostly on *R. mangle*, observations suggest it is omnivorous, supplementing a low nutritional leaf diet with animal matter (Beever et al., 1979; Erickson et al., 2003; I. Feller, pers. obs., 2003).

While gut content analyses, studies on crab behaviour, and crab damage patterns on leaves have revealed that this crab consumes a variety of food resources (Beever et al., 1979; Diaz and Conde, 1988; Brogim and Lana, 1997; Erickson et al., 2003), this study is the first that experimentally documents its feeding preferences through the use of multiple-choice feeding assays. In addition, the basis for food choice by this crab remains unknown. Few experimental studies have been conducted on mangrove herbivores and omnivores testing the effect of prey chemistry on feeding preferences (Fratini et al., 2001; Erickson et al., in prep.). While some research has been done that examines how chemistry of mangrove leaves correlates with crab damage (Erickson et al., 2004), experimental studies have not been conducted. Thus, this is the first study to use artificial feeding assays, where extracts of food resources are incorporated into an agar-based diet, to determine whether chemical defences or feeding stimulants are responsible for feeding preferences of this generalist mangrove tree crab. Studies were conducted in Florida and Belize, which are sites of ongoing research examining crab feeding ecology where abundant crab populations are present, to see whether crab populations respond similarly to available food items in each location and whether there is an interaction between chemistry and location in feeding. The questions being asked include: (1) what are the feeding preferences of *A. pisonii*; (2) are feeding preferences linked to food chemistry; and (3) does feeding behaviour of *A. pisonii* include diet mixing or compensatory feeding?

2. Materials and methods

2.1. Collection of organisms

Adult crabs (*Aratus pisonii*) used in feeding assays were collected from Fort Pierce, Florida, in the Indian River Lagoon (Mosquito Impoundment 23) and from Carrie Bow Cay, Belize. This crab is distributed in neotropical mangrove systems ranging from Florida to northern Brazil. Food resources for live assays were collected from the same habitats. *A. pisonii* has been shown in the field to feed on insects, such as crickets (Beever et al., 1979), beetles, and leaf miners (I. Feller, pers. obs., 2003; D. Devlin, pers. comm., 2004). House crickets (*Achetus domesticus*) were purchased from Pet Supermarket in Fort Pierce. They were used because they were readily available as an insect model and could be obtained in a large enough quantity for extraction purposes. The red alga *Gracilaria tikvahiae*, which was used in artificial feeding assays, was obtained from cultures maintained at Harbor Branch Oceanographic Institution by D. Hanisak.

2.2. Multiple-choice feeding assays

Multiple-choice feeding assays were conducted with food resources commonly found in mangrove habitats to gain perspective on how these items rank in palatability and the degree to which crabs maintain a generalized omnivorous diet. Individual adult crabs of each sex ($N=20$) were maintained in their own plastic mesh cages with enough seawater to submerge themselves. Water was replaced after evaporation. For feeding assays, crabs were offered various food items, including: *Rhizophora mangle* fruit, live *R. mangle* leaves, detrital *R. mangle* leaves, detrital *Thalassia testudinum* blades (Belize only), algae (*G. tikvahiae,* which washes up as drift in Florida and mangrove root algae composed primarily of *Bostrychia tenella* and *Caloglossa leprieurii* in Belize), and whole, dead adult *A. pisonii* (average carapace width of 2 cm) and *A. domesticus* (average body length of 1.9 cm). Food items were weighed prior to and after assays, which were run for ~ 3 d. Paired crab-exclusion controls were run simultaneously to account for changes in resources unrelated to feeding (Peterson and Renaud, 1989). Consumption of each item was determined using the following formula:

$$T_i\left(\frac{C_f}{C_i}\right) - T_f$$

where T_i is the initial food mass, T_f is the final food mass, C_i is the initial control food mass, and C_f is the final control food mass. The amount of each item consumed was expressed as the percent of the total food consumed by an individual crab (Lockwood, 1998). Crabs that consumed <10% or >90% of the total food mass cage^{-1} were excluded from statistical analysis given that no choice was demonstrated. Friedman's repeated measures ANOVA and multiple comparison tests (Tukey's and SNK) were used to identify significant differences in the percent of total consumption among food resources (Lockwood, 1998).

2.3. Preparation of extracts

Freshly collected food resources were homogenized in solvent and extracted three times in 1:1 ethyl acetate: methanol producing non-polar extracts and three times in 1:1 ethanol:di H_20 producing polar extracts. Extracts were filtered, dried by rotary evaporator, and stored at 4 °C until used in feeding assays. Non-polar extracts may include compounds such as fatty acids, triglycerides, sterols, and terpenes, while polar extracts may include compounds such as tannins and proteins.

2.4. Artificial feeding assays with extracts

Methods used were adopted from Hay et al. (1998). Artificial diet was made by dissolving 1 g agar in 30 ml di H_20 and heating in a microwave, after which 2 g dried, ground *G. tikvahiae* were added and stirred. Extracts were dissolved in 2 ml ethanol and added at natural concentrations (based on dry weight) into the food. Individual assays were done that tested non-polar extracts of food items against each other, polar extracts of food items against each other, and combinations of *R. mangle* and *A. domesticus* extracts yielding foods at various concentrations (100, 75, 50, 25, and 0%) of plant (*R. mangle*) versus animal (*A. domesticus*) extracts, in which non-polar and polar extracts also were tested separately. Extracts from *A. domesticus* and *R. mangle* leaves were used because crabs frequently encounter insects and feed heavily on *R. mangle* in the field. Ethanol without extracts (2 ml) was added to control food. Artificial food with extracts and control food were spread into a mold with parallel, rectangular wells placed over plastic window screen, allowed to cool, and cut into pieces of ~1 cm^2. Prior to assays, crabs were trained on artificial food to demonstrate that they would feed on it. For artificial assays, male and female crabs ($N=20$) simultaneously were offered one piece of each food type, including controls. They were allowed to feed until half of one piece of artificial food was consumed or 48 h passed. Preference was quantified as the number of window screen squares revealed after food was consumed. Squares that were partially consumed were counted as 0.5 square. Crabs were excluded from statistical analysis if they did not eat or consumed all food. Friedman's repeated measures ANOVA and Tukey's multiple comparison test were used to identify significant differences in the number of squares consumed.

3. Results

Multiple-choice feeding assays from Florida demonstrated that both male and female crabs significantly preferred animal matter to other food resources (Friedman's $\chi_r^2=95.94$, 41.57, 55.32, for sexes combined, females, and males, respectively, $P \le 0.001$ for all groups; Fig. 1A). Detrital *Rhizophora mangle* leaves and algae (*Gracilaria tikvahiae*) were intermediate in preference, while *R. mangle* fruit and green leaves were low in preference. These patterns differed somewhat from crabs residing in Belize, where preferences were not as well defined (Friedman's $\chi_r^2=37.34$, $P \le 0.001$ for sexes combined; $\chi_r^2=12.83$, $P=0.046$ for females; and $\chi_r^2=35.07$, $P \le 0.001$ for males; Fig. 1B). Root algae were preferred most by male crabs in Belize, closely followed by animal matter. The same trend was found for female crabs despite statistical tests being unable to determine which food types differed. Detritus,

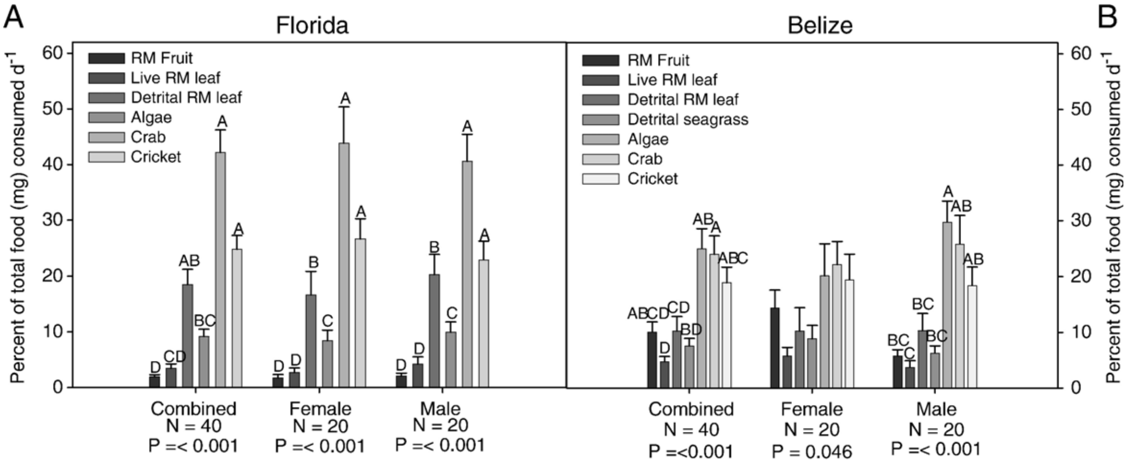

Fig. 1. Feeding preferences from multiple-choice feeding assays where *A. pisonii* were offered fruit, live, and detrital leaves of *R. mangle* (RM), detrital seagrass blades, algae, crabs, and crickets in Florida (A) and Belize (B). Different letters above bars indicate significant differences among treatments.

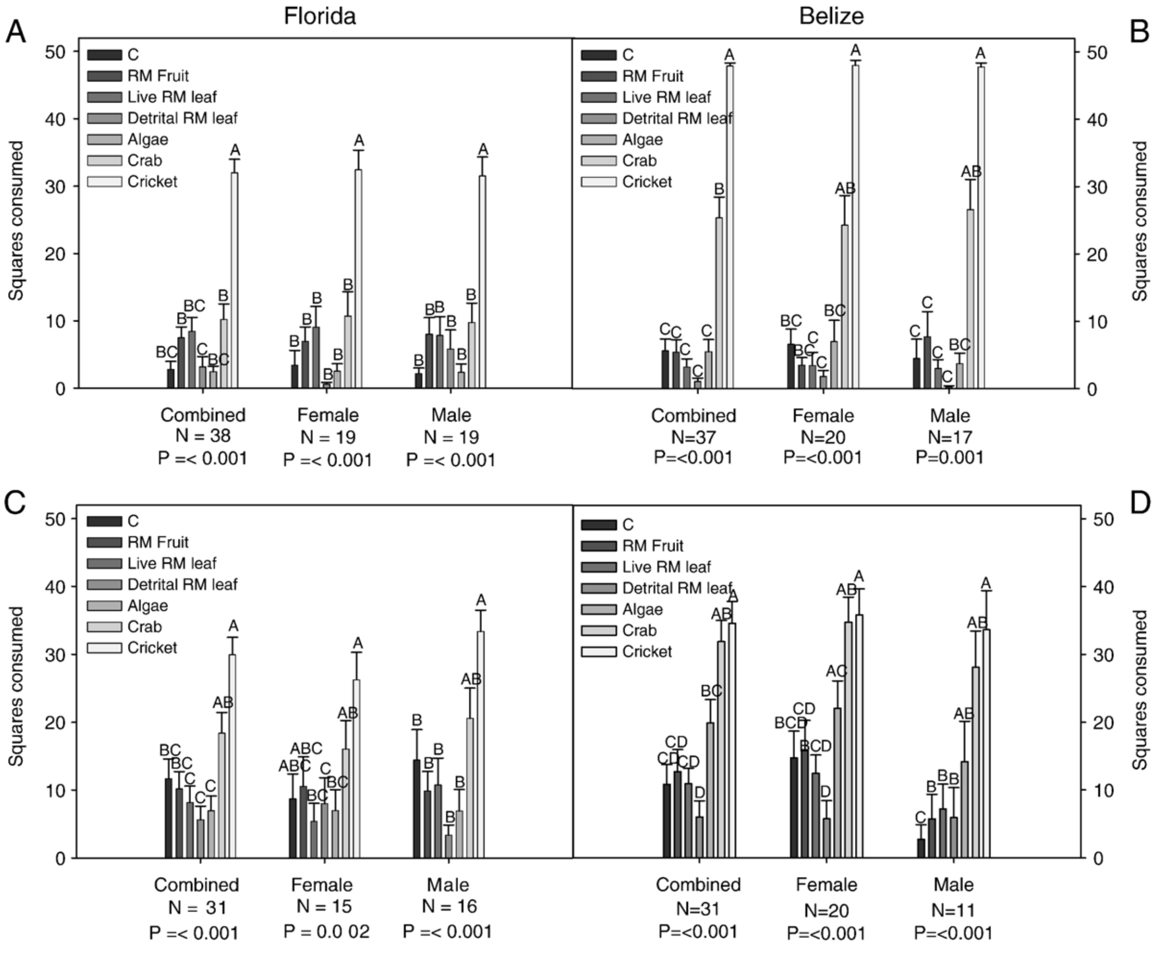

Fig. 2. Artificial feeding assays testing the influence of chemical composition of various food resources on consumption by crabs from Florida and Belize. Non-polar (A, B) and polar (C, D) extracts were incorporated into an agar-based artificial diet. Different letters above bars indicate significant differences among treatments. Abbreviations: see Fig. 1.

live *R. mangle* leaves, and fruits tended to be lower in preference.

Results from artificial feeding assays demonstrated that food with animal extracts (either non-polar or polar) was fed upon significantly more than food with extracts from other resources (Fig. 2) in both Florida and Belize. In Florida, non-polar food with *Achetus domesticus* extracts was consumed the most (Friedman's $\chi_r^2=105.70$, 54.18, 53.72, for sexes combined, females, and males, respectively, $P \leq 0.001$ for all groups; Fig. 2A), while in Belize, food with both *A. domesticus* and *Aratus pisonii* non-polar extracts was fed upon the most (Friedman's $\chi_r^2=127.69$, 66.02, 63.33 for sexes combined, females, and males, respectively, $P \leq 0.001$ for sexes combined and females, $P=0.001$ for males; Fig. 2B). Little difference in feeding existed among artificial food with non-polar extracts of other food items, regardless of location. Differences in feeding among food with polar extracts were not as well defined compared to non-polar extracts for both Florida and Belize populations (Friedman's $\chi_r^2=59.14$, $P \leq 0.001$ for sexes combined; $\chi_r^2=20.67$, $P=0.002$ for females; and $\chi_r^2=41.54$, $P \leq 0.001$ for males; Fig. 2C; Friedman's $\chi_r^2=73.14$, 48.88, 35.26, for sexes combined, females, and males, respectively, $P< 0.001$ for all groups, Fig. 2D). Male and female crabs showed similar feeding patterns.

As a follow-up to artificial assays that documented feeding preference of animal matter, artificial feeding assays were conducted that tested preference for food

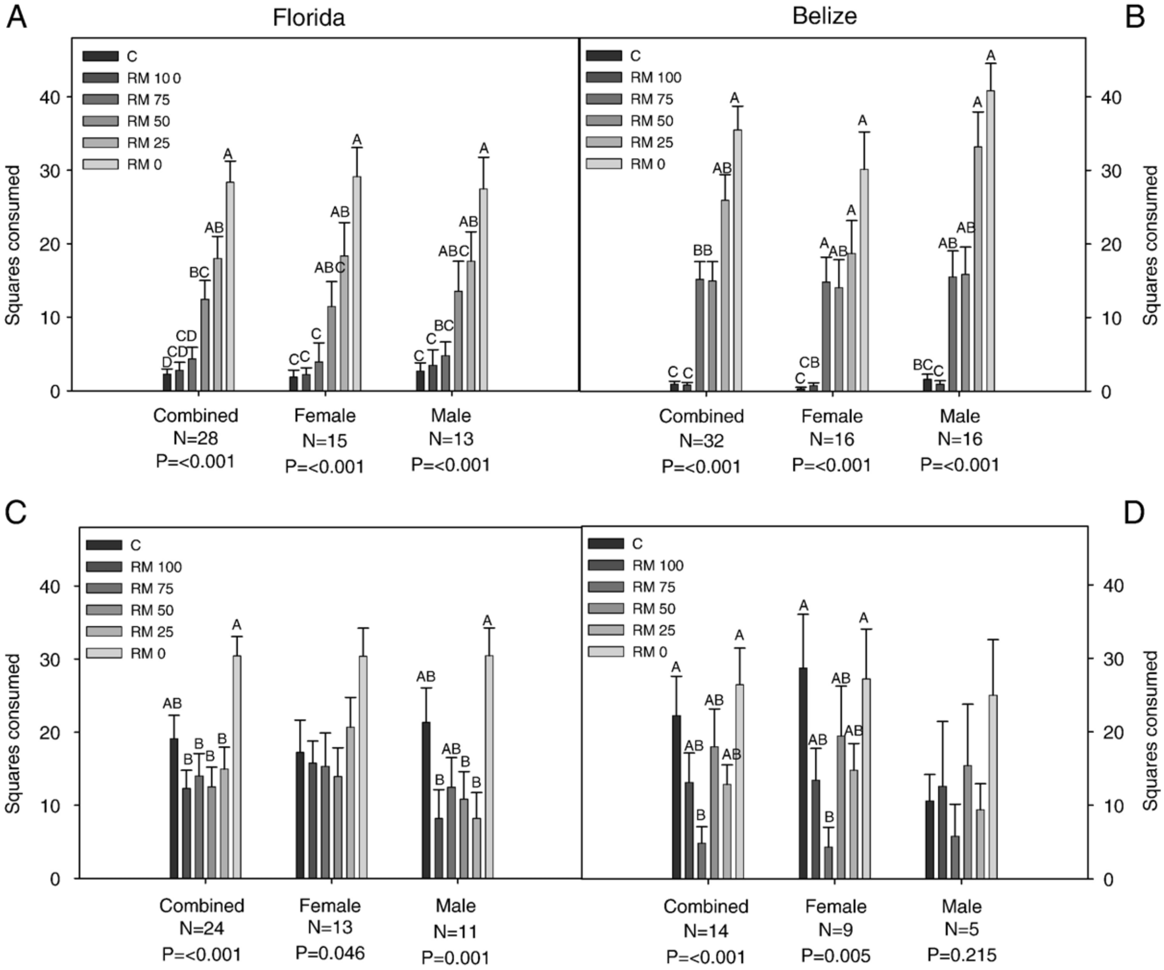

Fig. 3. Artificial feeding assays testing the influence of single and mixed animal and plant diets on consumption by crabs from Florida and Belize. Non-polar (A, B) and polar (C, D) extracts of *R. mangle* (RM) and *A. domesticus* were incorporated into an agar-based artificial diet so that food choices represented 100% RM, 75% RM, 50% RM, 25% RM, and 0% RM, with the remainder being composed of *A. domesticus*. Different letters above bars indicate significant differences among treatments.

with single diets containing animal or plant extracts (using natural concentrations based on dry weight) and mixed diets of both food types combined. Mixed diets ranged from 25 to 75% of either food type. Greater differences in feeding were seen across food with non-polar extracts as opposed to food containing polar extracts (Fig. 3). For crabs from Florida and Belize, feeding on artificial food with non-polar extracts increased as *R. mangle* extract concentration decreased and *A. domesticus* extract concentration increased (Friedman's $\chi_r^2=78.46$, 44.97, 33.99, for sexes combined, females, and males, respectively, $P \leq 0.001$ for all groups, Fig. 3A; Friedman's $\chi_r^2=101.29$, 46.75, 56.44, for sexes combined, females, and males, respectively, $P \leq 0.001$ for all groups, Fig. 3B). No major differences were found between sexes when non-polar extracts were incorporated into food. For polar extracts, the same strong patterns were not observed. In Florida, the only diet that was fed upon significantly more than others was the single diet of animal extract (Friedman's $\chi_r^2=24.09$, $P \leq 0.001$ for sexes combined, $\chi_r^2=11.30$, $P=0.046$ for females; and $\chi_r^2=20.36$, $P=0.001$ for males; Fig. 3C). There was no difference among food types with mixed diets or the single diet with plant extract. While the data from Belize demonstrate differences in feeding among mixed diets with polar extracts, the differences were only between the single diet with animal extract and the mixed diet with 75% plant and 25% animal extract (Friedman's $\chi_r^2=21.57$, $P \leq 0.001$ for sexes combined; $\chi_r^2=16.89$, $P=0.005$ for females; and $\chi_r^2=7.07$, $P=0.215$ for males; Fig. 3D). Significant differences were found in Belize among polar food types for females and none were found for males; however, male feeding trends were similar to that of females.

4. Discussion

Through the use of multiple-choice and artificial feeding assays, this study is the first to experimentally document feeding preferences of the mangrove tree crab *Aratus pisonii* and demonstrate the role of food chemistry on food selection. The fact that live *Rhizophora mangle* leaves were low preference food items was surprising given that *A. pisonii* consumes significant amounts of *R. mangle* leaf material (Erickson et al., 2003, 2004), and this crab is the primary folivore of *R. mangle* leaves in the field (Feller and Chamberlain, in review). Animal matter was significantly preferred over plant matter. This study provides experimental evidence supporting other observations that *A. pisonii* will feed opportunistically when animal resources become available (Beever et al., 1979; Diaz and Conde, 1988; Brogim and Lana, 1997; Erickson et al., 2003). *A. pisonii* has been known to feed on insects, gastropods, dead fish, and crabs of their own and other species (Beever et al., 1979; Diaz and Conde, 1988; Brogim and Lana, 1997; Erickson et al., 2003). Preliminary work done on carbon stable isotopes in Belize mangrove systems has determined that the dietary signature of *A. pisonii* is of mixed influence (insects and algal/cyanobacterial mats) (M. Fogel, D. Akob, pers. comm., 2001). Supplemental feeding on animal matter has been documented through observational or experimental studies for many other mangrove and salt marsh crabs, such as *Armases cinereum*, *Cardisoma carnifex*, *Chiromanthes onychophorum*, *Neosarmatium meinerti*, *Neosarmatium smithii*, *Selatium elonagtum*, *Parasesarma leptosoma*, and *Perisesarma guttatum* (Malley, 1978; Giddins et al., 1986; Dahdouh-Guebas et al., 1997, 1999; Buck et al., 2003; Thongtham and Kristensen, 2005), as well as other marine herbivores such as sea urchins (McClintock et al., 1982) and amphipods (Cruz-Rivera and Hay, 2000a,b, 2001).

Differences in feeding preferences between sexes could be expected due to sexual dimorphism in chelae size or differential energy and reproductive requirements (Cannicci et al., 1996; Buck et al., 2003). Dimorphism in crab claw size has allowed males to feed on a wider variety of food items (Kyomo, 1992; Brousseau et al., 2001; Buck et al., 2003). Adult *A. pisonii* males tend to have larger club-shaped chelae (Warner, 1979), which may allow greater ability and force with which to grasp food items, and possibly greater breadth in diet as well. Erickson et al. (2003) demonstrated that the male diet of *A. pisonii* is more variable with respect to leaves of different mangrove species but did not address other food types. The female diet may be constrained by energetic requirements or physical location within mangrove habitat that are necessary to maximize fitness. However, in Florida and Belize, there was no difference in preference between males and females. No difference in feeding between sexes also has been found for other marine crabs (Cannicci et al., 1996; Sukumaran and Neelakantan, 1997; Fratini et al., 2000).

Artificial feeding assays, where non-polar and polar food extracts were incorporated into an artificial diet, corroborated feeding preferences from multiple-choice feeding assays and supported the role of chemical composition in food selection. Assays demonstrated that animal extracts stimulated feeding while extract from live *R. mangle* leaves failed to do so. Experimental studies using artificial diets with protein also demonstrated stimulation of feeding by *A. cinereum* (Pennings et al., 1998). The fact that *A. pisonii* preferred animal matter over other resources is not necessarily surprising given that animal matter is significantly higher than plant matter in nitrogen and protein, which are both important for crab growth and reproduction (Wolcott and Wolcott, 1987). Protein in marine animal matter can be as high as 50% dry weight (Duffy and Paul, 1992). For plant matter to be nutritious to marine invertebrates, it needs to have a C:N ratio equal to or less than 17:1 (Russell-Hunter, 1970); however, live *R. mangle* leaves in Tampa Bay, Florida have an average C:N ratio of 38:1, with as little as 1–1.5% nitrogen and 7–8% protein per dry weight (Erickson et al., 2004). Other studies throughout the neotropics have reported similar values for *R. mangle* (Conde et al., 1995; Feller, 1995; Fry et al., 2000). While proteins probably were confined to polar extracts, greater differences were observed among food with non-polar extracts, suggesting these extracts may play more of a crucial role in food selection (Kanazawa, 2001; Sheen and Wu, 2003). Chemical constituents in non-polar extracts include fatty acids, triglycerides, and sterols, which have received significantly less attention than protein in feeding and nutritional studies of marine invertebrates. Experimental feeding assays should be conducted to determine the extent to which these constituents influence feeding preferences, as well as growth, survivorship, and reproduction. Studies on marine crustaceans have demonstrated superior growth when grown on animal versus plant matter (Cruz-Rivera and Hay, 2000a; Buck et al., 2003); however, studies also have yielded species-specific results as far as survivorship and fitness (Cruz-Rivera and Hay, 2000a,b). Alternatively, non-polar extracts of *R. mangle* may have been avoided if they contain feeding deterrents that are lacking in animal tissue, such as terpenes, whose role in mangrove defence have gone virtually unnoticed. *Rhizophora mangle* leaves contain a variety of compounds associated with non-polar extracts, including: n-alkanes, n-alkanoic acids, wax ester acids, hydroxyacids, triterpenones, pentacyclic triterpenoids, and various sterols (Killops and Frewin, 1994; Williams, 1999). Two such compounds, taraxerol and cinnamoyl-lupeol, have demonstrated significant insecticidal activity against agricultural pests (Williams, 1999), therefore having the potential to alter feeding by herbivores in natural systems.

Based on these crab feeding preferences, optimal foraging theory would predict that animal matter would be consumed most in the field (Schoener, 1971); however, this is not the case. In the feeding assays conducted in this study, adult crabs were offered dead prey as food. While *A. pisonii* are highly mobile, it is possible that they only feed on animal matter when it is easy to obtain or catch. The fact that more animal matter was not found in crabs guts (Erickson et al., 2003) could relate to the difficulty in catching mobile insects as well as associated energy costs. It also could relate to the fact that animal matter tends to digest more quickly than plant matter (Williams, 1981).

Other food items also were high or intermediate in preference. For instance, root algae were highly preferred in Belize but not in Florida. Algal root communities in Florida are not developed to the same extent as they are in Belize. Mangrove tree crabs spend a significant amount of time crawling among roots especially at receding, low, and incoming tides (Erickson, pers. obs.). Algae likely are of greater nutritional value than mangrove leaves. Other mangrove crabs that frequently consume root algae along with mangrove leaves are *Metopograpsus* spp. (Dahdouh-Guebas et al., 1999; Fratini et al., 2000). In Florida, artificial assays demonstrated that algae, *R. mangle* fruit, and live leaves were similar in palatability. At the same time, in Belize, *R. mangle* fruit, live leaves, and detritus were of similar palatability. In Florida, detritus was of intermediate palatability, but detritus was of low palatability in Belize. It is not surprising that detrital leaves were fed upon more than live leaves. Aging of leaves may increase nitrogen content through bacterial or fungal growth or it may increase digestibility through the leaching of tannins (Neilson et al., 1986). Litter-feeding crabs from the paleotropics have been suggested to cache leaves in burrows to age them, thus reducing tannins and increasing nitrogen content (Giddins et al., 1986); however, this theory was disproved by Skov and Hartnoll (2002), who demonstrated no difference in carbon, nitrogen, and C/N ratio between cached and freshly fallen senescent leaves.

One discrepancy from this study between whole food and artificial assays was found for detrital *R. mangle* leaves. While they were fed upon readily in whole food assays, food with non-polar extract was fed upon the least in artificial assays. The fact that chemical composition failed to support feeding on detrital leaves suggests that some other quality may be responsible for feeding on detrital leaves, such as toughness or water content. For instance, plant toughness was shown to correlate negatively with leaf damage by *A. pisonii* (Erickson et al., 2004) and to be a major determinant of feeding preferences by the salt marsh crab *A. cinereum* and the opisthobranch gastropod *Dolabella auricularia* (Pennings and Paul, 1992; Pennings et al., 1998). In addition, feeding preferences documented in this study may have resulted based on the decision to use specific organisms as food resources and results may have been different if other animal or algal species had been used.

While crabs feed significantly on *R. mangle*, the extent to which they feed on animal matter in the field is unknown. Given significant feeding on these leaves and the opportunistic feeding behaviour of *A. pisonii*, we expected that a mixed diet would be fed upon more than single diets where extracts of either plant or animal matter were incorporated into artificial food. However, a single diet where non-polar extract of animal matter was incorporated into artificial food was fed upon most across locations and sexes, which suggests that something other than protein is important. Between 25–50% of non-polar animal extract increased feeding. Polar extracts did not necessarily support the same pattern or show the same magnitude of differences among the mixed diets. Based on these results, it cannot be determined whether there are basic dietary requirements present in *R. mangle* leaves or whether mixed diets of both animal and plant matter would yield greater growth, survival, and fitness. Mixed diets with complementary resources have been consumed in the field or preferred in experimental trials by other marine organisms, such as crustaceans, gastropods, and fish, beyond single diets of either plant or animal matter (Lobel and Ogden, 1981; Pennings et al., 1993; Cruz-Rivera and Hay, 2000a,b, 2001; Buck et al., 2003; Hall et al., 2006). While mixed diets tend to increase growth, evidence suggests they may be of limited benefit to survivorship and reproduction of some amphipod species (Pennings et al., 1993; Cruz-Rivera and Hay, 2000a,b, 2001; Buck et al., 2003).

So why does *A. pisonii* feed so heavily on *R. mangle* leaves in the field? As *R. mangle* is a nutritionally poor food source (based on nitrogen and protein) that is relatively unpalatable in feeding assays, it may be fed upon because it is a readily available and highly abundant food source. Feeding behaviour in the field suggests that crabs may be using compensatory feeding, consuming greater amounts of *R. mangle* leaf material than expected given its nutritional value. Compensatory feeding has been observed for other herbivorous and omnivorous crustaceans (copepods, amphipods, crabs), sea urchins, and fish (Stachowicz and Hay, 1996, 1999; Poore and Steinberg, 1999; Cruz-Rivera and Hay, 2000a, 2001, 2003; Valentine and Heck, 2001; Thongtham and Kristensen, 2005; Prince et al., 2006). However, effects of compensatory feeding on growth, survivorship, and fitness have been species-specific in the above studies, demonstrating that it may not always be an effective feeding strategy. Further, to determine whether this is actually occurring, no-choice experiments need to be performed in conjunction with multiple-choice ones to demonstrate increased consumption when *R. mangle* is the only food choice available.

Another possibility, rather than compensatory feeding, is that these crabs are capable of breaking down metabolites of significant concentration that may be nutritionally unavailable or toxic. Many invertebrate herbivores harbour gut symbionts, including bacteria or fungi, which contribute enzymes, further breaking down food and making it more available for absorption (Gulmann and Mullineaux, 2001; Zimmer et al., 2001; Kimura et al., 2002). Red mangrove leaves have high concentrations of condensed tannins (which often range between 20–40% dry weight) (Hernes et al., 2001; Erickson et al., 2004). While these tannins do not deter feeding by this crab, tannins have the ability to reduce digestion of protein by binding to it (Hagerman et al., 1992). *Aratus pisonii* has been shown to have significant gut populations of trichomycete fungi in Tampa Bay, Florida, populations (Mattson, 1988); however, it is unknown how prevalent these fungi are in *A. pisonii* and whether they influence digestion, absorption, or availability of resources.

A third possibility is that while high levels of feeding on *R. mangle* are not correlated to nitrogen or protein (Erickson et al., 2004), feeding on leaves may be related to other constituents such as amino or fatty acids and lipids (Harrsion, 1990; Jonasdottir, 1994). For instance, lipid concentration has been shown to be important to copepod egg production (Giese, 1966). Hall et al. (2006) demonstrated significant uptake and tissue incorporation of fatty acids by the mangrove crab *Parasesarma erythodactyla* through a series of feeding trials that alternated feeding and starvation. The authors also suggest that the crabs are capable of synthesizing and storing highly unsaturated fatty acids de novo from chemical precursors in mangrove leaves. Given this example, it is possible that *A. pisonii* also produces similar fatty acids and derives a significant amount of nutrition from the leaves. Meziane et al. (2006) demonstrated fatty acid signatures representing either mangrove or microbial origin in the mangrove crab *P. erythodactyla*; they also suggested that crabs may selectively feed on the microbial community of mangrove leaves, rendering consumption of leaf material merely as incidental. Silliman and Newell (2003) also document that salt marsh snails (*Littoraria irrorata*) found on live rather than detrital *Spartina alterniflora* feed within and around self-created wounds made by their radulae. Interestingly, this same behaviour has been observed by *A. pisonii* (Erickson et al., in preparation); in feeding trials, *A. pisonii* selectively fed 70% of the time in and adjacent to wounds that they previously created on live *R. mangle* leaves. Thus, it appears that these crabs may be able to promote the generation of more abundant and nutritious microbial resources for their consumption.

It also is possible that factors unrelated to nutrition constrain feeding preferences. For instance, high levels of feeding on mangrove leaves may relate to the crabs' proximity to the shoreline. *A. pisonii* releases fertilized eggs at new and full moon into the water column, where larval stages develop as plankton before emerging as juveniles into the mangroves (Warner, 1967). In addition, *A. pisonii* may feed on a less than optimal food (*R. mangle* leaves) as this may provide a refuge from predation. Predators, such as birds and raccoons may have difficulty moving through the prop roots of *R. mangle* allowing crabs time to escape up to the canopy. Use of associational defences has been demonstrated by other small herbivores (Duffy and Hay, 1994; Poore and Steinberg, 1999; Stachowicz and Hay, 1999; Cruz-Rivera and Hay, 2000a). However, *A. pisonii* is fairly mobile and does not restrict itself completely to *R. mangle*. The crabs have been seen in high number resting on the black mangrove *Avicennia germinans*, of which they consume very little leaf material (Erickson et al., 2004). It also has been suggested that *A. pisonii* feeds predominantly at night (Warner, 1977), thus avoiding diurnal predators that rely on visual cues. This behaviour has been observed by other small marine herbivores that may be susceptible to predation if moving about to acquire a mixed diet (Rogers et al., 1998).

In conclusion, more studies need to be conducted that examine how single and mixed diets, as well as individual nutritional characteristics, influence crab growth, survival, and fitness. Bioassay-guided fractionation will aid in identifying chemical constituents responsible for stimulating feeding by *A. pisonii*. Finally, efforts should be made to identify the extent to which crabs actually consume animal matter and to which dietary mixing or compensatory feeding occurs in the field. Techniques including stable isotope analyses (Bouillon et al., 2004) as well as fatty acid tracers (Jonasdottir, 1994; Hall et al., 2006) should facilitate a better understanding of feeding preferences as well as trophic dynamics. These studies should help to identify nutritional requirements of an abundant mangrove crab and aid in understanding the true diet of *A. pisonii* and its trophic significance in mangrove food webs. Through studying trophic relationships, a greater understanding of mangrove ecosystem function can be gained.

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References

Barile, P.J., Lapointe, B.E., Capo, T.R., 2004. Dietary nitrogen availability in macroalgae enhances growth of the sea hare *Aplysia californica* (Opisthobranchia: Anaspidea). J. Exp. Mar. Biol. Ecol. 303, 65–78.

Beever, J.W., Simberloff, D., King, L., 1979. Herbivory and predation by the mangrove tree crab *Aratus pisonii*. Oecologia 43, 317–328.

Bouillon, S., Moens, T., Overmeer, I., Koedam, N., Dehairs, F., 2004. Resource utilization patterns of epifauna from mangrove forests with contrasting inputs of local versus imported organic matter. Mar. Ecol., Prog. Ser. 278, 77–88.

Brogim, R.A., Lana, P.C., 1997. Feeding habits of *Aratus pisonii*, *Chasmagnathus granulata*, and *Sesarma rectum* (Decapoda, Grapsidae) in a Mangrove of Paranagua Bay, Parana. Iheringia, Ser. Zool. 83, 35–43.

Brousseau, D.J., Filipowicz, A., Baglivo, J.A., 2001. Laboratory investigations of the effects of predator sex and size on prey selection by the Asian crab, *Hemigrapsus sanguineus*. J. Exp. Mar. Biol. Ecol. 262, 199–210.

Buck, T.L., Breed, G.A., Pennings, S.C., Chase, M.E., Zimmer, M., Carefoot, T.H., 2003. Diet choice in an omnivorous salt-marsh crab: different food types, body size, and habitat complexity. J. Exp. Mar. Biol. Ecol. 292, 103–116.

Camilleri, J., 1989. Leaf choice by crustaceans in a mangrove forest in Queensland. Mar. Biol. 102, 453–459.

Cannicci, S., Dahdouh-Guebas, F., Anyona, D., Vannini, M., 1996. Natural diets and feeding habitats of *Thalamita crenata* (Decapoda: Portunidae). J. Crustac. Biol. 16, 678–683.

Conde, J., Alarcón, C., Flores, S., Díaz, H., 1995. Nitrogen and tannins in mangrove leaves might explain interpopulation variations in the crab *Aratus pisonii*. Acta Cient. Venez. 46, 303–304.

Cruz-Rivera, E., Hay, M., 2000a. Can quantity replace quality? Food choice, compensatory feeding, and fitness of marine mesograzers. Ecology 81, 201–219.

Cruz-Rivera, E., Hay, M., 2000b. The effects of diet mixing on consumer fitness: macroalgae, epiphytes, and animal matter as food for marine amphipods. Oecologia 123, 252–264.

Cruz-Rivera, E., Hay, M., 2001. Macroalgal traits and the feeding and fitness of an herbivorous amphipod: the roles of selectivity, mixing, and compensation. Mar. Ecol., Prog. Ser. 218, 249–266.

Cruz-Rivera, E., Hay, M., 2003. Prey nutritional quality interacts with chemical defenses to affect consumer feeding and fitness. Ecol. Monogr. 73, 483–506.

Dahdouh-Guebas, F., Verneirt, M., Tack, J.F., Koedam, N., 1997. Food preferences of *Neosarmatium meinerti* de Man (Decapoda: Sesarminae) and its possible effect on the regeneration of mangroves. Hydrobiologia 347, 83–89.

Dahdouh-Guebas, F., Giuggioli, M., Oluoch, A., Vannini, M., Cannicci, S., 1999. Feeding habits of non-ocypodid crabs from two mangrove forests in Kenya. Bull. Mar. Sci. 64, 291–297.

Diaz, H., Conde, D.E., 1988. On the food sources for the mangrove tree crab *Aratus pisonii* (Brachyura: Grapsidae). Biotropica 20, 348–350.

Duffy, J.E., Hay, M.E., 1991. Food and shelter as determinants of food choice by an herbivorous marine amphipod. Ecology 72, 1286–1298.

Duffy, J.E., Hay, M.E., 1994. Herbivore resistance to seaweed chemical defense: the roles of mobility and predation risk. Ecology 75, 1304–1319.

Duffy, J.E., Paul, V.J., 1992. Prey nutritional quality and the effectiveness of chemical defenses against tropical reef fishes. Oecologia 90, 333–339.

Emmerson, W.D., McGwynne, L.E., 1992. Feeding and assimilation of mangrove leaves by the crab *Sesarma meinerti* de Man in relation to leaf-litter production in Mgazana, a warm-temperate southern African mangrove swamp. J. Exp. Mar. Biol. Ecol. 157, 41–53.

Erickson, A.A., Saltis, M., Bell, S.S., Dawes, C.J., 2003. Herbivore feeding preferences as measured by leaf damage and stomatal ingestion: a mangrove crab example. J. Exp. Mar. Biol. Ecol. 289, 123–138.

Erickson, A.A., Bell, S.S., Dawes, C.J., 2004. Does mangrove leaf chemistry help explain crab herbivory patterns? Biotropica 36, 333–343.

Feller, I.C., 1995. Effects of nutrient enrichment on growth and herbivory of dwarf red mangrove (*Rhizophora mangle*). Ecol. Monogr. 65, 477–505.

Feller, I.C., Chamberlain, A., in review. Herbivore responses to nutrient enrichment and landscape heterogeneity in a mangrove ecosystem.

Fratini, S., Cannicci, S., Vannini, M., 2000. Competition and interaction between *Neosarmatium smithi* (Crustacea, Grapsidae) and *Terebralia palustris* (Mollusca, Gastropoda) in a Kenyan mangrove. Mar. Biol. 137, 309–316.

Fratini, S., Cannicci, S., Vannini, M., 2001. Feeding clusters and olfaction in the mangrove snail *Terebralia palustris* (Linnaeus) (Potamididae: Gastropoda). J. Exp. Mar. Biol. Ecol. 261, 173–183.

Fry, B., Bern, A.L., Ross, M.S., Meeder, J.F., 2000. δ^{15}N studies of nitrogen use by the red mangrove, *Rhizophora mangle* L. in South Florida. Estuar. Coast. Shelf Sci. 50, 291–296.

Giddins, R.L., Lucas, J.S., Neilson, M.J., Richards, G.N., 1986. Feeding ecology of the mangrove crab *Neosarmatium smithii* (Crustacea: Decapoda: Sesarmidae). Mar. Ecol., Prog. Ser. 33, 147–155.

Giese, A.C., 1966. Lipids in the economy of marine invertebrates. Physiol. Rev. 46, 244–291.

Gulmann, L.K., Mullineaux, L.S., 2001. Exploring the role of gut microbiota in the fiddler crab,*Uca pugilator*. Abstr. Pap. Am. Chem. Soc. 221, U542.

Hagerman, A.E., Robbins, C.T., Weerasuriya, Y., Wilson, T.C., McArthur, C., 1992. Tannin chemistry in relation to digestion. J. Range Manag. 45, 57–62.

Hall, D., Lee, S.Y., Meziane, T., 2006. Fatty acids as trophic tracers in an experimental estuarine food chain: Tracer transfer. J. Exp. Mar. Biol. Ecol. 336, 42–53.

Harrsion, K.E., 1990. The role of nutrition in maturation, reproduction and embryonic development of decapod crustaceans: a review. J. Shellfish Res. 9, 1–28.

Hay, M.E., Stachowicz, J.J., Cruz-Rivera, E., Bullard, S., Deal, M.S., Lindquist, N., 1998. Bioassays with marine and freshwater organisms. In: Haynes, K.F., Millar, J.G. (Eds.), Methods in Chemical Ecology. . Bioassay Methods, vol. 2. Chapman and Hall, New York, NY, pp. 39–141.

Hernes, P.J., Benner, R., Cowie, G.L., Goni, M.A., Bergamaschi, B.A., Hedges, J.I., 2001. Tannin diagenesis in mangrove leaves from a tropical estuary: A novel molecular approach. Geochim. Cosmochim. Acta 65, 3109–3122.

Jonasdottir, S.H., 1994. Effects of food quality on the reproductive success of *Acartia tonsa* and *Acartia hudsonica*: laboratory observations. Mar. Biol. 121, 67–81.

Kanazawa, A., 2001. Sterols in marine invertebrates. Fish. Sci. 67, 997–1007.

Killops, S.D., Frewin, N.L., 1994. Triterpenoid diagenesis and cuticular preservation. Org. Geochem. 21, 1193–1209.

Kimura, H., Harada, K., Hara, K., Tamaki, A., 2002. Enzymatic approach to fungal association with arthropod guts: A case study for the crustacean host, *Nihonotrypaea harmandi*, and its foregut fungus, *Enteromyces callianassae*. Mar. Ecol. 23, 157–183.

Kyomo, J., 1992. Variations in the feeding habits of males and females of the crab *Sesarma intermedia*. Mar. Ecol., Prog. Ser. 83, 151–155.

Lee, S.Y., 1997. Potential trophic importance of the faecal material of the mangrove Sesarmine crab *Sesarma messa*. Mar. Ecol., Prog. Ser. 159, 275–284.

Lobel, P.S., Ogden, J.C., 1981. Foraging by the herbivorous parrotfish *Sparisoma radians*. Mar. Biol. 64, 173–183.

Lockwood, J.R., 1998. On the statistical analysis of multiple-choice feeding preference experiments. Oecologia 116, 475–481.

Malley, D.F., 1978. Degradation of mangrove leaf litter by the tropical sesarmid crab *Chiromanthes onychophorum*. Mar. Biol. 49, 377–386.

Mattson, R.A., 1988. Occurrence and abundance of eccrinaceous fungi (Trichomycetes) in brachyuran crabs from Tampa Bay, Florida. J. Crustac. Biol. 8, 20–30.

McClintock, J.B., Klinger, T.S., Lawrence, J.M., 1982. Feeding preferences of echinoids for plant and animal food models. Bull. Mar. Sci. 32, 365–369.

Meziane, T., d'Agata, F., Lee, S.Y., 2006. Fate of mangrove organic matter along a subtropical estuary: small-scale exportation and contribution to the food of crab communities. Mar. Ecol., Prog. Ser. 312, 15–27.

Micheli, F., 1993. Feeding ecology of mangrove crabs in Northeastern Australia: mangrove litter consumption by *Sesarma messa* and *Sesarma smithi*. J. Exp. Mar. Biol. Ecol. 171, 165–186.

Neilson, M.J., Giddins, R.L., Richards, G.N., 1986. Effect of tannins on the palatability of mangrove leaves to the tropical sesarminid crab *Neosarmatium smithi*. Mar. Ecol., Prog. Ser. 34, 185–186.

Nordhaus, I., Wolff, M., Diele, K., 2006. Litter processing and population food intake of the mangrove crab *Ucides cordatus* in a high intertidal forest in northern Brazil. Estuar. Coast. Shelf Sci. 67, 239–250.

Olmos, F., Silva-Silva, R., Prado, A., 2001. Breeding season diet of scarlet ibises and little blue herons in a Brazilian mangrove swamp. Waterbirds 24, 50–57.

Onuf, C.P., Teal, J.M., Valiela, I., 1977. Interactions of nutrients, plant growth, and herbivory in a mangrove ecosystem. Ecology 58, 514–526.

Pennings, S.C., Paul, V.J., 1992. Effect of plant toughness, calcification, and chemistry on herbivory by *Dolabella auricularia*. Ecology 73, 1606–1619.

Pennings, S.C., Nadeau, M.T., Paul, V.J., 1993. Selectivity and growth of the generalist herbivore *Dolabella auricularia* feeding upon complementary resources. Ecology 74, 879–890.

Pennings, S.C., Carefoot, T.H., Siska, E.L., Chase, M.E., Page, T.A., 1998. Feeding preferences of a generalist salt-marsh crab: relative importance of multiple plant traits. Ecology 79, 1968–1979.

Peterson, C.H., Renaud, P.E., 1989. Analysis of feeding preference experiments. Oecologia 80, 82–86.

Poore, A.G.B., Steinberg, P.D., 1999. Preference-performance relationships and effects of host plant choice in an herbivorous marine amphipod. Ecol. Monogr. 69, 443–464.

Prince, E.K., Lettieri, L., McCurdy, K.J., Kubanek, J., 2006. Fitness consequences for copepods feeding on a red tide dinoflagellate: deciphering the effects of nutritional value, toxicity, and feeding behavior. Oecologia 147, 479–488.

Risley, L.S., Crossley Jr., D.A., 1988. Herbivore-caused greenfall in the southern Appalachians. Ecology 69, 1118–1127.

Rogers, C.N., Williamson, J.E., Carson, D.G., Steinberg, P.D., 1998. Diel vertical movement by mesograzers on seaweeds. Mar. Ecol., Prog. Ser. 166, 301–306.

Russell-Hunter, W.D., 1970. Aquatic Productivity: an Introduction to Some Basic Aspects of Biological Oceanography and Limnology. Collier-Macmillan, London.

Schoener, T.W., 1971. Theory of feeding strategies. Annu. Rev. Ecol. Syst. 11, 369–404.

Sheen, S.S., Wu, S.W., 2003. Essential fatty acid requirements of juvenile mud crab, *Scylla serrata* (Forskal, 1775) (Decapoda, Scyllaridae). Crustaceana 75, 1387–1401.

Silliman, B.R., Newell, S.Y., 2003. Fungal farming in a snail. Proc. Natl. Acad. Sci., USA 100, 15643–15648.

Skov, M.W., Hartnoll, R.G., 2002. Paradoxical selective feeding on a low-nutrient diet: why do mangrove crabs eat leaves? Oecologia 131, 1–7.

Stachowicz, J.J., Hay, M., 1996. Facultative mutualism between an herbivorous crab and a coralline alga: advantages of eating noxious seaweeds. Oecologia 105, 377–387.

Stachowicz, J.J., Hay, M., 1999. Reduced mobility is associated with complementary feeding and increased diet breadth of marine crabs. Mar. Ecol., Prog. Ser. 188, 169–178.

Steinke, T.D., Holland, A.J., Singh, Y., 1993. Leaching losses during decomposition of mangrove leaf litter. S. Afr. J. Bot. 59, 21–25.

Sukumaran, K.K., Neelakantan, B., 1997. Food and feeding of *Portunas* (Portunas) *sanguinolentus* (Herbst) and *Portunus* (Portunus) *pelagicus* (Linnaeus) (Brachyura: Portunidae) along Karnataka coast. Indian J. Mar. Sci. 26, 35–38.

Thongtham, N., Kristensen, E., 2005. Carbon and nitrogen balance of leaf-eating sesarmid crabs (*Neoepisesarma versicolor*) offered different food sources. Estuar. Coast. Shelf Sci. 65, 213–222.

Valentine, J.F., Heck Jr., K.L., 2001. The role of leaf nitrogen content in determining turtlegrass (*Thalassia testudinum*) grazing by a generalist herbivore in the northeastern Gulf of Mexico. J. Exp. Mar. Biol. Ecol. 258, 65–86.

Warner, G.F., 1967. The life history of the mangrove tree crab, *Aratus pisonii*. J. Zool. London 153, 321–335.

Warner, G.F., 1977. The Biology of Crabs. Van Nostrand Reinhold Co., New York.

Warner, G.F., 1979. Behavior of two species of grapsid crab during intraspecific encounters. Behavior 36, 9–19.

Werry, J., Lee, S.Y., 2005. Grapsid crabs mediate link between mangrove litter production and estuarine planktonic food chains. Mar. Ecol., Prog. Ser. 293, 165–176.

Williams, M.J., 1981. Methods for analysis of natural diet in portunid crabs (Crustacea: Decapoda: Portunidae). J. Exp. Mar. Biol. Ecol. 52, 103–113.

Williams, L.A.D., 1999. *Rhizophora mangle* (Rhizophoraceae) triterpenoids with insecticidal activity. Naturwissenschaften 86, 450–452.

Wilson, K.A., 1989. Ecology of mangrove crabs: predation, physical factors and refuges. Bull. Mar. Sci. 44, 263–273.

Wolcott, D.L., Wolcott, T.G., 1987. Nitrogen limitation in the herbivorous land crab *Cardiosoma guanhumi*. Physiol. Zool. 60, 262–268.

Zimmer, M., Danko, J.P., Pennings, S.C., Danford, A.R., Ziegler, A., Uglow, R.F., Carefoot, T.H., 2001. Hepatopancreatic endosymbionts in coastal isopods (Crustacea: Isopoda), and their contribution to digestion. Mar. Biol. 138, 955–963.

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Diversity of Polychaeta (Annelida) and other worm taxa in mangrove habitats of Darwin Harbour, northern Australia

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Abstract

In this paper data on the diversity, distribution and abundance of polychaetes and other worm taxa in the mangroves of Darwin Harbour, northern Australia, are presented and compared with those of other tropical mangrove areas. Aspects of the feeding guild ecology and the effects of disturbance on mangrove worms are also examined. Data were collected over a period of four years, across four mangrove assemblages. Samples were obtained using three sampling techniques: 1 m × 1 m quadrat searches, epifauna searches and a new infaunal sampling technique, the anoxic mat. A total of 76 species (68 polychaetes, 1 oligochaete, 1 echiuran, 3 sipunculans, 2 nemerteans, 1 turbellarian) were recorded from the four main mangrove assemblages. Of these, 30 species are widespread, occurring in mangrove and non-mangrove habitats throughout the Indo-west Pacific. Only seven species (all polychaetes) appear to be restricted to the mangroves of Darwin Harbour and northern Australia. Polychaetes are predominant, comprising 80–96% of all worms sampled, with three families—Nereididae, Capitellidae and Spionidae—accounting for 46% of all species. The highest diversity and abundance was recorded in the soft, unconsolidated substrates of the seaward assemblage, with diversity and abundance decreasing progressively in the landward assemblages. Most of the worm fauna was infaunal (70%), but the intensive sampling regime revealed a hitherto unknown significant percentage of epifaunal species (18%) and species occurring as both infauna and epifauna (12%). Univariate analyses showed annual and seasonal differences in worm species richness and abundance—presumably associated with the intensity of the monsoon and recruitment success. The worm fauna differed between mangrove assemblages but the proportion of species in each feeding guild was relatively consistent across the four assemblages studied. Herbivores were the most species-rich and abundant, followed by carnivores and sub-surface deposit feeders. Multivariate analyses showed that the species composition of urbanised mangroves differed from that of undisturbed sites, with surface deposit feeders more numerous in urbanised habitats. Overall, the findings demonstrate a dynamic spatial and temporal variation in diversity and abundance, and provide insight on the range of microhabitats in which mangrove worms occur and their response to anthropogenic disturbance.

Keywords: Polychaete worms; Macrobenthos; Feeding guild; Disturbance; Mangroves; Australia

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1. Introduction

Invertebrate fauna surveys conducted by the senior author in the mangroves of Darwin Harbour, northern Australia between 2001 and 2005 yielded a considerable

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amount of data on the distribution, diversity and abundance of macro-invertebrates (Metcalfe, 2004, 2005, 2007). Crustaceans, molluscs and worms (mainly polychaetes) were the most species-rich groups sampled during these surveys. This study presents the results for the worm fauna, including diversity, abundance and distribution, within the four main mangrove assemblages (hinterland margin, tidal flat, tidal creek and seaward). Although worms comprise an ecologically important element of the macro-invertebrate fauna of mangroves (e.g. Hutchings and Recher, 1982), they have been relatively poorly studied or neglected (e.g. MacIntosh et al., 2002). Previous studies in tropical Australia include those of Wells (1983), who found 15 and 12 polychaete species (and one flatworm in each) in *Avicennia* and *Rhizophora* assemblages respectively in North-west Cape, Western Australia; Hanley (1985), who listed nine polychaete species from mangroves at several sites in the Northern Territory; and Dittmann (2001), who found 19 species of polychaetes and a couple of oligochaetes at Missionary Bay, north Queensland.

The worm fauna of other tropical Indo-west Pacific mangroves has been documented in several studies including Sasekumar (1974), Frith et al. (1976), Kumar (1995), and Guerreiro et al. (1996). All showed a diverse and abundant polychaete fauna, especially in more seaward parts of the mangroves (also true for Australian mangroves, e.g. Wells, 1983; Hanley, 1985). Kumar (1995) reported higher faunal diversity during pre-and post-monsoon months compared to the monsoon months of June and July. Frith et al. (1976) found ‘a distinct and characteristic mangrove fauna’ dominated by molluscs, crustaceans and polychaetes in Phuket, Thailand. Several other studies have examined the worm fauna of mudflats immediately adjacent to mangrove areas (e.g. Hsieh, 1995; Dittmann, 2002; López et al., 2002). Although these areas may support a similar worm fauna, the habitat is sufficiently different—especially in terms of insolation, exposure to currents, and degree of inundation—that a comparison of species composition and abundance would not be useful. A few studies have attempted to compile the invertebrate mangrove fauna of entire regions (e.g. Saenger et al., 1978; Hutchings and Recher, 1982; Kumar, 2003), but they are also not comparable with this study because of the taxonomic inconsistency between source studies.

Polychaetes in general are good subjects for research on the impacts of anthropogenic disturbance (reviewed by Giangrande et al., 2005), because of their highly diverse range of feeding and reproductive strategies, which give them different potentials for responding to disturbance. The use of worm feeding guilds as indicators of ecological change was first proposed by Fauchald and Jumars (1979) and recently examined in the context of environmental assessment by Pagliosa (2005). This study represents an opportunity to further examine the relationship between feeding guild and anthropogenic disturbance, in this case potential differences between disturbed and undisturbed mangrove habitats. It is based on two data sets from Darwin Harbour: a one-year survey in 2001 of three relatively pristine mangrove sites and four sites affected directly or indirectly by anthropogenic disturbance (Metcalfe, 2007); and a three-year study (2003–2005) of six mangrove sites—including two of the three sites in the 2001 study—which was part of a mangrove monitoring program examining invertebrate biodiversity (Metcalfe, 2004, 2005). Collectively these data were compared with specimen records in the database of the Museum and Art Gallery of the Northern Territory (NTM)—built from various baseline surveys and environmental assessment projects—and an annotated list of polychaete and other worm species was compiled. Where possible, the feeding guild, ecology and distribution of each species in the wider context of the tropical Indo-Pacific region were recorded.

The specific aims of the study were:

1. To describe the spatial and temporal changes in the diversity and abundance of worm fauna in mangrove habitats of Darwin Harbour;
2. To test for the effects of anthropogenic disturbance on diversity, abundance and trophic composition;
3. To compare the diversity of worm fauna of Darwin Harbour with that of other tropical mangrove regions in northern Australia and the wider Indo-Pacific and assess the level of endemism.

2. Study area

All data were collected within Darwin Harbour, situated on the north-western coastline of the Northern Territory between latitudes 12°20′ and 12°40′ S and longitudes 130°45′ and 131°05′ E. Darwin Harbour is bounded to the west and east by Charles Point and East Point, respectively, and contains ~ 20400 ha of healthy and relatively intact mangrove and saltflat habitat—representing one of the largest tracts of mangroves in the Northern Territory (Fig. 1).

Darwin's climate is tropical, seasonally humid, with mean annual temperature of 28 °C and 54% relative humidity. Annual rainfall is ~ 1713 mm, with wet summer monsoon and dry winter seasons (Bureau of Meteorology, 2006). The region is macrotidal, with a maximum tidal range of 7.8 m and strong bi-directional tidal velocities. Tides are diurnal (two per day) with a

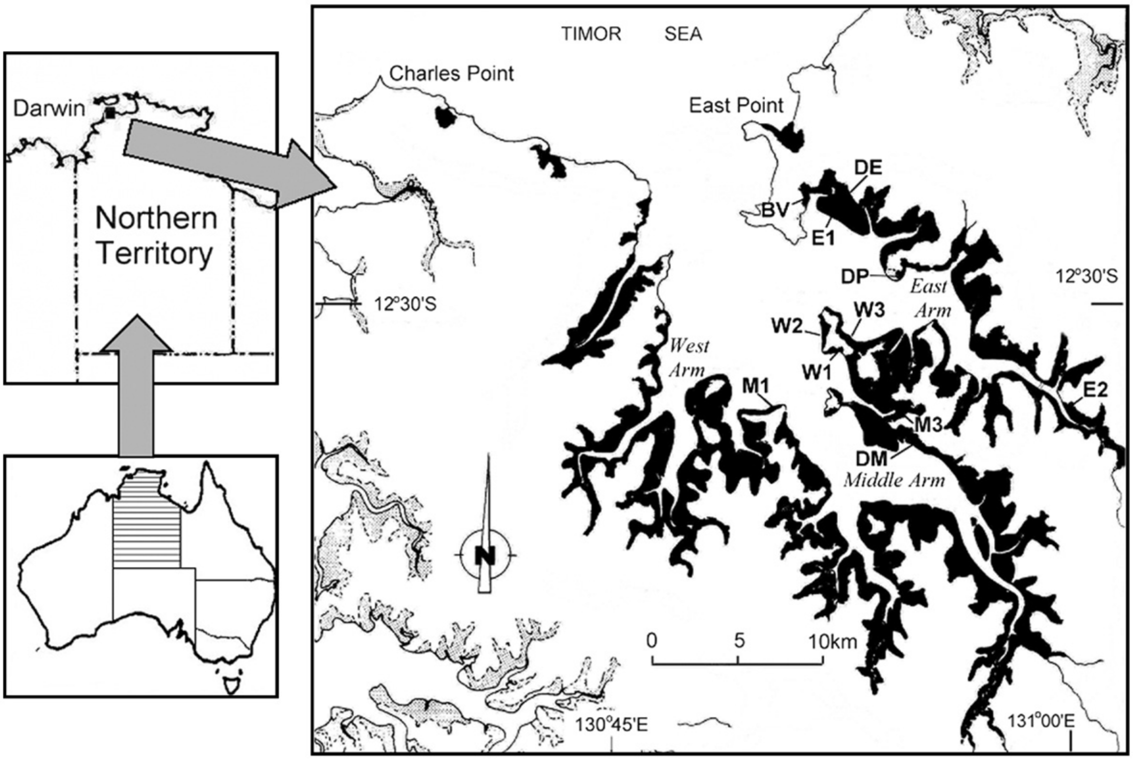

Fig. 1. Map showing location of Darwin in the Northern Territory, Australia (left) and the distribution of mangroves (shaded in black) within Darwin Harbour (right). The seven study sites (E1, E2, M1, M3, W1, W2 and W3) and four disturbed sites (BV, DE, DP and DM) are indicated.

mean spring range of 5.5 m and mean neap range of 1.9 m (Woodroffe, 1995). Despite strong tidal currents, the Darwin Harbour estuary is relatively poorly flushed (Williams et al., 2006), which contributes to characteristically high turbidity levels, particularly during the wet season. Mangrove substrates generally comprise root-structured and bioturbated mud and muddy sands with fine-grained, unconsolidated marine muds in the seaward assemblages (Semeniuk, 1985).

Over 30 species of mangrove are known from the Darwin area, with 21 shrub and tree species commonly occurring in the intertidal zone (Wightman, 1989). Collectively they form dense mangrove forests that comprise a number of distinct habitats, indicated by a predictable pattern of species distribution—each of the major floristic assemblages are confined to discrete elevation ranges (Semeniuk, 1985; Woodroffe and Bardsley, 1987; Metcalfe, 1999). Four of the ten assemblages recognised in Darwin Harbour (Brocklehurst and Edmeades, 1996) occupy 88.2% of the total mangrove area (Fig. 2). The tidal flooding regime and the seasonality of the climate are primary factors influencing the distribution and extent of mangroves in Darwin Harbour (Woodroffe and Bardsley, 1987).

At around mean sea level, open woodlands with *Sonneratia alba* occur in soft, unconsolidated substrates. Further landward, tall *Rhizophora stylosa* forests occur between ~ 0.5 and 2 m Australian Height Datum (AHD). These two assemblages occupy the lower intertidal zone of the mangrove and are largely shaped by marine processes—including wave action, tidal currents and two high tides per day. Only 58% of annual tides exceed 2 m AHD, however, and assemblages in the upper intertidal zone are inundated only by spring tides, for one week of every fortnight (Metcalfe, 1999). The landward assemblages are thus more influenced by terrestrial rather than marine processes, including freshwater seepage, seasonal deposition of sediments and desiccation. Dense, low (2 to 4 m high) thickets of *Ceriops australis* occur in this habitat, partly in response to increasing soil salinities.

3. Methods

3.1. Sampling

Sampling for the 2001 study was conducted at three undisturbed mangrove sites (E1, E2 and M3) during wet

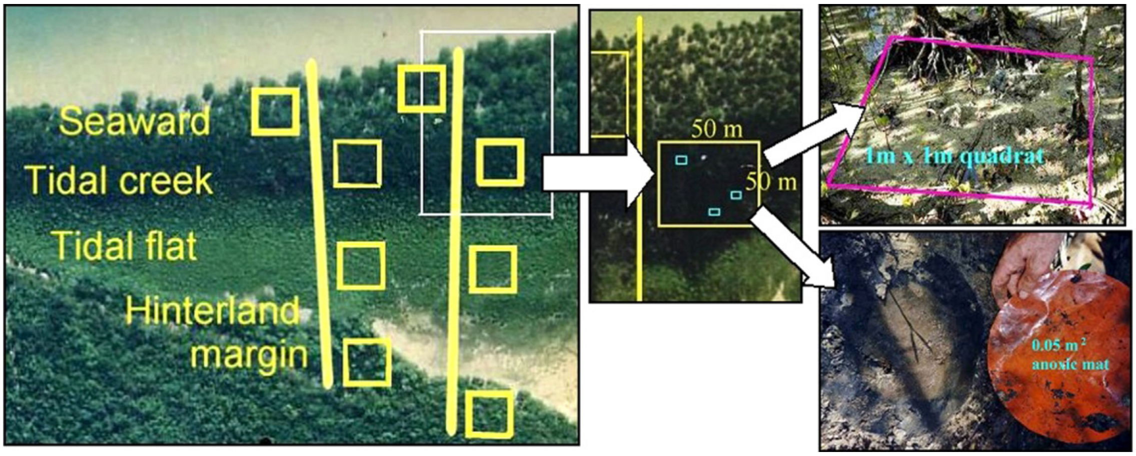

Fig. 2. Permanent study plots were placed within the four assemblages on paired transects from the landward to seaward margin (left). Sampling was conducted at three randomly placed subplots within each study plot (middle) using quadrats and anoxic mats (right).

and dry seasons, and at four disturbed mangrove sites (BV, DE, DP and DM) during the dry season of the same year. Disturbed sites were located adjacent to the Bayview housing development situated on 103 ha of reclaimed mangroves (site BV), on bulldozed tracks through relatively pristine mangroves (site DE), adjacent to the Darwin Port precinct, a major industrial port development (site DP), and adjacent to an earthen channel for a prawn farm in Middle Arm (site DM). Sampling for the three-year monitoring program (2003–2005) was done at six sites (W1, W2, W3, E1, M3 and M1) during the wet and dry seasons (Fig. 1).

At each site, transects traversing each of the four main assemblages were established from the landward to seaward margin of the mangroves, viz. hinterland margin, tidal flat, tidal creek and seaward (Fig. 2). Transect length varied between ~ 350 and 1500 m and along each transect, one permanent study plot was established in each assemblage (Fig. 2). Study plots for the 2001 study were 50 m × 50 m in size and two transects were established at each site. For the monitoring study, study plots were 20 m × 20 m in size and one transect was established per site. In all other respects, the methodology for both studies was identical.

Worms were sampled from four distinct micro-habitats: (i) on the mud surface, (ii) within the substrate, (iii) on the surface of tree trunks, roots and rocks, and (iv) within rotting logs. Worms in the first two micro-habitats were considered infauna and those in the latter two, epifauna. Within each 0.25 ha or 0.04 ha study plot, three randomly selected sampling stations were located at which one pitfall trap, one 0.05 m^2 'anoxic mat' and one 1m × 1m quadrat were used. The quadrat was placed against the tree nearest to the point designated by random number co-ordinates. Active searches of the quadrat and all surfaces of the tree to a height of 2 m (including roots and foliage) were conducted and quadrats were also dug to a depth of ~ 5–10 cm.

The anoxic mat comprised a plastic disc that temporarily created a localised area of anoxic mud. It was placed flat on the mud surface, covered with a mound of mud to maintain anoxic conditions and left for up to 24 h. The following day the mat was peeled back and specimens collected, by eye, from the mud surface. The mud beneath the mat was also searched, by digging with a trowel to a depth of approximately 5 cm. The technique was very effective at capturing small polychaetes overlooked by other methods, but possibly under-sampled taxa having a high tolerance of anaerobic conditions (e.g. some oligochaetes); the effectiveness of the anoxic mat compared to other benthic sampling devices is described elsewhere (Metcalfe, 2007). All specimens sampled were preserved in 70% ethanol, and lodged with the NTM for identification (references specimens were registered with the NTM).

3.2. Analyses

Specimens identified to genus or species levels were included in statistical analyses and species tallies. Specimens identified only to family (usually because they were in poor condition) or phylum level (lack of taxonomic expertise) were omitted from the analyses, unless they represented the only member of that family, or phylum. Thus 98 of the total of 1026 specimen records obtained during all surveys were omitted. Each of the analysed taxa was assigned to one of 22 feeding guilds and five trophic categories—herbivore, carnivore, filter feeder, surface deposit feeder and subsurface deposit feeder [=burrower, after Fauchald and Jumars (1979) and Pagliosa (2005)]—in order to assess trophic characteristics of the worm fauna.

For the three-year study, species richness and abundance data were compared between years, seasons, sites and assemblages using a 4-factor ANOVA with all factors fixed. Tests for ANOVA assumptions were run prior to the analysis, by examination of normal plots of within-cell residuals and plots of means versus standard deviations, before and after transformation. Abundance data was transformed ($\log_{10}(x+1)$) but transformation was not necessary for species richness data. Analyses were conducted using either *Statistica* or the General Linear Model in *Minitab*. By convention, significance levels were set at $p<0.05$.

All comparisons of disturbed and undisturbed mangroves were based on the dry season survey of 2001. The sampling effort for that survey was double that for surveys in 2003–2005, as paired transects were sampled at each location. ANOVA for species richness, abundance and feeding guild data involved 4-factor, nested analyses with the factors disturbance, location, transect and assemblage, in which all factors were fixed except transect, which was random and nested in location and disturbance.

The two data sets from undisturbed sites were merged for multivariate analyses, to permit examination of community data spanning four years. Ordination by non-metric multi-dimensional scaling (nMDS) procedures in *PRIMER* (Clarke and Warwick, 1994; Clarke and Gorley, 2001) was used to examine community patterns in worm diversity and abundance, and for comparison of disturbed and undisturbed sites. Ordinations were generated using Bray Curtis dissimilarity on untransformed data after 50 random restarts.

4. Results

A total of 216 records were obtained for worms during three surveys in 2001 (one wet season, two dry seasons) and 810 records for the three-year survey of six sites (three wet and three dry seasons).

4.1. Diversity, distribution and habitat

The two data sets yielded a total of 76 species of worms from mangrove habitats comprising 68 polychaetes, 1 oligochaete (Annelida), 1 echiuran, 3 sipunculans, 2 nemerteans and 1 turbellarian (online table, http://www.nt.gov.au/nreta/museums/magnt/collectionsresearch/naturalsciences/annelids.html). In any one sample, polychaetes were predominant, comprising 80–96% of all taxa. Only one species, *Mastobranchus* sp., previously reported from Darwin Harbour mangroves was not recollected in this study. Seven species appear to be restricted to mangrove habitats of Darwin Harbour and northern Australia – the polynoid *Lepidonotus* sp. 1, three capitellids (*Heteromastus* sp. 1, sp. 2 and *Mastobranchus* sp.) and three nereidids (*Ceratonereis* sp. NTM6742, *Namalycastis nicolea* and *Paraleonnates bolus*). Thirty-three species occur in mangrove and non-mangrove habitats throughout the Indo-West Pacific; the remainder are too poorly known taxonomically for distributions to be analysed.

In terms of microhabitat, the majority of species are infaunal (70%), but a substantial portion also occurs as epifauna (18%) and about 12% of species occur as both (http://www.nt.gov.au/nreta/museums/magnt/collectionsresearch/naturalsciences/annelids.html). Most species avoided the sediment surface, the exceptions being the large nereidid *Paraleonnates bolus* and the phyllodocid *Phyllodoce* sp., which mostly was collected in pitfall traps. Epifaunal species mostly occurred under the bark of mangrove trees, but also in fallen timber. Particularly productive microhabitats were beneath the large flakes of bark on the lower trunks of *Sonneratia alba* in the seaward assemblage and within rotting, burrow-structured roots and limbs of *Rhizophora stylosa* in the tidal creek assemblage. Certain species including *Lepidonotus* sp. 1, *Neanthes* cf. *biseriata* and *Perinereis singaporiensis* were almost exclusively sampled from the trunks of *Sonneratia alba*.

4.2. Species richness and abundance

Within the mangroves, the overall species richness and abundance of worms at the six sites sampled during

Table 1
Mean species richness and abundance of worms per m^2 (±SE) in the four mangrove assemblages during wet and dry seasons over three years

Assemblage	Dry Season		Wet season	
	Mean species richness± SE	Mean abundance± SE	Mean species richness± SE	Mean abundance± SE
Hinterland margin	0.1±0.03	0.06±0.03	0.1±0.05	0.13±0.05
Tidal flat	0.2±0.05	0.15±0.05	0.5±0.12	0.56±0.13
Tidal creek	1.0±0.16	1.34±0.26	0.7±0.17	0.93±0.22
Seaward	3.1±0.27	6.06±0.64	1.9±0.19	3.19±0.39
TOTAL	1.1±0.12	1.92±0.24	0.83±0.09	1.20±0.14

Data from 1 × 1 m quadrats and epifaunal counts were used to calculate means.

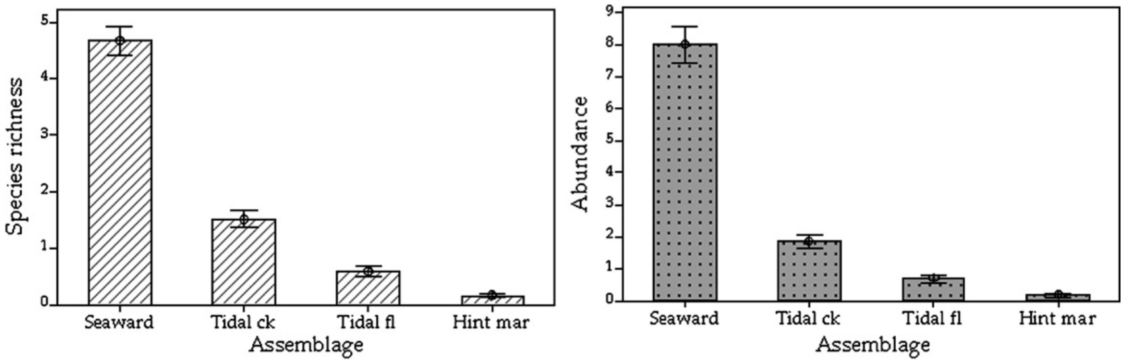

Fig. 3. Variation in mean worm species richness (left) and abundance (right) per sampling station (±SE) in the four main mangrove assemblages. Data are pooled over six sites and three years.

the three-year monitoring program were not significantly different. Also, diversity levels for each of the four assemblages were reasonably consistent between sites. However, within each site univariate analysis showed significant annual and seasonal differences in species richness and abundance between assemblages. The seaward assemblage had the highest diversity of worms, with species richness and abundance decreasing progressively to landward, with few worms sampled in the hinterland margin (Table 1; Fig. 3). This distribution pattern reflects the frequency of tidal inundation and the suitability of substrates—muds become increasingly moist and unconsolidated to seaward and the habitat opportunities for infauna increase.

Significant year × assemblage and season × assemblage interactions were also found, indicating distinct annual differences amongst assemblages and that the effects of season on diversity are dependent on assemblage. For instance, species richness is higher in the seaward assemblages in the dry season, whereas it decreases in the two landward assemblages in the dry season (Fig. 4). The mean squares indicated that the most significant factor determining worm species richness and abundance was mangrove assemblage.

Overall mean abundance decreased by almost 50% in the seaward assemblage during the wet (monsoon) season, when rainfall, erosion and wave action peak. In contrast, abundance increased in both the tidal flat and hinterland margin assemblages during the wet season Fig. 5). Worm abundance varied between years but this was determined by assemblage, as was the effect of season. Overall worm abundance showed an apparent increase from 2001 to 2005 (Fig. 5), a pattern that was mirrored by other invertebrate groups, e.g. crustaceans and molluscs (Metcalfe, 2007).

Multivariate analyses showed that mangrove assemblage is the primary determinant of species composition. nMDS ordinations indicated the strong similarity between study plots in the seaward mangrove assemblage based on the presence and abundance of worms (Fig. 6). The worm fauna of the tidal creek assemblage shows similar affinity between the different locations sampled, but there is also

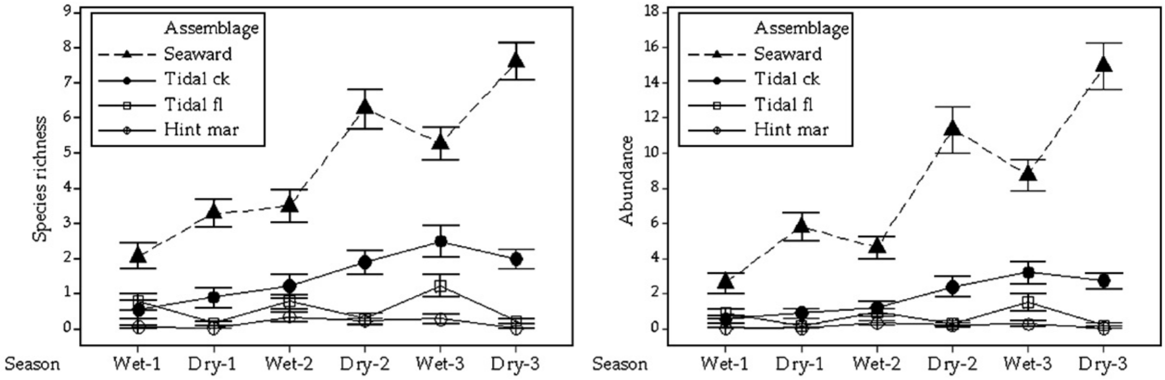

Fig. 4. Annual (and seasonal) variation in worm species richness (left) and abundance (right) in the four main assemblages. Points are means per sampling station (±SE); data are pooled over six sites.

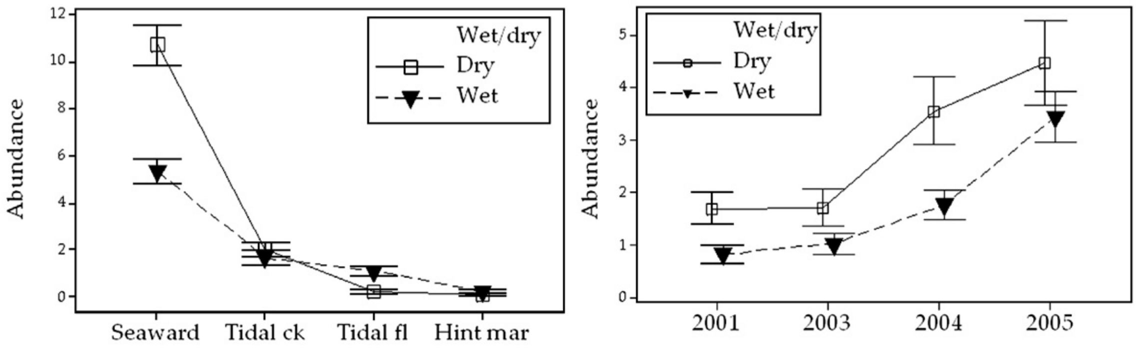

Fig. 5. Mean worm abundance (±SE) indicating seasonal and annual variation. Differences in mean abundance in the four assemblages (left) and during wet and dry season during four years of sampling (right). Points represent mean numbers of worms per sampling station, averaged over three locations (2001 data) or six locations (2003–2005 data) shown from seaward (left) to landward (right).

some overlap with study sites from both other assemblages. The tidal flat and hinterland margin assemblages have a distinct worm fauna, although not as prolific as the seaward assemblages (Fig. 6). Typical species in the hinterland margin and tidal flat are the nereidids *Namanereis malaitae* and *Paraleonnates bolus* and *Phyllodoce* sp. (Phyllodocidae). The tidal creek and seaward assemblages are characterised by a greater number of species including the ampharetid *Isolda pulchella*, the lumbrinerid *Scoletoma* sp. 1, the magelonid *Magelona* sp. 1, the nereidids *Nereis* sp. 1 and *Perinereis singaporiensis*, the orbiniid *Leitoscoloplos latibranchus* and the polynoid *Lepidonotus* sp. 1. Only two species—the nereidid polychaete *Perinereis aibuhitensis* and the sipunculan *Phascolosoma arcuatum*—occurred in all four mangrove assemblages, and both have a widespread Indo-west Pacific distribution.

Mangrove assemblage also plays a role in the frequency of occurrence of worms in different microhabitats—few species occur as epifauna in the hinterland margin and tidal flat but they are highly numerous and almost as common as infauna in the tidal creek and seaward assemblages. Typical epifaunal species include the eunicid *Nematonereis* sp., the nereidids *Ceratonereis australis*, *Neanthes* cf. *biseriata*, *Perinereis singaporiensis*, the scaleworm *Lepidonotus* sp. 1, the serpulid *Pomatoleios kraussii* and a syllid, *Syllis* sp. 1. A few infaunal species are also characteristic of the seaward assemblage including *Isolda pulchella* (Ampharetidae), the lumbrinerids *Arabelloneris broomensis* and *Scoletoma* sp. 1, *Nephtys mesobranchia* (Nephtyidae) and *Nereis* sp. 1 (Nereididae).

4.3. Feeding guild

All five trophic categories and 13 of the 22 feeding guilds were identified among the worm taxa collected in this study; filter feeders were the only trophic category not well represented (http://www.nt.gov.au/nreta/museums/magnt/collectionsresearch/naturalsciences/annelids.html). The proportion of worms per feeding guild remained relatively consistent in each of the main assemblages, with the exception of the tidal flat (*Ceriops australis*) assemblage where subsurface deposit feeders were more numerous than carnivores and herbivores. Overall, herbivores were the most numerous, with carnivores, subsurface deposit feeders and surface deposit feeders in decreasing order of abundance (Fig. 7). Although herbivores were treated together in one group in this analysis, they can be subdivided further into diatom-and macrophyte-feeders (Fauchald and Jumars, 1979). Probably the majority of herbivores in this study are of the former type (i.e., microphagous), and feed not only on diatoms, but also algae and detritus. Polychaetes are also potentially capable of breaking down whole mangrove leaves (e.g. Camilleri, 1992) so it is likely that some species would also utilise this abundant food source.

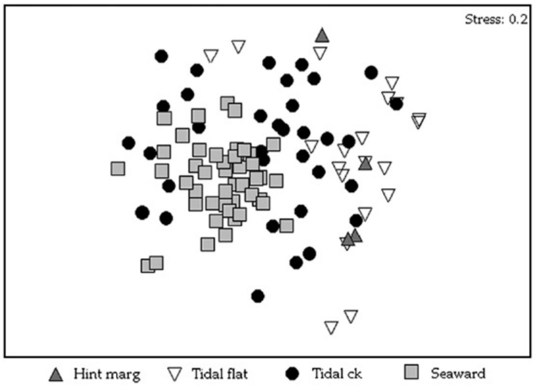

Fig. 6. nMDS ordination of 107 study plots surveyed over four years based on the abundance of 69 polychaete species indicating the similarity of study plots in different assemblages. Points represent data pooled for each sampling technique at three replicate sampling stations per study plot.

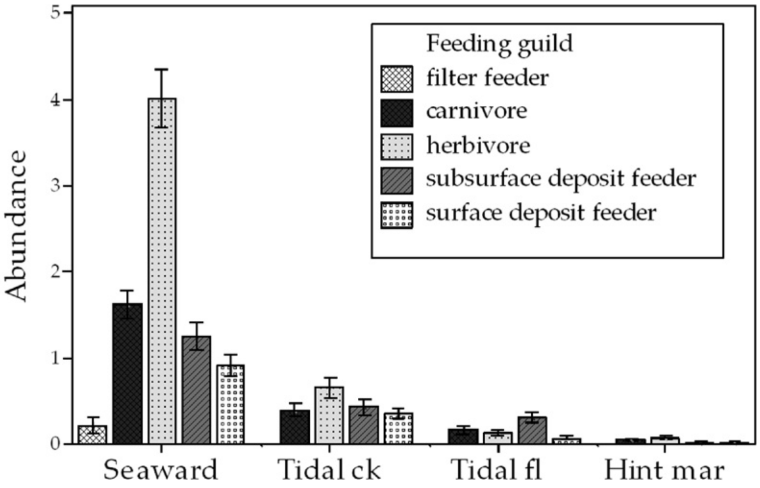

Fig. 7. Mean abundance of worms in the five main feeding guilds at six sites during 2003–2005. Means per sampling station (±SE) in the four assemblages are shown from seaward (L) to landward (R).

4.4. Fauna of disturbed mangroves

The one-year survey of three undisturbed and four disturbed sites conducted in 2001 allowed comparison of the worm faunal assemblages in mangroves directly or indirectly affected by anthropogenic development, with undisturbed sites. Although mean diversity was lower and abundance slightly higher in disturbed mangroves, univariate analyses found no significant differences in overall mean species richness and abundance between disturbed and undisturbed mangroves. A significant disturbance × assemblage interaction for worm abundance indicated that abundance in disturbed and undisturbed sites differed between assemblages. Mean worm abundance is apparently higher in disturbed sites in the tidal creek and to a lesser extent the seaward assemblage, but is apparently lower than undisturbed sites in the landward assemblages (Fig. 8).

Multivariate analyses illustrated that the worm fauna of urbanised mangroves differs somewhat from that of undisturbed sites (Fig. 9). Seventeen species, of the total of 49, were recorded only from disturbed sites. Subsequent sampling, however, spanning three years and both wet and dry seasons, revealed a wider distribution for many of those species, including undisturbed sites. Although not always exclusive to disturbed habitats, the surface deposit feeders *Aphelochaeta* sp. 1, *Leonnates stephensoni*, *Scolelepis* sp. 1, *Terebellides kowinka*, and *Terebella tantabiddycreekensis* and the herbivore (detrital) feeder, *Simplisetia* cf *erythraensis* appear characteristic of urbanised mangroves.

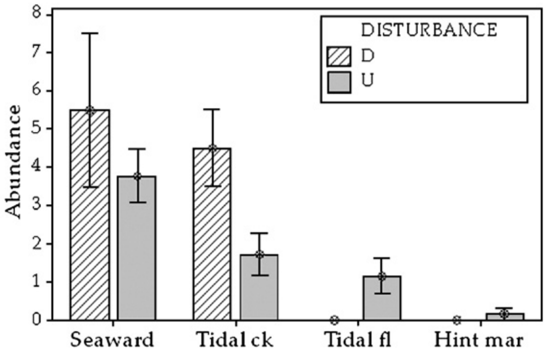

Fig. 8. Mean abundance of worms (±SE) in disturbed (D) and undisturbed (U) sites, in the four assemblages. Means are pooled across three undisturbed and two disturbed sites from one dry season survey in 2001.

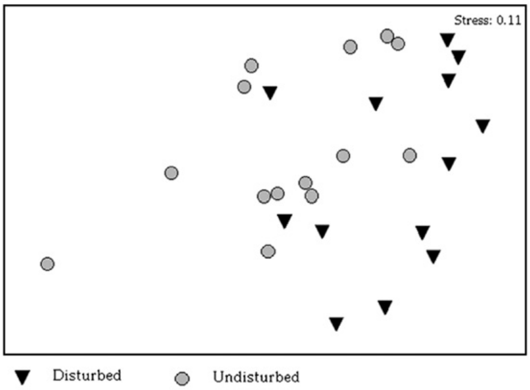

Fig. 9. Ordination of 13 disturbed and 14 undisturbed study plots based on worm taxon presence/absence. Dry season data from three replicate sampling stations were pooled for each study plot.

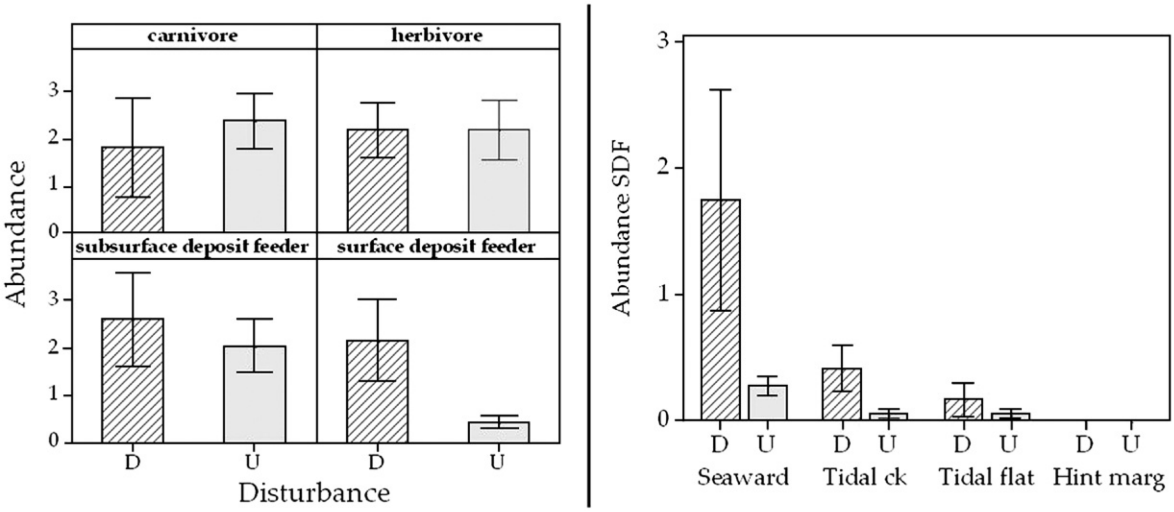

Fig. 10. Mean abundance of worms in the four main feeding guilds in disturbed (D) and undisturbed (U) mangroves (left). Means represent average abundance per sampling station, pooled across 78 disturbed and 72 undisturbed replicates. Mean abundance of surface deposit feeders (±SE) in disturbed (D) and undisturbed sites (U) in the four assemblages (right). Means are pooled for two disturbed (BV, DP) and two undisturbed sites (E2 , M3).

The abundance of worms in three of the four main feeding guilds varied little between disturbed and undisturbed sites (Fig. 10). Univariate analyses found that the abundance of surface deposit feeders differed between disturbed and undisturbed sites; this trophic group was more numerous in disturbed sites. A significant disturbance × assemblage interaction also indicated that the effects of disturbance on surface deposit feeders varied between assemblages—impacts of disturbance were most pronounced in the seaward assemblage (Fig. 10). These results were, however, based on one dry season survey during 2001 and further sampling is required to substantiate these findings.

5. Discussion

5.1. Diversity and abundance

The diverse and extensive mangrove environments of Darwin Harbour, provide habitat for a surprisingly rich worm fauna in which polychaetes predominate, comprising 80–96% of all worms sampled. Three polychaete families—Nereididae, Capitellidae and Spionidae—accounted for 46% of all species. The dominance of these three polychaete families coincides with the results of other studies of mangrove systems (Frith et al., 1976; Hutchings and Recher, 1982; Kumar, 1995). The total number of taxa reported in the study (76 species; 56 genera) is, however, far in excess of any other mangrove study in the Indo-west Pacific, but this is likely to be the result of the more extensive sampling regime over a longer period of time. Studies of one-year duration or less and those that consider only the infauna have yielded less than half the number of genera (e.g. Sasekumar, 1974; Guerreiro et al., 1996; Dittmann, 2001). Multi-year studies, therefore, are more likely to sample short-lived species (one year or less), which may be absent altogether in years following poor recruitment. The four-year period of this study was sufficient in duration to sample almost all of the polychaete species currently known from Darwin Harbour mangroves, based on literature records and polychaete specimen records (spanning over 30 years) in the database of NTM. The only species known to occur in Darwin Harbour mangroves but not sampled in this study is the capitellid, *Mastobranchus* sp., which was also reported by Hanley (1985) as *Heteromastus* sp. A; it may have a specialised habitat (tailings of mud lobster burrows).

Of the other worm taxa recorded in this study, nemerteans were also abundant (8.5% of all records) but the taxonomy of this group is poorly known and apart from the large, rarely encountered *Cerebratulus* species of the seaward zones, other species could not be identified. Sipuncula were also abundant (6.5% of all records) with most belonging to the widely distributed Indo-west Pacific estuarine species, *Phascolosoma arcuatum;* two other, possibly undescribed, species were also found in the tidal creek zone.

The spatial patterns in diversity and abundance were remarkably consistent between locations in Darwin Harbour such that the species richness and abundance of polychaetes around Darwin Harbour appear reasonably predictable—with highest diversity and abundance in the seaward mangrove assemblage, decreasing progressively to landward, with few worms sampled in the hinterland margin. This distribution pattern presumably reflects the frequency of tidal inundation and the suitability of substrates—muds become increasingly moist and unconsolidated to seaward and the habitat opportunities for epifauna increase. In addition, frequency of tidal inundation directly influences recruitment such that the more frequently inundated seaward zones have a greater potential to receive larvae, and for larvae to survive. For example, species occurring in the tidal creek assemblage (~ 1 m AHD) are inundated by 93% of annual tides, whereas those living in the tidal flat assemblage and above (> 2 m AHD) are only bathed by 58% of tides. High dry season evaporation rates in the tidal flat create hypersaline conditions which further add to the harshness of the mid- to upper-intertidal zone. Seasonal rainfall and higher tides during the wet season moderate the harsh environmental conditions in the tidal flat and the hinterland margin, which may contribute to the higher diversity and abundance observed in landward zones during the wet season. Desiccation and high salinity are likely to be important factors limiting worm populations in these habitats.

On the contrary, the levels of diversity in the seaward assemblages decreased during the wet season. Monsoonal conditions during the wet season generate swell and wave action, typically leading to erosion of surface sediment in the seaward assemblages during this period (K. Metcalfe, pers. obs.). Monsoonal conditions may drastically alter sediment characteristics, such as particle size and can exert a strong seasonal impact on the macrobenthos (Alongi and Sasekumar, 1992), especially polychaetous worms (Sarkar et al., 2005). Kumar (1995) also reported lessened faunal diversity during the monsoonal period in the mangroves of Cochin, India. Polychaetes may be seriously affected by erosion and reduced salinity (Kurian, 1984), while other phyla are not (Nandi and Choudhury, 1983 as cited in Alongi and Sasekumar (1992)). Recent research in north Queensland indicates that during intense, short-term freshwater inundations, the majority of benthic species in mudflats just seaward of mangroves are lost and do not return; a small remnant fauna remains—comprising euryhaline ‘resident’ species—which slowly recover to pre-disturbance levels (J. Sheaves, pers. comm., 2006).

The gradual increase in diversity and abundance observed during 2001 to 2005 may be a response to the impact of one or more extreme wet season events. The wet season of 2003–2004 had an above average rainfall and strong monsoonal activity, which may have contributed to lower worm diversity and abundance during that year, but 2001 values were, however, even lower than 2003. Nevertheless, the observed increase may represent gradual recovery of invertebrate populations during years in which the monsoon was more moderate. It is unlikely, given the methodological consistency that the increase is due to an artefact of sampling or improved discrimination in the field or laboratory. Determination of the factors influencing worm populations is, however, beyond the scope of this project. Forthcoming surveys may provide further insight into the long-term patterns in diversity and abundance of mangrove worms.

The higher number of subsurface deposit feeders in the tidal flat may be associated with the number of mud lobster mounds, which provide excellent habitat (soft, reworked mud) for worms. The capitellids – *Heteromastus* sp. 1, *Mediomastus* sp. 1 and *Notomastus* sp. – appear to be the main taxa responsible for this pattern. The higher number of surface deposit feeders in disturbed sites is the only significant difference detected between disturbed and undisturbed mangroves, but it was only based on one year’s sampling and therefore requires corroboration. If supported, it suggests that a shift in polychaete trophic assemblages, such as the sudden dominance of surface deposit feeders, could be a good indicator of disturbance, such as increased sedimentation.

5.2. Effect of anthropogenic disturbance

Probably the most significant type of anthropogenic disturbance to the mangroves of Darwin Harbour is associated with urbanisation. Urbanisation can affect sediment properties when runoff, currents, tidal flow and the ability of mangrove trees to capture sediments are altered (Kaly et al., 1997). By contrast, organic enrichment associated with pollution is anticipated to be relatively minor, if present, at the disturbed study sites in Darwin Harbour. Sediment properties are a primary factor determining polychaete populations, especially grain size (Alongi, 1987; Pagliosa, 2005; Sarkar et al., 2005) and silt and clay content (Hsieh, 1995). Increased populations of polychaetes at several sites and increases in the abundance of surface deposit feeders may have been related to changes in the sediment.

The findings of this study in relation to anthropogenic disturbance need to be interpreted with caution, however, as the work did not document the direct response of the worm fauna to disturbance. The faunal differences observed in disturbed sites may, to some extent, also be due to intrinsic environmental differences between sites. Substrates at the port site, for example, may naturally have been more sandy, gravely or rocky than at the undisturbed sites studied—with a specialised worm fauna that reflected this. Pre-disturbance surveys are required to eliminate such possibilities. Nevertheless, these studies have provided valuable baseline information and further research on the response of mangrove polychaetes to anthropogenic disturbance is seen as a priority for environmental assessment and management of mangrove communities in Darwin Harbour. The preliminary results obtained here suggest that of all the invertebrate groups studied in mangrove environments, polychaetes may be the most useful as key indicators of anthropogenic disturbances.

5.3. Mangrove worms: characteristic or specialised fauna?

Hutchings and Recher (1982: p. 102) point out that ‘Relatively few animals are restricted to mangroves or show specific adaptations to the mangrove environment.’ This appears to be the case for the majority of species encountered in this study. Of the 76 worm species reported in this study from Darwin Harbour mangroves, only seven (~ 10%) may be restricted to this environment. The remainder that are well enough known (at least 33 species) are also present on adjacent mudflats and channels, and other intertidal non-mangrove shallow coastal habitats in northern Australia. Several species including the polychaetes *Marphysa mossambica*, *Dendronereides heteropoda*, *Namalycastis abiuma*, *Perinereis aibuhitensis*, *Simplisetia* cf *erythraensis*, and the sipunculan, *Phascolosoma arcuatum* have been reported from other mangrove areas in northern Australia and the Indo-west Pacific and are characteristic members of the Indo-west Pacific mangrove fauna.

No previous study has identified an endemic or specialised mangrove worm fauna, perhaps because the knowledge of polychaetes and other worms (especially of the tropics) is not mature enough to know with any degree of confidence the taxonomic limits and distributions of each species. This is also true of the seven species identified here as possible endemics (http://www.nt.gov.au/nreta/museums/magnt/collectionsresearch/naturalsciences/annelids.html). Of these seven species, the three most likely to be endemics are: *Mastobranchus* sp., which appears to be confined to the mounds of the mud-lobster *Thalassina squamifera*. This species was not collected in the present study, possibly because *Thalassina* mounds were rarely sampled in the sampling strategy, which placed 1 m × 1 m quadrats against randomly selected trees. It was one of only two species found by Hanley (1985) to be exclusively associated with *Thalassina* mounds; the other one *Neanthes* sp. B (=*Perinereis aibuhitensis*) was found here to occur more widely across all mangrove assemblages both as epifauna and infauna. Another nereidid, the epifaunal *Namalycastis nicoleae*, is mainly found under the bark of *Sonneratia alba* and within fallen mangrove timber, and so far is only known from Darwin Harbour mangroves and a drainage channel of reclaimed mangroves near Brisbane (Glasby, 1999). The epifaunal scaleworm *Lepidonotus* sp. 1 also appears to be restricted to Darwin Harbour mangroves. The occurrence of endemic polychaetes in Darwin Harbour mangroves may be the result of isolation, spatial extent, floristic diversity and the habitat complexity they provide. Other mangrove specialists/endemics are known from other animal groups occurring in tropical mangroves (Hutchings and Recher, 1982: p.102).

At the generic level, a similar suite of ‘characteristic’ worm taxa exists. Polychaete genera common to both Darwin Harbour mangroves and the mangroves of other Indo-west Pacific mangroves include, the ampharetid *Amphicteis*, the nereidids *Composetia*, *Dendronereides*, *Dendronereis, Neanthes, Nereis, Perinereis and Simplisetia,* the onuphid *Diopatra,* the maldanid *Euclymene,* the glycerid, *Glycera,* the capitellids *Heteromastus and Mediomastus,* the polynoid *Lepidonotus,* the eunicid *Marphysa,* the phyllodocid *Phyllodoce,* the lumbrinerid *Scoletoma,* the spionids *Polydora, Prionospio* and the orbiniid, *Scoloplos.* The only non-polychaete worm so far reported from more than one Indo-Pacific mangrove area is the sipunculan, *Phascolosoma*, which is a genus typical of Indo-west Pacific hard substrates (Cutler and Cutler, 1990). Most of these are species-rich genera whose members occupy a wide variety of habitats globally. Thus, while these genera can be considered characteristic of mangroves, they are not mangrove specialists. The high number of genera (56) in Darwin Harbour mangroves that have not been previously reported from other Indo-west Pacific mangroves probably reflects the poor state of taxonomic knowledge of polychaetes, particularly in the tropics.

6. Conclusions

1. The diverse mangrove worm fauna of Darwin Harbour is dominated by polychaetes, especially Nereididae, Capitellidae and Spionidae.
2. The majority of species, and many genera, are characteristic of mangrove areas across the Indo-Pacific; only about 10% of species may be endemic to the mangroves of northern Australia, but further studies are required to test this hypothesis.

3. The distribution and abundance of species in Darwin Harbour mangroves was found to vary in time (between years and seasons) and space (between mangrove assemblages). High consistency was observed from site to site, however, with a reasonably predictable suite of species occurring at particular tidal elevations.
4. The microhabitats from which worms were sampled and the species composition of landward assemblages differed markedly from the seaward assemblages.
5. The seasonal pattern of increased dry season diversity and abundance to seaward is reversed to landward, where it declined in response to desiccation.
6. A different species and trophic composition between disturbed and undisturbed mangroves is also suggested by the data.
7. Herbivores are the most abundant trophic group overall, but in disturbed habitats surface deposit feeders are relatively more common.

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References

Alongi, D.M., 1987. Intertidal zonation and seasonality of meiobenthos in tropical mangrove estuaries. Mar. Biol. 95, 447–458.

Alongi, D.M., Sasekumar, A., 1992. Benthic communities. In: Robertson, A.I., Alongi, D.M. (Eds.), Tropical Mangrove Ecosystems. American Geophysical Union, Washington, DC, pp. 137–172.

Brocklehurst, P.S., Edmeades, B.F., 1996. Mangrove Survey of Darwin Harbour, Northern Territory, Australia. Land Conservation Unit, Conservation Commission of the Northern Territory, Darwin, NT.

Bureau of Meteorology, 2006. Climate averages for Station 014015 Darwin Airport, NT during the period 1941–2006, Commonwealth Bureau of Meteorology Website www.bom.gov.au. 2006.

Camilleri, J.C., 1992. Leaf-litter processing by invertebrates in a mangrove forest in Queenland. Mar. Biol. 114, 139–145.

Clarke, K.R., Gorley, R.N., 2001. Primer v5: User Manual. Plymouth Marine Laboratory.

Clarke, K.R., Warwick, R.M., 1994. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation. Plymouth Marine Laboratory, Primer-E Ltd.

Cutler, N.J., Cutler, E.B., 1990. Revision of the genus Phascolosoma (Sipuncula: Phascolosomatidae). Proc. Biol. Soc. Wash. 103, 691–730.

Dittmann, S., 2001. Abundance and distribution of small infauna in mangroves of Missionary Bay, North Queensland Australia. Rev. Biol. Trop. 49, 535–544.

Dittmann, S., 2002. Benthic fauna in tropical tidal flats of Hinchinbrook Channel, NE Australia: diversity, abundance and their spatial and temporal variation. Wetlands Ecol. Manag. 10, 323–333.

Fauchald, K., Jumars, P.A., 1979. The diet of worms: a study of polychaete feeding guilds. Oceanogr. Mar. Biol. Ann. Rev. 17, 193–284.

Frith, D.W., Tantanasiriwong, R., Bhatia, O., 1976. Zonation of macrofauna on a mangrove shore, Phuket Island. Res. Bull. - Phuket Mar. Biol. Cent. 10, 1–37.

Giangrande, A., Licciano, M., Musco, L., 2005. Polychaetes as environmental indicators revisited. Mar. Pollut. Bull. 50, 1153–1162.

Glasby, C.J., 1999. The Namanereidinae (Polychaeta: Nereididae). Part 1. Taxonomy and Phylogeny. Rec. Aust. Mus., Suppl. 25, 1–129.

Guerreiro, J., Freitas, S., Pereira, P., Paula, J., Macia Jr., A., 1996. Sediment macrobenthos of mangrove flats at Inhaca Island, Mozambique. Cah. Biol. Mar. 37, 309–327.

Hanley, J.R., 1985. Why are there so few Polychaetes (Annelida) in northern Australian mangroves? In: Bardsley, K.N., Davie, J.D.S., Woodroffe, C.D. (Eds.), Coasts and Tidal Wetlands of the Australian Monsoon Region. North Australia Research Unit, Australian National University, Darwin, NT, pp. 239–250.

Hsieh, H.-L., 1995. Spatial and temporal patterns of polychaete communities in a subtropical mangrove swamp: influences of sediment and microhabitat. Mar. Ecol. Prog. Ser. 127, 157–167.

Hutchings, P., Recher, H.F., 1982. The fauna of Australian mangroves. Proc. Linn. Soc. N. S. W. 106, 83–121.

Kaly, U.L., Eugelink, G., Roberston, A.I., 1997. Soil conditions in damaged north Queensland mangroves. Estuaries 20, 291–300.

Kumar, R.S., 1995. Macrobenthos in the mangrove ecosystem of Cochin backwaters, Kerala (southwest coast of India). Ind. J. Mar. Sci. 24, 56–61.

Kumar, R.S., 2003. A checklist of polychaete species some mangroves of Asia. Zoos' Print J. 18, 1017–1020.

Kurian, C.V., 1984. Fauna of the mangrove swamps in Cochin estuary. In: Soepadmo, E., Rao, A.N., MacIntosh, D.J. (Eds.), Proc. Asian Symp. Mangrove Environments: Research and Management. University of Malaya and UNESCO, Kuala Lumpur, pp. 226–230.

López, E., Cladera, P., San Martín, G., Laborda, A., Aguado, M.T., 2002. Polychaete assemblages inhabiting intertidal soft bottoms associated with mangrove systems in Coiba National Park (East Pacific, Panama). Wetlands Ecol. Manag. 10, 233–242.

MacIntosh, D.J., Ashton, E.C., Havanond, S., 2002. Mangrove rehabilitation and intertidal biodiversity: a study in the Ranong mangrove ecosystem, Thailand. Estuar. Coast. Shelf Sci. 55, 331–345.

Metcalfe, K., 1999. Mangrove litter production, Darwin Harbour. A study of litter fall as a measure of primary productivity in the mangrove communities of Darwin Harbour. Master of Tropical Environmental Management Thesis, Faculty of Biological and Environmental Science, Northern Territory University, 84 pp.

Metcalfe, K., 2004. Mangrove Invertebrate Fauna. Darwin LNG Project Environmental Monitoring Program, Darwin, NT. Prepared for URS Australia Pty Ltd, 55 pp.

Metcalfe, K., 2005. Mangrove Invertebrate Fauna. Darwin LNG Project Mangrove Monitoring Program, Annual Report 2004–2005. Prepared for URS Australia, 94 pp.

Metcalfe, K., 2007. The biological diversity, recovery from disturbance and rehabilitation of mangroves, Darwin Harbour, NT. Ph.D.

Thesis, Faculty of Education, Health and Science, Charles Darwin University, Darwin, Northern Territory, Australia.

Pagliosa, P.R., 2005. Another diet of worms: the applicability of polychaete feeding guilds as a useful conceptual framework and biological variable. Mar. Ecol. 26, 246–254.

Saenger, P., Specht, M.M., Specht, R.L., Chapman, V.J., 1978. Mangal and coastal salt-marsh communities in Australasia. In: Chapman, V.J. (Ed.), Ecosystems of the World. Wet Coastal Ecosystems, vol. I. Elsevier, Amsterdam, pp. 293–345.

Sarkar, S.K., Bhattacharya, S.G., Bhattacharya, B., Sarkar, D., Nayak, D.C., Chattopadhaya, A.K., 2005. Spatiotemporal variation in benthic polychaetes (Annelida) and relationships with environmental variables in a tropical estuary. Wetlands Ecol. Manag. 13, 55–67.

Sasekumar, A., 1974. Distribution of macrofauna on a Malayan mangrove shore. J. Anim. Ecol. 43, 51–69.

Semeniuk, V., 1985. Mangrove environments of Port Darwin, Northern Territory: the physical framework and habitats. J. R. Soc. West. Aust. 67, 81–97.

Wells, F.E., 1983. An analysis of marine invertebrate distributions in a mangrove swamp in northwestern Australia. Bull. Mar. Sci. 33, 736–744.

Wightman, G.M., 1989. Mangroves of the Northern Territory. Conservation Commission of the Northern Territory, Palmerston.

Williams, D., Wolanski, E., Spagnol, S., 2006. The hydrodynamics of Darwin Harbour. In: Wolanski, E. (Ed.), The Environments in Asia Pacific Harbours. Springer, Dordrecht, Netherlands, pp. 461–476.

Woodroffe, C.D., 1995. Response of tide-dominated mangrove shorelines in northern Australia to anticipated sea-level rise. Earth Surf. Proc. Landf. 20, 65–85.

Woodroffe, C.D., Bardsley, K.N., 1987. The distribution and productivity of mangroves in Creek H, Darwin Harbour. In: Larson, H.K., Michie, M.G., Hanley, J.R. (Eds.), Proc. Workshop on Research and Management Held in Darwin, 2–3 September 1987. Mangrove Monograph, vol. 4. North Australia Research Unit, Australian National University, Darwin, pp. 82–122.

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Leaf litter dynamics and litter consumption in two temperate South Australian mangrove forests

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Abstract

The dynamics and consumption of mangrove litter were investigated in two temperate *Avicennia marina* dominated forests in South Australia in order to compare production and fate of leaf litter with records from tropical and temperate mangroves. Litterfall was measured using traps over four months in the summer of 2004/2005. Average amount of litter was 2.1 and 3.2 g dwt m^{-2} d^{-1}, respectively, at the two study sites. Leaves accounted for most of the litterfall, followed by propagules and wood. Litterfall varied over time, and depending on the site and inundation time. The standing stock of leaf litter on the forest floor amounted to 15.5 g m^{-2} dwt in March 2005. Decomposition determined by litter bags suggested that leaves lost ~ 50% of their weight in the first two weeks of exposure, with little further weight loss over longer exposure times. Leaf consumption was investigated with a series of laboratory experiments, using the grapsid crab *Helograpsus haswellianus*, two snail species (*Salinator fragilis* and *Austrocochlea concamerata)* and the polychaete *Neanthes vaalii* as potential consumers. There was no consumption of new leaves, and the only significant consumption of aged leaves was found for female *H. haswellianus*. *H. haswellianus* consumed 0.1 g dwt d^{-1} of senescent leaves in the experiment, equivalent to 0.18 g m^{-2} d^{-1} in the field (average crab density 1.8 ind m^{-2}), or 9.4% of the average daily leaf litterfall. Experiments with propagules revealed no significant consumption by the crabs. High decomposition and low consumption rates of crabs account for the high accumulation and possible export of leaf litter from these mangroves. Leaf litter availability is not a limiting factor for invertebrate consumers in these temperate mangrove forests, and the low consumption rates imply a major difference in the fate of leaf litter between tropical and temperate mangrove systems.

Keywords: Temperate mangroves; Litterfall; Brachyuran crabs; Decomposition; Leaf consumption

1. Introduction

Mangroves contribute organic matter to the environment, mainly through the production of leaf litter (Ashton et al., 1999; Hogarth, 1999; Lee, 1999). When leaf litter is mineralised within the forest, nutrients are retained in the system, supporting further production. In systems where decomposition is minimal, tidal export of leaf litter may provide nutrients to nearby coastal waters (Alongi, 1998). Processes that promote the breakdown of leaf litter within the forest are therefore also important to the productivity of coastal ecosystems (Lee, 1995; Werry and Lee, 2005). The flux of energy in mangroves is essentially a two-step process; the first being the transfer of fixed synthesised energy to the benthic environment in the form of leaf litter (Hogarth, 1999).

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The second step consists of the breakdown of this litter to a form fit for heterotrophy (Wafar et al., 1997).

Numerous studies in tropical mangrove forests have substantiated how litter dynamics contribute to nutrient cycles and support food webs in coastal habitats (Twilley et al., 1986; Dawes et al., 1999; Holmer and Olsen, 2002; Jennerjahn and Ittekkot, 2002; Mfilinge et al., 2002). Organic production and carbon turnover in mangroves tend to be higher near the equator and decrease towards temperate latitudes (Saenger and Snedaker, 1993). Yet, there have been comparatively few studies on leaf litter in temperate mangroves, dominated by *Avicennia marina* in the southern hemisphere (Goulter and Allaway, 1979; Clarke and Myerscough, 1991; 1993; Fairweather, 1999), in which dynamics may be very different.

Quantification of litterfall and decomposition is important for assessing the productivity of a mangrove ecosystem and its relevance for food webs in coastal environments (Dawes et al., 1999; Lee, 1999). Litter production is influenced by tidal position (Feller et al., 1999), salinity (Day et al., 1996) pollution (Silva et al., 1998), mangrove tree species, weather and season (Saenger and Snedaker, 1993). Typical production rates of *A. marina* in tropical latitudes range from 3.42 to 14.02 t ha^{-1} y^{-1} (Saenger and Snedaker, 1993), with higher values generally reported in the summer months.

The rate and extent of *in situ* decomposition governs how much organic matter is recycled within the mangrove forest, and how much is exported to near-shore waters (Boulton and Boon, 1991). Greater levels of decomposition within the forest result in nutrient retention, whilst slow decomposition increases the chance of leaves being exported (Ashton et al., 1999). Stand-specific management strategies, such as reforestation, may further influence decay rates of mangrove litterfall (Bosire et al., 2005). Submersion in water results in the rapid leaching of nutrients from mangrove leaves, which can then be broken down by microbial action, macrofauna such as crabs, or the physical impact of tides (Boulton and Boon, 1991).

Crustaceans, molluscs and annelids dominate most mangrove communities (Macnae, 1968; Bouillon et al., 2002; Erseus, 2002; Ashton et al., 2003) and may play a role in the structure and function of these habitats through their burrowing activities (Warren and Underwood, 1986), as nutritional resources for higher predators (Robertson, 1988) and through processing of leaf litter (Lee, 1998). The shredding of leaves into smaller particles by consumers can increase the rate of breakdown by increasing the surface area available for microbial colonisation. Organisms such as crabs, worms and snails can potentially process leaf litter in this manner (Alongi, 1998), resulting in the retention and recycling of organic matter within the mangrove system (Lee, 1997).

To further understand differences between tropical and temperate mangroves, we investigated litter dynamics (litterfall rates, litterfall composition and leaf decomposition) and consumption by grapsid crabs and other macrofauna in two temperate *A. marina* mangrove forests, through a series of field and laboratory experiments.

2. Material and methods

2.1. Study sites

The study was carried out in South Australia, at two sites on the eastern shore of Gulf St. Vincent and ~30 km north of Adelaide (Fig. 1). Gulf St. Vincent, South Australia, is a reverse estuary that supports some of the southernmost mangroves in the world. The two sites, Port Gawler (34°38′ S, 138°26′ E) and Middle Beach (34°36′ S, 138°24′ E), are ~7 km apart and were chosen to assess possible site-specific variation in litterfall dynamics. South Australia is characterised by a dry temperate climate with 398 mm annual rainfall on average and temperature extremes from −3 °C to +44 °C. During the study period, the average temperature was 21 °C (range 7.9 °C to 42 °C), with 73 mm rainfall.

Both sites support extensive monospecific *Avicennia marina* mangrove forests. Sparse salt marsh occurs on the landward side of the mangroves, whilst extensive mudflats and seagrass beds lie on the seaward side of the forest. The tides in Gulf St. Vincent are mesotidal and mixed (Bye, 1976). The mangroves are interspersed by several small creeks, allowing easy access to the forest and good drainage. Both sites are used heavily for recreational purposes.

To investigate variation in litterfall and decomposition rates with the duration of submergence, three tidal levels were differentiated at each site: the landward fringe, the seaward fringe and mid-forest.

2.2. Litterfall

Measurements were made using litter traps (616 cm^2 surface area, 65 cm height), constructed of a metal frame with 2 mm mesh and a lid insert to prevent leaves from washing out at high tide. The traps were tied to tree branches and suspended at a maximum height of 1 m above the sediment. Three traps were placed at each tidal level at each site.

A total of 18 traps were placed in the field at the beginning of December 2004. Care was taken to place

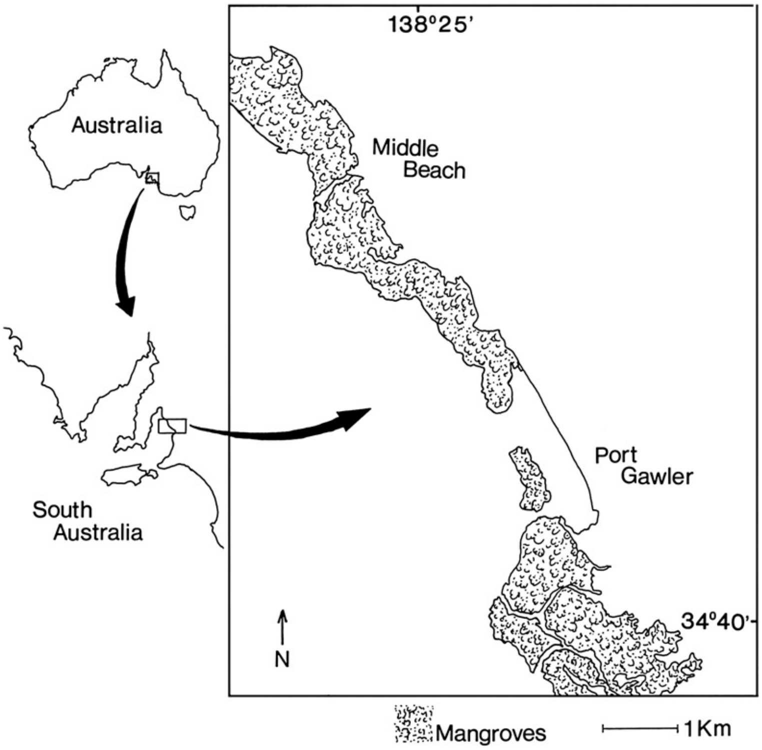

Fig. 1. Map of the South Australian coast showing the location of the two study sites, Port Gawler and Middle Beach.

traps randomly under trees of similar height. However, due to the high recreational use of the sites in some cases randomness was traded for secure and discreet placement of the traps. To investigate temporal changes in litterfall, trap contents were collected over the study period of four months. Each trap was emptied into respective bags every two weeks to minimise any leaching or decomposition of leaves within the basket (Ukonmaanaho and Starr, 2001). The litter was then rinsed with freshwater to remove any excess salt, and air dried for 48 h to reduce variability due to differing water content (Boulton and Boon, 1991). Once dried, the samples were sorted into three categories: leaves, propagules/reproductive parts, and wood, and weighed.

In order to compare values with other studies, a conversion factor between dry weight and air-dried weight (0.6675) was established by first air drying 130 leaves and subsequently drying them to constant weight at 80 °C. All values reported in this study were accordingly converted to dry weight (dwt).

2.3. Decomposition and standing stock measurements

The breakdown of *A. marina* leaves was measured over a period of eight weeks at both study sites. Freshly senescent leaves, chosen by a green/yellow colour, were collected from the forest floor (Boulton and Boon, 1991). As *A. marina* has a nutrient resorption of up to 61% before senescence (Ocheing and Erftemeijer, 2002), leaves were not picked directly from the trees. Once collected, leaves were rinsed with freshwater and air-dried for 48 h. The dried leaves were weighed into 10 g samples, and placed into decomposition bags (26 × 20 cm), made of 1 mm mesh. This design allows microbial decomposition, but excludes any large consumers such as crabs. The small mesh also prevents most particulate organic matter from washing out of the bag.

Three bags were placed at each tidal level in February 2005 at both sites, tied to pneumatophores or low-lying branches ($n=18$). To compare decomposition over different exposure time intervals, retrieval was repeated every fortnight for eight weeks, resulting in a total of 72 bags. All bags were removed from the field in April 2005 and returned to the laboratory, where they were once again rinsed and air-dried before being weighed.

To determine the standing stock of leaf litter, a quadrat (50 × 50 cm) was haphazardly placed five times at each tidal level of the mangroves at Port Gawler, and all leaf litter on the forest floor was collected from within the quadrats. In the laboratory, the samples were rinsed and air-dried for 48 h before being weighed. This

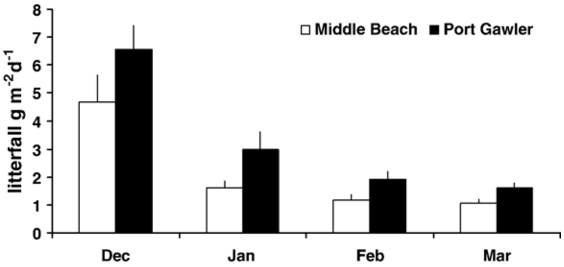

Fig. 2. Daily *Avicennia marina* litterfall (dry weight; mean+SE) for each of the study months in 2004/2005 at mangrove forests at Middle Beach and Port Gawler, South Australia. The figure shows total litterfall, composed of leaves, propagules, and wood.

measurement was carried out only in March 2005, coinciding with the litterfall collection times.

2.4. Leaf and propagule consumption experiments

To investigate whether grapsid crabs are the main consumers of leaf litter (Lee, 1998) in this temperate mangrove system, or whether other benthic organisms consume mangrove leaf litter as well (e.g. Camilleri, 1992; Fratini et al., 2004), laboratory experiments were carried out to determine consumption rates. Benthic surveys had identified several snail and polychaete species as possible leaf litter consumers, and had determined their densities in the field (Imgraben, unpubl. data). For the leaf consumption experiments, six treatments were applied, and the respective species were added according to their natural density in the field: (1) one male crab *Helograpsus haswellianus*; (2) one female *H. haswellianus* (3) 10 individuals of the snail *Austrocochlea concamerata*; (4) 20 individuals of the snail *Salinator fragilis*; (5) five individuals of the polychaete *Neanthes vaalii*; and (6) a control with no organisms. Ten replicates were run for each treatment. The organisms were randomly allocated to a tank and left for 24 h for acclimatisation and gut evacuation (Camilleri, 1989; Lee, 1997; Nordhaus, 2004; Olafsson et al., 2002).

Sediment was collected from the field sites and air-dried before being placed at the bottom of each tank, which was then filled with filtered seawater. Each tank was cleaned and the water exchanged between trials. When the organisms were not in use they were kept in a holding tank under identical conditions. The aquarium room was set to a 12-h light/dark cycle and a constant temperature of 17–18 °C. Glass tanks (18 × 25 × 12 cm) were used for all trials. Leaves were collected from the field prior to the experiments, and their surface area measured and weight recorded after being air-dried as described above. The organisms were offered a choice between one freshly senescent leaf and one aged leaf, which were placed on the sediment of each tank. After 24 h, the leaves were removed, air dried, re-weighed and the new surface area was obtained. Weight loss rather than surface area was used as an indication of consumption, as in many cases crabs consumed from the base of the stem where surface area was not proportional to weight.

Propagule consumption was only determined for the crab *H. haswellianus*. The same tank set-up and conditions were used as for the leaf consumption

Table 1
Results of a repeated measures ANOVA for *Avicennia marina* litterfall

Source of variation	df	Total litterfall			Leaves			Wood		
		MS	F	p	MS	F	p	MS	F	p
Month (M)	3	13.059	148.558	≤0.001	7.224	140.323	≤0.001	.079	.497	ns
Error(M)	6	.088			.051			.158		
Site (S)	1	6.023	290.517	≤0.001	.338	24.729	<0.05	.205	2.572	ns
Error(S)	2	.021			.014			.080		
Level (L)	2	.007	.022	ns	.470	1.708	ns	.799	2.424	ns
Error(L)	4	.308			.275			.330		
M * S	3	.075	.289	ns	.790	4.563	ns	.065	.573	ns
Error(M*S)	6	.258			.173			.113		
M * L	6	.791	2.592	ns	.039	.096	ns	.222	1.542	ns
Error(M*L)	12	.305			.405			.144		
S * L	2	1.943	3.596	ns	2.205	12.173	<0.05	.017	.364	ns
Error(S*L)	4	.540			.181			.046		
M * S * L	6	.759	3.227	<0.05	.558	4.486	<0.05	.136	5.906	<0.01
Error(M*S*L)	12	.235			.124			.023		

Data were square-root transformed prior to analysis. Months (December to March), site (Port Gawler and Middle Beach) and tidal level (high, mid and low) are fixed factors. ns=non significant.

experiments. Twelve replicates were run of each of the following three treatments: (1) male *H. haswellianus*, (2) female *H. haswellianus*, and (3) a control with no organisms. Crabs were randomly allocated to tanks and left for 24 h to acclimatise. Propagules were collected and weighed, as surface area would be inappropriate given their complex three-dimensional structure. One propagule was placed in each tank, and treatments were assigned randomly. After 24 h, each propagule was removed and reweighed.

2.5. Data analysis

All litterfall and decomposition data were square-root transformed prior to analysis of variance (ANOVA). Litterfall data were analysed with a repeated measures ANOVA, with fixed factors being month (4 levels), site (2 levels) and tidal level (3 levels). For decomposition data, a three-way ANOVA was run using site (2 levels), tidal level (3 levels) and exposure time (4 levels), with Tukey's Honestly Significant Difference (HSD) test for post-hoc analyses and one-way ANOVA to explore interaction effects. For the propagule component of the litterfall data, the standing stock data, as well as the data from the consumption experiment, normality could not be achieved by transformation, and in these cases non-parametric Mann-Whitney U-test or Kruskal-Wallis H-test was used for analyses. For the new leaf trials in the consumption experiments, one replicate each for treatments with female crabs, polychaetes, and a control were removed from the analysis, as weight gains were measured in these cases. All data analysis was undertaken using SPSS 11.5 for Windows.

3. Results

3.1. Litterfall

At the two studied temperate mangrove forests, litterfall varied in composition and amount over time, as

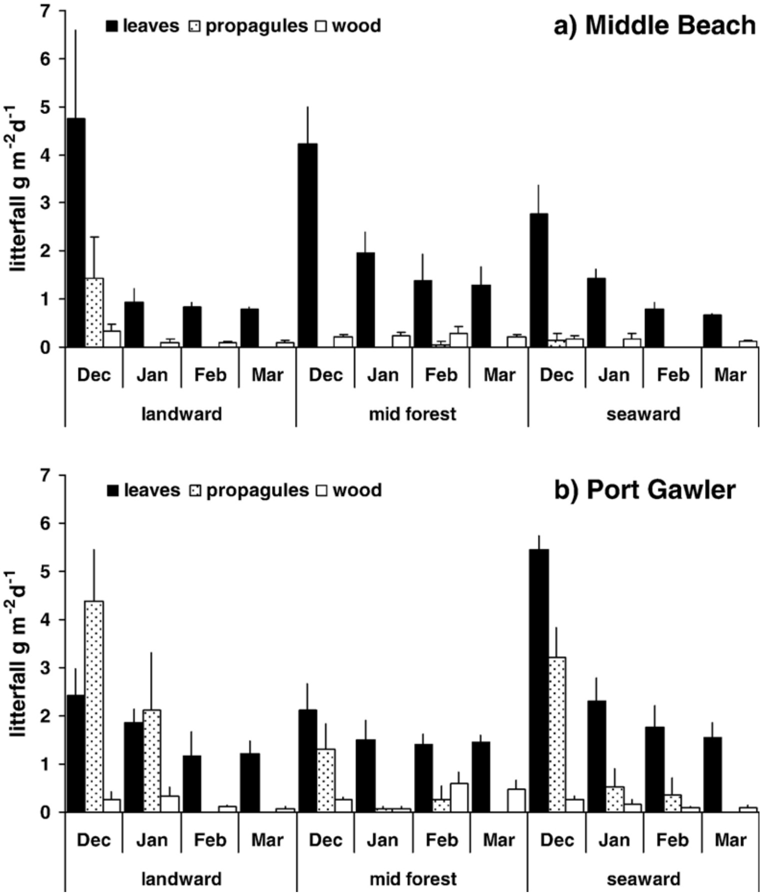

Fig. 3. Daily litterfall (dry weight; mean + SE) at three tidal levels (landward, seaward and mid-forest) in the *Avicennia marina* mangrove forests at (a) Middle Beach and (b) Port Gawler, shown for each month and separated into litterfall components (leaves, propagules, wood).

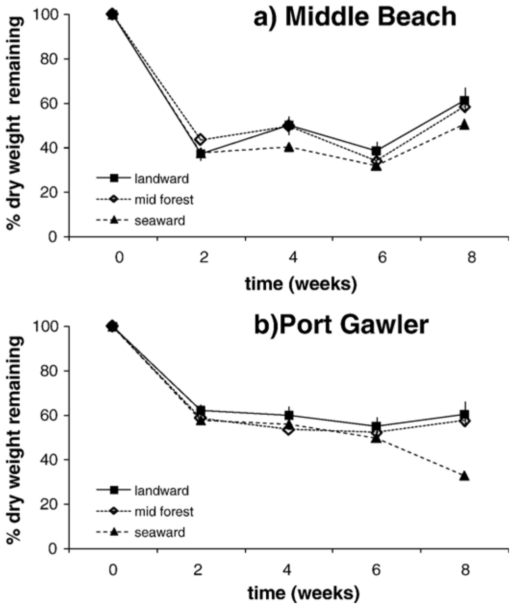

Fig. 4. Decomposition of *Avicennia marina* leaves in litter bags, exposed at Middle Beach and Port Gawler, South Australia, in February and March 2005. Three litter bags each were placed in the field at three tidal levels (landward, mid-forest, seaward) at each site. Bags were exposed for 2, 4, 6 and 8 wk. The figure shows weight loss as percent of initial weight remaining (mean+SE).

well as with site and tidal level. The average amount of mangrove litter was significantly higher at Port Gawler (3.2 ± 0.3 g dwt m^{-2} d^{-1}, mean±SE) than at Middle Beach (2.1 ± 0.3 g dwt m^{-2} d^{-1}) (Fig. 2, Table 1). Litterfall decreased at both sites from summer (December) towards autumn (March) (Fig. 2). Litter was composed of leaves, propagules and wood, and the composition varied over time as well as between sites and between tidal levels within sites (Fig. 3). Leaves contributed 85% to litterfall at Middle Beach, with propagules making up 6% and wood contributing 9%. The leaf component of the litterfall differed significantly over time, between the sites, and depended on the tidal level only in interaction with site and time components (Table 1). Since leaves constitute most of the litterfall, the total litterfall differed as the leaf component (Table 1). At Port Gawler, propagules contributed a much higher percentage of 30%, whilst leaves made up about 62% and wood 8% of the total litterfall. The amount of propagules in the litter traps was significantly higher at Port Gawler than at Middle Beach in December and January ($p<0.05$ and $p<0.01$, respectively; U-Tests), while there were no significant differences between tidal levels ($p>0.05$; H-Test). The wood component showed no significant variation, apart from an interaction effect between months, site and tidal level (Table 1).

The average standing stock of litter on the forest floor amounted to 15.5 ± 3.9 g dwt m^{-2} (mean±SE) at Port Gawler. This measurement was taken in March, when few propagules were caught in the litter traps, yet propagules contributed 35% to the weight of the standing stock, especially in the mid forest. Leaves accounted for 65% of the standing stock. There was no significant difference between tidal levels for any component of the standing stock.

3.2. Decomposition

The average decay rate recorded in this study was 0.15 ± 0.02 g dwt d^{-1} (mean±SE) at Middle Beach, and 0.12 ± 0.01 g dwt d^{-1} at Port Gawler. Decomposition of leaf litter did not increase with longer exposure time of litter bags in this temperate mangrove forest (Fig. 4). Leaves lost about half of their weight during the early stages of decomposition, with little further weight loss over a two-month period. Litter bags exposed for six weeks had the highest weight loss (65% on average), yet those exposed for eight weeks had lower weight losses of 43%. Decomposition rates were significantly higher at Middle Beach (55%) than at Port Gawler (45%) (Table 2). There was a significant interaction effect for site and exposure time (Table 2), with significant differences between sites for leaves exposed for six (ANOVA, $F=31.95$, $p<0.001$), four (ANOVA, $F=9.38$, $p<0.01$) and two weeks (ANOVA, $F=34.66$, $p<0.001$). Decomposition rates varied not only between sites, but also within the forest, being highest at the seaward fringe of the mangroves compared to the other tidal levels (Table 2, Fig. 4).

Table 2
Results of a three-way ANOVA for decomposition of *Avicennia marina* leaves at Port Gawler and Middle Beach, South Australia

Source of Variation	df	Mean-Square	F-ratio	p
Site	1	9.379	26.831	<0.001
Exposure	3	1.710	4.892	<0.01
Level	2	2.202	6.300	<0.01
Site*Exposure	3	2.923	8.363	<0.001
Site*Level	2	0.114	0.325	ns
Exposure*Level	6	0.483	1.381	ns
Site*Exposure*Level	6	0.259	0.742	ns
Error	48	0.350		

Data were square-root transformed prior to analysis. Fixed factors are site, level and exposure time. Exposure time refers to the number of weeks leaf litter bags were in the field. ns=non significant.

3.3. Leaf and propagule consumption

All organisms that consumed leaf litter picked on old rather than freshly senescent leaves, apart from one snail species (Fig. 5). Weight losses of old leaves were significantly different between all treatments (H-Test, $p < 0.01$), yet in pairwise tests, female crabs were the only ones to show any significant consumption of old leaves over the control (U-Test, $p < 0.05$) (Fig. 5), and significantly preferred old over new leaves (U-Test, $p < 0.01$). Old leaves had lost weight in the controls as well, even more than in the treatment with *Austrocochlea concamerata* (U-Test, $p < 0.05$). There were no significant results for fresh leaf consumption. On average, crabs consumed 0.1 ± 0.02 g dwt d^{-1} (mean ± SE) of senescent leaves in the experiment, which equates to 0.18 g m^{-2} d^{-1} based on an average density of 1.8 crabs m^{-2} in the field (Imgraben, unpubl. data). There was no significant difference in weight loss of fresh or aged leaves between the experiments using male and female crabs.

The experiment on propagule predation did not reveal consumption of propagules by either male or female *Helograpsus haswellianus*. Weight losses were very minimal, with a maximum of 7% over all trials, and not significantly different from the control.

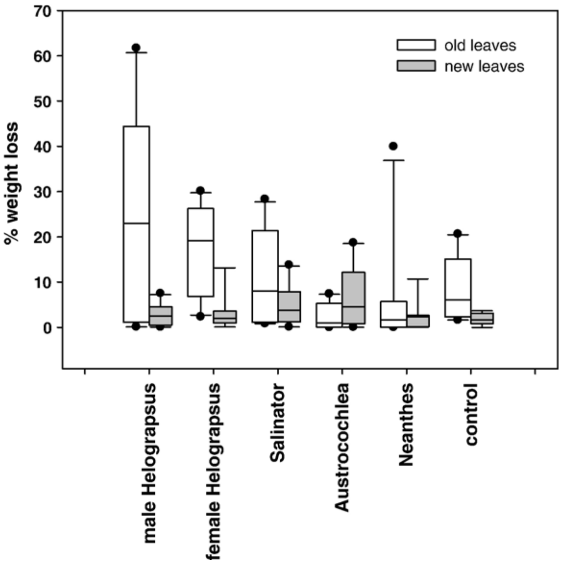

Fig. 5. Consumption of old and fresh *Avicennia marina* leaves offered to possible benthic consumers (male and female grapsid crab (*Helograpsus haswellianus*), pulmonate snail (*Salinator fragilis*), trochid snail (*Austrocochlea concamerata*), and the nereidid polychaete *Neanthes vaalii*) over 24 h trials (mean+SE, n=10 per treatment). Percent weight loss was used as an indicator of consumption as surface area was not accurate. The control consisted of a treatment with no organisms.

4. Discussion

Although latitudinal differences in mangrove litterfall dynamics are to be expected (Saenger and Snedaker, 1993), this study on temperate *Avicennia* mangroves revealed similarities in litterfall and decomposition with some tropical mangroves. Leaf consumption by grapsid crabs, however, appears to be of less importance in these temperate mangroves.

4.1. Litterfall

In order to compare litterfall values to other tropical and temperate mangrove systems, and to investigate seasonal patterns, an annual litterfall cycle is needed. This project was, however, confined in time, and annual data could not be obtained. Yet several comparisons can still be made to evaluate differences between mangrove systems.

The composition of litterfall, with leaves accounting for 62 – 85% of the total at our study sites, followed by propagules and wood components, is comparable to tropical mangroves. Other studies have reported similar litterfall compositions, with leaf contributions ranging from 40 to 83% (Bunt, 1995; Mackey and Smail, 1995; May, 1999; Ocheing and Erftemeijer, 2002).

The amount and composition of litterfall changed over time at our temperate mangrove sites, corroborating previous findings on seasonality in mangrove litterfall (Duke, 1990; Mackey and Smail, 1996; Mfilinge et al., 2005). As flowering and fruiting varies with the geographic setting (latitude, rainfall, temperature), the phenology of litterfall varies throughout a year (Duke, 1990). Yet, in many mangroves, flowering and fruiting coincide with the summer months (Clarke and Myerscough, 1991; Clarke, 1994; May, 1999) and many stands have one peak reproductive period (Twilley et al., 1997; Shunula and Whittick, 1999; Ocheing and Erftemeijer, 2002). In temperate mangroves, litterfall has been reported to be unimodal and highest in summer (Duke, 1990; May, 1999). Previous records from one of our study sites (Port Gawler) (Duke, 1990) showed highest leaf litterfall between December and March, and highest fruit fall between December and January. Thus, litterfall would have been negligible in the months not covered by our study.

The daily litterfall rate recorded at our two study sites (2.7 g dwt m^{-2} d^{-1} on average) lies within the range of litterfall values reported for *Avicennia marina* in the tropics, which can vary from 1.49 g m^{-2} d^{-1} (Ocheing and Erftemeijer, 2002) to 6 g m^{-2} d^{-1} (Shunula and Whittick, 1999). The daily litterfall rates were lower than those reported for *Avicennia alba* in Malaysia (Sasekumar and Loi, 1983), but higher than those for *Avicennia germinans* in Brazil (Schories et al., 2003).

We found further differences in the amount and composition of litterfall between as well as within our study sites, yet with no clear pattern. Variations in litterfall have been found between adjacent mangrove sites, or with shore height (Mackey and Smail, 1995; May, 1999), and tidal flushing or water movement might account for such differences (e.g. Twilley et al., 1997).

About 31% of the monthly litterfall for March 2005 was found on the forest floor in our study, indicating possible retention of litter. Monthly standing stock measurements would be needed to assess any seasonal patterns. The standing stock of 15.5 g dwt m^{-2} recorded at the end of summer in this study falls within the range of values reported by Goulter and Allaway (1979) for temperate mangroves in Sydney (9 g m^{-2} in winter and 62 g m^{-2} in summer), but was lower than the maximum value for *A. germinans* in a macrotidal tropical mangrove (Schories et al., 2003).

4.2. Decomposition

Leaves inside decomposition bags may face different micro-climatic conditions than naturally decomposing leaves (Boulton and Boon, 1991), so that results from litter bag experiments indicate only possible breakdown rates of *A. marina* in the field.

Mangrove litter has been reported to decompose quickly, with high leaching rates in the first few weeks of exposure in the field (Van der Valk and Attiwill, 1984; Mfilinge et al., 2005). In our study, the highest weight loss occurred in the first two weeks as well, but prolonged exposure did not cause further weight loss. Contrary to the expectation, litter bags left in the field for eight weeks showed even slower decomposition than litter bags left for shorter time spans. Meiofaunal colonisation of the leaf litter inside the bags may have affected the weight over time (Gwyther, 2003); however, this would need to be explored further.

The decomposition half-time of two weeks found in our study sites was much faster than the eight weeks reported for another temperate *A. marina* forests in Sydney (Goulter and Allaway, 1979). However, decomposition can be even faster, as Wafar et al. (1997) found a complete loss of leaf material in eight weeks for *Avicennnia officinalis* in a mangrove forest in India. Decomposition can be influenced by seasonal variations (Mackey and Smail, 1996) and tidal inundation (Lee, 1989; Mackey and Smail, 1996; Dick and Osunkoya, 2000; Mfilinge et al., 2002). The higher decomposition rate at the seaward fringe of the mangroves reported here corroborates previous findings that increased submergence accelerates decomposition. Variability in leaf litter decomposition occurs not only between tidal levels, but over larger spatial scales, too, as is indicated by the site specific decomposition rates found in this study.

4.3. Litter consumption

Brachyuran crabs of the families Grapsidae and Ocypodidae are the main consumers of mangrove leaf litter and propagules worldwide (Lee, 1998; Nordhaus et al., 2006), yet gastropods have been shown to consume leaf litter as well (Slim et al., 1997; Fratini et al., 2004). Two gastropod species related to those tested in our experiments have been found to feed on senescent leaves in subtropical mangroves (Camilleri, 1992), while we found no indication of their leaf consumption, except for *A. concamerata,* which might graze on fresh leaves. Further benthic invertebrates have been identified as leaf shredders in tropical mangroves, including isopods, amphipods, and polychaetes (Camilleri, 1992). Polychaetes of the family Nereididae can increase the decay of macroalgal detritus in sediments (Kristensen and Mikkelsen, 2003), yet we obtained no indication from our experiment that *N. vaalii* would consume mangrove litter.

Of all the possible consumers tested, only *Helograpsus haswellianus* emerged as consumer of leaf litter in the temperate mangroves of South Australia. The lack of consumption in the experiment by other species could reflect differences in metabolism or feeding rates. The gastropod *Terebralia palustris* shows selective behaviour when feeding on mangrove leaves, with the ability to choose less damaged or different aged leaves (Fratini et al., 2004). As shown from tropical studies, crabs have a preference for aged leaves (Lee, 1989; Micheli, 1993), which also applied to the crab species found in our temperate mangroves. In many studies *A. marina* leaves are preferred by crabs over leaves from other mangrove species (Camilleri, 1989; Dahdouh-Guebas et al., 1999; Olafsson et al., 2002), presumably due to their lower tannin concentrations and thinner blades (Micheli, 1993). While leaf consumption by semi-terrestrial *H. haswellianus* was observed in the aquaria, it remains unknown whether consumption rates would have been higher if the crabs and leaves had not been submerged. Initial leaf tethering trials in the field had shown no signs of consumption within two days. Entanglement with seagrass detritus washed into the mangroves at the study sites made a further field experimental approach not feasible.

The experiment demonstrated that the grapsid crab *H. haswellianus* has the ability to process 0.1 g dwt d^{-1} of senescent leaves, and consumption was not sex dependent. Other studies on leaf consumption by mangrove crabs did find that female crabs consumed more leaf litter than males (Olafsson et al., 2002), yet male *Aratus pisonii* had a much greater variation in diet than females (Erickson et al., 2003). Female crabs might have higher energy requirements related to differences in reproductive costs or investments than males (Hartnoll, 2006). Therefore, future studies should assess how the reproductive stage of crabs, or the sex-ratio of the population, affects how much litter is consumed in a forest.

Based on the leaf consumption rate by crabs determined in the experiments and crab density recorded in the field, we estimated that *H. haswellianus* can consume 0.18 g dwt m^{-2} d^{-1} of leaf litter, equivalent to 9.4% of the average daily leaf litterfall at our study sites. Many studies in tropical mangroves have reported consumption values between 10 and 100% of the daily litterfall (Slim et al., 1997; Lee, 1998), which are much higher than the values obtained in this study. Thus, although *H. haswellianus* can process a small proportion of litterfall, leaf litter consumption by grapsid crabs appears to be of less relevance to temperate than to tropical mangroves.

In tropical mangroves, grapsid crabs are not only important to the forest as leaf litter consumers, but as predators of propagules as well (Smith et al., 1989; Dahdouh-Guebas et al., 1998; Clarke and Kerrigan, 2002; Lindquist and Carroll, 2004). Although Clarke and Myerscough (1993) report chew marks of *H. haswellianus* on propagules in mangroves near Sydney, we found no significant consumption of propagules by crabs during this study.

4.4. Conclusion

The results of this study support Robertson and Daniel's (1989) hypothesis that physical factors may be more significant in governing the fate of leaf litter in temperate than in tropical mangroves. Crabs were consuming <10% of the daily leaf litterfall in the temperate mangroves studied, leaving the majority of the litterfall to decompose or accumulate on the forest floor and, possibly, be exported as detritus to nearshore waters (Van der Valk and Attiwill, 1984). Yet, the high decomposition rate and standing stock recorded would imply a minimal export of leaf litter from these temperate mangrove systems. Future research needs to establish the relevance of exported particulate and dissolved organic matter from temperate mangroves to fuel productivity of temperate shelf seas, especially for oligotrophic waters such as those off the coast of southern Australia.

This is the first study integrating litterfall dynamics and litter consumption in a temperate mangrove system. Composition, seasonality and amount of leaf litter in an *A. marina* dominated mangrove forest in South Australia were comparable to *Avicennia* forests in other temperate and tropical locations. Whilst leaf litter cannot be considered a limiting factor for invertebrate consumer populations in this temperate mangrove system, the limited consumption by crabs suggests major differences in the fate of leaf litter between tropical and temperate mangrove systems.

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References

Alongi, D.M., 1998. Coastal Ecosystem Processes. CRC Press, Boca Raton.

Ashton, E.C., Hogarth, P.J., Ormond, R., 1999. Breakdown of mangrove leaf litter in a managed mangrove forest in Peninsular Malaysia. Hydrobiologia 413, 77–88.

Ashton, E.C., Macintosh, D.J., Hogarth, P.J., 2003. A baseline study of the diversity and community ecology of crab and molluscan macrofauna in the Sematan mangrove forest, Sarawak, Malaysia. J. Trop. Ecol. 19, 127–142.

Bosire, J.O., Dahdouh-Guebas, F., Kairo, J.G., Kazungu, J., Dehairs, F., Koedam, N., 2005. Litter degradation and CN dynamics in reforested mangrove plantations at Gazi Bay, Kenya. Biol. Conserv. 126, 287–295.

Bouillon, S., Koedam, N., Raman, A.V., Dehairs, F., 2002. Primary producers sustaining macro-invertebrate communities in intertidal mangrove forests. Oecologia 130, 441–448.

Boulton, A.J., Boon, P.I., 1991. A review of methodology used to measure leaf litter decomposition in lotic environments: time to turn over an old leaf? Aust. J. Mar. Freshw. Res. 42, 1–43.

Bunt, J.S., 1995. Continental scale patterns in mangrove litterfall. Hydrobiologia 295, 135–140.

Bye, J.A.T., 1976. Physical oceanography of Gulf St Vincent and Investigator Strait. In: Twidale, C.R., Tyler, M.J., Webb, B.P. (Eds.), Natural History of the Adelaide Region. Royal Society of South Australia, Adelaide, pp. 143–160.

Camilleri, J., 1989. Leaf choice by crustaceans in a mangrove forest in Queensland. Mar. Biol. 102, 453–459.

Camilleri, J., 1992. Leaf-litter processing by invertebrates in a mangrove forest in Queensland. Mar. Biol. 114, 139–145.

Clarke, P.J., 1994. Baseline studies of temperate mangrove growth and reproduction; demographic and litterfall measures of leafing and flowering. Aust. J. Bot. 42, 37–48.

Clarke, P.J., Kerrigan, R.A., 2002. The effect of seed predators on the recruitment of mangroves. J. Ecol. 90, 728–736.

Clarke, P.J., Myerscough, P.J., 1991. Floral biology and reproductive phenology of *Avicennia marina* in South-Eastern Australia. Aust. J. Bot. 39, 283–293.

Clarke, P.J., Myerscough, P.J., 1993. The intertidal distribution of the grey mangrove (*Avicennia marina*) in southeastern Australia: The effects of physical conditions, interspecific competition, and predation on propagule establishment and survival. Aust. J. Ecol. 18, 307–315.

Dahdouh-Guebas, F., Verneirt, M., Tack, J.F., Van Speybroeck, D., Koedam, N., 1998. Propagule predators in Kenyan mangroves and their possible effect on regeneration. Mar. Freshw. Res. 49, 345–350.

Dahdouh-Guebas, F., Giuggioli, M., Oluoch, A., Vannini, M., Cannicci, S., 1999. Feeding habits of non-ocypodid crabs from two mangrove forests in Kenya. Bull. Mar. Sci. 642, 291–297.

Dawes, C., Siar, K., Marlett, D., 1999. Mangrove structure, litter and macroalgal productivity in a northern-most forest of Florida. Mangroves Salt Marshes 3, 259–267.

Day Jr., J.W., Coronado-Molina, C., Vera-Herrera, F.R., Twilley, R., Rivera-Monroy, V.H., Alvarez-Guillen, H., Day, R., Conner, W., 1996. A 7 year record of above-ground net primary production in a southeastern Mexican mangrove forest. Aquat. Bot. 55, 39–60.

Dick, T.M., Osunkoya, O.O., 2000. Influence of tidal restriction floodgates on decomposition of mangrove litter. Aquat. Bot. 68, 273–280.

Duke, N.C., 1990. Phenological trends with latitude in the mangrove tree *Avicennia marina*. J. Ecol. 78, 113–133.

Erickson, A.A., Saltis, M., Bell, S.S., Dawes, C.J., 2003. Herbivore feeding preferences as measured by leaf damage and stomatal ingestion: a mangrove crab example. J. Exp. Mar Biol. Ecol. 289, 123–138.

Erseus, C., 2002. Mangroves and marine oligochaete diversity. Wetlands Ecol. Manag. 10, 197–202.

Fairweather, P.G., 1999. Determining the 'health' of estuaries: Priorities for ecological research. Aust. J. Ecol. 24, 441–451.

Feller, I.C., Whigham, D.F., O'Neill, J.P., McKee, K.L., 1999. Effects of nutrient enrichment on within stand cycling in a mangrove forest. Ecology 8, 2193–2205.

Fratini, S., Vigiani, V., Vannini, M., Cannicci, S., 2004. *Terebralia palustris* (Gastropoda; Potamididae) in a Kenyan mangal: size structure, distribution, and impact on the composition of leaf litter. Mar. Biol. 144, 1173–1182.

Goulter, P.F.E., Allaway, W.G., 1979. Litter fall and decomposition in a mangrove stand, *Avicennia marina* (Forsk.) Vierh. Aust. J. Mar. Freshw. Res., vol. 30. Middle Harbour, Sydney, pp. 541–546.

Gwyther, J., 2003. Nematode assemblages from *Avicennia marina* leaf litter in a temperate mangrove forest in south-eastern Australia. Mar. Biol. 142, 289–297.

Hartnoll, R.G., 2006. Reproductive investment in Brachyura. Hydrobiologia 557, 31–40.

Hogarth, P.J., 1999. The Biology of Mangroves. Oxford University Press, New York.

Holmer, M., Olsen, A.B., 2002. Role of decomposition of mangrove and seagrass detritus in sediment carbon and nitrogen cycling in a tropical mangrove forest. Mar. Ecol. Prog. Ser. 230, 87–101.

Jennerjahn, T.C., Ittekkot, V., 2002. Relevance of mangroves for the production and deposition of organic matter along tropical coastlines. Naturwissenschaften 89, 23–30.

Kristensen, E., Mikkelsen, O.L., 2003. Impact of the burrow-dwelling polychaete *Nereis diversicolor* on the degradation of fresh and aged macroalgal detritus in a coastal marine sediment. Mar. Ecol. Prog. Ser. 265, 141–153.

Lee, S.Y., 1989. The importance of sesarminae crabs *Chiromanthes* spp. and inundation frequency on mangrove (*Kandelia candel* (L.) Druce) leaf litter turnover in a Hong Kong tidal shrimp pond. J. Exp. Mar. Biol. Ecol. 131, 23–43.

Lee, S.Y., 1995. Mangrove outwelling: a review. Hydrobiologia 295, 203–212.

Lee, S.Y., 1997. Potential trophic importance of the faecal material of the mangrove sesarmine crab *Sesarma messa*. Mar. Ecol. Prog. Ser. 159, 275–284.

Lee, S.Y., 1998. Ecological role of grapsid crabs in mangrove ecosystems: a review. Mar. Freshw. Res. 49, 335–343.

Lee, S.Y., 1999. Tropical mangrove ecology: Physical and biotic factors influencing ecosystem structure and function. Aust. J. Ecol. 24, 355–366.

Lindquist, E.S., Carroll, C.R., 2004. Differential seed and seedling predation by crabs: impacts on tropical coastal forest composition. Oecologia 141, 661–671.

Mackey, A.P., Smail, G., 1995. Spatial and temporal variation in litter fall of *Avicennia marina* (Forssk.) Vierh. in the Brisbane River, Queensland, Australia. Aquat. Bot. 52, 133–142.

Mackey, A.P., Smail, G., 1996. The decomposition of mangrove litter in a subtropical mangrove forest. Hydrobiologia 332, 93–98.

Macnae, W., 1968. A general account of the fauna and flora of mangrove swamps and forests in the Indo-West-Pacific region. Adv. Mar. Biol. 6, 73–270.

May, J.D., 1999. Spatial variation in litter production by the mangrove *Avicennia marina* var. *australasica* in Rangaunu Harbour, New Zealand. N. Z. J. Mar. Freshw. Res. 33, 163–172.

Mfilinge, P.L., Atta, N., Tsuchiya, M., 2002. Nutrient dynamics and leaf litter decomposition in a subtropical mangrove forest at Oura Bay, Okinawa, Japan. Trees 16, 172–180.

Mfilinge, P.L., Meziane, T., Bachok, Z., Tsuchiya, M., 2005. Litter dynamics and particulate organic matter outwelling from a subtropical mangrove in Okinawa Island, South Japan. Estuar. Coast. Shelf Sci. 63, 301–313.

Micheli, F., 1993. Feeding ecology of mangrove crabs in North Eastern Australia: mangrove litter consumption by *Sesarma messa* and *Sesarma smithii*. J. Exp. Mar. Biol. Ecol. 171, 165–186.

Nordhaus, I., 2004. Feeding ecology of the semi-terrestrial crab *Ucides cordatus cordatus* (Decapoda: Brachyura) in a mangrove forest in Brazil. Ph.D. Thesis, University of Bremen, ZMT Contribution 18, Bremen, Germany.

Nordhaus, I., Wolff, M., Diele, K., 2006. Litter processing and population food intake of the mangrove crab *Ucides cordatus* in a high intertidal forest in northern Brazil. Estuar. Coast. Shelf Sci. 67, 239–250.

Ocheing, C.A., Erftemeijer, P.L.A., 2002. Phenology, litterfall and nutrient resorption in *Avicennia marina* (Forskk.) Vierh. Trees, vol. 16. Gazi Bay, Kenya, pp. 167–171.

Olafsson, E., Buchmayer, S., Skov, M.W., 2002. The east African decapod crab *Neosarmatium meinerti* (de Man) sweeps mangrove floors clean of leaf litter. Ambio 31, 569–573.

Robertson, A.I., 1988. Abundance, diet and predators of juvenile banana prawns, *Penaeus merguiensis*, in a tropical mangrove estuary. Aust. J. Mar. Freshw. Res. 39, 467–478.

Robertson, A.I., Daniel, P.A., 1989. The influence of crabs in litter processing in high intertidal mangrove forests in tropical Australia. Oecologia 78, 191–198.

Saenger, P., Snedaker, S.C., 1993. Pantropical trends in mangrove above-ground biomass and annual litterfall. Oecologia 96, 293–299.

Sasekumar, A., Loi, J.J., 1983. Litter production in three mangrove forest zones in the Malay Peninsula. Aquat. Bot. 17, 283–290.

Schories, D., Barletta-Bergan, A., Barletta, M., Krumme, U., Mehlig, U., Rademaker, V., 2003. The keystone role of leaf-removing crabs in mangrove forests of North Brazil. Wetlands Ecol. Manag. 11, 243–255.

Shunula, J.P., Whittick, A., 1999. Aspects of litter production in mangroves from Unguja Island, Zanzibar, Tanzania. Estuar. Coast. Shelf Sci. 49, 51–54.

Silva, C.A.R., Lacerda, L.D., Ovalle, A.R., Rezende, C.E., 1998. The dynamics of heavy metals through litterfall and decomposition in a red mangrove forest. Mangroves Salt marshes 2, 149–157.

Slim, F.J., Hemminga, M.A., Ocheing, C.A., Jannick, N.T., Cocheret de la Moriniere, E., Van der Velde, G., 1997. Leaf litter removal by the snail *Terebralia palustris* (Linnaeus) and sesarmid crabs in an East African mangrove forest (Gazi Bay, Kenya). J. Exp. Mar. Biol. Ecol. 215, 35–48.

Smith, T.J., Chan, H.T., McIvor, C.C., Robblee, M.B., 1989. Comparisons of seed predation in tropical, tidal forests from three continents. Ecology 70, 146–151.

Twilley, R.R., Lugo, A.E., Patterson-Zucca, C., 1986. Litter production and turnover in basin mangrove forests in southwest Florida. Ecology 67, 670–683.

Twilley, R.R., Pozo, M., Garcia, V.H, Rivera-Monroy, V.H., Zambrano, R., Bodero, A., 1997. Litter dynamics in riverine mangrove forests in the Guayas River Estuary, Ecuador. Oecologia 111, 109–122.

Ukonmaanaho, L., Starr, M., 2001. The importance of leaching from litter collected in litterfall traps. Environ. Monit. Assess. 66, 129–146.

Van der Valk, A.G., Attiwill, P.M., 1984. Decomposition of leaf and root litter of *Avicennia marina* at Westernport Bay, Victoria, Australia. Aquat. Bot. 18, 205–221.

Wafar, S., Untawale, A.G., Wafar, M., 1997. Litter fall and energy flux in a mangrove ecosystem. Estuar. Coast. Shelf Sci. 44, 111–124.

Warren, J.H., Underwood, A.J., 1986. Effects of burrowing crabs on the topography of mangrove swamps in New South Wales. J. Exp. Mar. Biol. Ecol. 102, 223–235.

Werry, J., Lee, S.Y., 2005. Grapsid crabs mediate link between mangrove litter production and planktonic food chains. Mar. Ecol. Prog. Ser. 293, 165–176.

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Effect of temperature on leaf litter consumption by grapsid crabs in a subtropical mangrove (Okinawa, Japan)

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Abstract

Litter consumption by grapsid crabs enhances detritus turnover and nutrient cycling in mangrove ecosystems. However, unlike tropical mangroves, subtropical mangroves are subjected to pronounced seasonal changes in weather; particularly, low winter temperatures may slow down important ecological processes such as litter decay. This study aimed at evaluating the effect of temperature (low winter and high summer temperatures) on leaf litter consumption by two grapsid crabs (*Parasesarma pictum* and *Helice leachi*) in a subtropical mangrove forest of Okinawa Island, south Japan. We also tested whether leaf litter consumption between the low winter and summer temperatures could be affected by leaf species type and quality. A leaf-tethering technique was used to conduct field feeding experiments in the high and low intertidal sites of the mangroves using leaves of *Bruguiera gymnorrhiza* and *Kandelia obovata*. Leaves of different stages of decay: fresh (green), yellow, brown, two and four weeks were used. Results showed significant differences in leaf consumption between seasons, leaf species and shore heights. More leaves were consumed during summer than winter. In both seasons and shore heights, crabs consumed significantly more leaves of *K. obovata* than *B. gymnorrhiza.* Consumption was higher in the high than low intertidal mangrove. Although crabs preferred aged leaves in summer, during the winter season they consumed significantly more green leaves of *K. obovata* than yellow and brown leaves of *B. gymnorrhiza*. The slow litter processing during winter was consistent with lower carbon contents and lower C/N ratios in the surface sediments, signifying low input of organic matter. Results of this study suggest that temperature affects mangrove litter processing in Oura Bay mangroves, and consequently the amounts of organic matter and nutrients conserved inside subtropical mangrove sediments.

Keywords: Mangrove; Litter consumption; Grapsid crabs; *Bruguiera gymnorrhiza*; *Kandelia obovata*; Okinawa Japan

1. Introduction

Leaves make a substantial contribution (>70%) of the total litter fall in many tropical and subtropical mangroves (Steinke and Ward, 1988; Chale, 1996; Twilley et al., 1997; Mfilinge et al., 2005). By consuming leaf litter, mangrove crabs substantially reduce export, shorten decomposition time, and enhance nutrient cycling (Robertson, 1986; Robertson and Daniel, 1989; Lee, 1998, 1999; Ashton, 2002). More importantly, their bioturbation activities help to retain organic matter and nutrients within the mangrove ecosystem (Lee, 1998; Nordhaus et al., 2006). Studies show that leaf litter consumption rates vary among crab species and leaf species (Micheli, 1993a; Ashton, 2002), probably because the variable nutritional qualities of leaves determine the preference for consumption by crabs (Ashton, 2002; Skov and Hartnoll, 2002). Crabs generally prefer aged to fresh leaves (Giddins et al.,

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1986; Lee, 1989; Micheli, 1993a) because of lower tannin content or lower C/N ratio and higher nutritional value (Ashton, 2002; Skov and Hartnoll, 2002), though preference for green leaves has also been shown (Micheli, 1993b; Ashton, 2002).

In contrast to their tropical counterparts, subtropical mangroves of southern Japan are subjected to large seasonal changes in weather. In particular, low temperatures are present during the winter season and sometimes fall below 14 °C in Okinawa Island (Mfilinge et al., 2002). The low temperatures slow down important ecological processes such as litter production (Mfilinge et al., 2005) and decay (Mfilinge, 2004). The low temperature during winter is likely to reduce crab activity on the sediment surface, slow leaf consumption and breakdown, and possibly the amount of organic matter retained in the sediments.

The objective of this study was to quantify leaf litter consumption by grapsid crabs at low and high temperatures (during winter and summer respectively), by using the leaf tethering-method (McGuinness, 1997), and assess its impact on sedimentary organic matter composition in the subtropical mangrove of Oura Bay. We also tested whether leaf consumption between the seasons could be affected by leaf species type and quality, namely, fresh green leaves, senescent leaves (yellow and brown) and decayed leaves (2 and 4 weeks). Since the low shore mangrove is occupied mostly by a mixture of juvenile (<10 mm carapace width) and adult crabs (>10 mm carapace width), and the high shore mangrove is occupied mostly by adults, we carried out an additional experiment to test whether crabs would choose similar leaf types and quality at both shore heights, and whether the amount of leaf consumed between the shore heights would be the same.

2. Material and methods

2.1. Study area

The leaf-feeding experiments were carried out at Oura Bay estuary located in the northern part of Okinawa Island in southern Japan (26.5°N, 128°E, Fig. 1). The mangrove forest consists of mixed stands of *Bruguiera gymnorrhiza*, *Kandelia obovata* and *Rhizophora stylosa* that cover an area of ~10 ha at the mouth of Oura River. The tree species of *B. gymnorrhiza* and *K. obovata* dominate in the

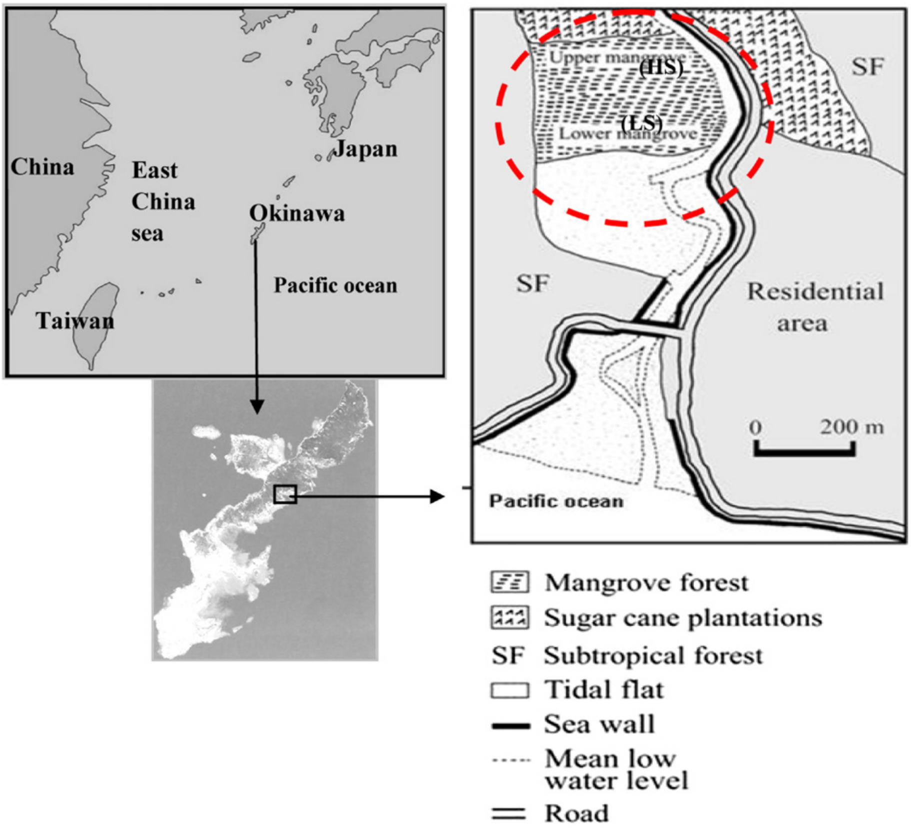

Fig. 1. Map of Okinawa island showing the location of Oura Bay estuary and experimental sites.

forest. *B. gymnorrhiza* is distributed throughout the mangrove forest, while *K. obovata* occurs abundantly in the lower intertidal and river banks. The two mangrove species are also the most common in Okinawa Island mangrove forests. Therefore they were selected for the crab feeding experiments. The species *R. stylosa* was not used in the feeding experiments because it is the least dominant species with <10 stands in the 10 ha mangrove forest.

The herbivorous grapsid crabs *Parasesarma pictum* and *Helice leachi* inhabit the mangrove forest of Oura bay. Enumeration of crab population density performed by visual count of animals active on the surface and burrow count methods (Salgado Kent and McGuinness, 2006) on two transects 4 m wide running perpendicular to the shore line, showed that the species *P. pictum* dominates the macrobenthos in terms of both adults and juveniles that feed on mangrove leaves. It is followed by *H. leachi,* with both species showing no apparent zonation in the mangrove. Overall, higher density of crabs was found in the high than low shore mangrove. However, in terms of size distribution (*P. pictum*; 18.3±3.2 mm and *H. leachi*; 14.5±2.8 mm carapace width), the abundance of adults was higher in the high shore mangrove than in the low shore mangrove, whereas the reverse was true about the abundance of juveniles (<10 mm carapace width).

The mean annual litter production is 12.95±2.95 t ha^{-1} with leaves contributing $>70\%$ (9.09±1.8 t ha^{-1}) of the total litter production. Litter production is highest during autumn and lowest during winter, with no significant differences between the high and low shore mangroves (Mfilinge et al., 2005). The tidal range is 2 m and both the high and low shore mangrove sites are frequently (twice a day) inundated by tides. The sediment surface in the mangroves varies from hard to soft mud, comprising the highest percentage of fine sand in the high shore and coarse sand in the low shore mangrove. Organic carbon, nitrogen and the C:N ratio are higher in the high shore than in the low shore mangrove, while litter decay rate is faster in the low shore than in the high shore mangrove (Mfilinge et al., 2002). The annual mean air temperature is 22.9 °C, the highest monthly mean occurs in July (28 °C), and the lowest monthly mean in January (14 °C) (Mfilinge et al., 2002, 2005). Precipitation peaks at a mean of 218 mm month^{-1} during the rainy season (May–July) and is at its lowest during the dry season (October–November), and winter through spring, with a mean of 116 mm month^{-1} (Mfilinge et al., 2002).

2.2. Experiments

For the feeding experiments we used fresh (green), senescent (yellow and brown) and decayed leaves (2 and 4 weeks) of the two dominant species (*B. gymnorrhiza* and *K. obovata*). The green leaves were picked from trees and senescent yellow leaves were picked from a shaken tree. Brown leaves were collected from the sediment surface. The decayed leaves (2 and 4 weeks) were obtained by placing senescent yellow leaves inside mesh bags, and then kept on the forest floor in the field for 2 and 4 weeks (Mfilinge et al., 2002). These leaves were specifically used for the comparison of leaf consumption and leaf choices of crabs between the winter and summer seasons.

Before experiments began, we determined nutrient levels, carbon (C) and nitrogen (N), in the leaves of *B. gymnorrhiza* and *K. obovata*, as they are important factors that may influence leaf species preferences for consumption by crabs (Micheli, 1993a; Ashton, 2002). For each species, twelve fresh (mature green leaves), senescent (yellow and brown) and decomposed leaves (2 and 4 weeks) were dried at 60 °C to constant weight. The dried leaf material was ground to a fine powder, which was then used for determining C and N contents in a Shimadzu high-sensitivity CN analyser (Model Sumigraph NC-80). Three replicates of powdered leaf material for each leaf category were measured.

2.2.1. Experiment 1: Effect of temperature on leaf litter consumption

Experiment 1 was specifically concerned with effects related to temperature; it tested whether temperature, leaf species, leaf type (decay state) and the duration of exposure in the field had significant effects on crab leaf consumption. The field feeding experiments were conducted during winter (December 2002–January 2003) and summer (July–August 2003). The average surface sediment (top 20 mm) temperature in the mangrove was 12.9 °C during the winter and 26.4 °C during the summer experiments. Since leaf abundance in the forest floor is the lowest during winter (Mfilinge et al., 2005), and the addition of tethered leaves would have increased the number of leaves available to crabs, the feeding experiments were performed in a relatively large area (2500 m^2 at each experimental site with 250 m^2 sub areas).

The experiments were conducted in the low shore mangroves dominated by *B. gymnorrhiza*. Twenty replicates of each leaf species and status, fresh (mature green leaves), senescent (yellow and brown), or decayed (2 and 4 weeks), were tethered to strings and deployed in the low shore mangroves. Each leaf was tied to a piece of a nylon string ~2 m long. Different colours (e.g. white, blue, yellow, red or black) of nylon strings were used to distinguish the tied leaf groups. At the same time, additional leaves for each species and litter type were placed in mesh bags and used as controls for losses in mass due to leaching and decay (Ashton, 2002). For each species 12 fresh leaves (mature green leaves), senescent leaves (yellow and brown) and decomposed leaves (2 and 4 weeks) were placed in mesh bags and deployed on the forest floor.

After 24 h, 48 h and 8 d from the beginning of the experiment, leaf remains were collected. Both tethered and control leaves were weighed to the closest 0.0001 g. After drying (60 °C) to constant weight, leaves were reweighed and used for subsequent conversion of wet weight to dry weight. The dry weight-wet weight regressions were used to convert the initial wet weights of the leaves to dry weights. The amount of leaves consumed in the low shore mangrove during winter was compared with the amount consumed in the low shore mangrove during summer. Experiments were repeated three times to take into account any possible and probable temporal differences that may occur within the winter and summer experiments.

At the end of the feeding experiments in winter and summer, surface sediment (upper 10 mm) was collected from nine locations located randomly in the high and low shore mangroves, and along the river (three samples per each sub location), and then analysed for C and N contents. Prior to analysis, 5 g of sediment for each sample was treated with 100 ml solution of 1N HCl to remove carbonates. Total organic C and N contents were measured in a Shimadzu high-sensitivity CN analyser (model Sumigraph NC-80).

2.2.2. Experiment 2: Effect of shore level on leaf consumption

Experiment 2 was specifically concerned with effects related to shore level and was carried out during the winter; it tested whether shore level, leaf species, leaf type (decay state) and the duration of exposure in the field had significant effects on crab leaf consumption. Only green, yellow and brown leaves were used. The tethered leaves were placed randomly in the high and low shore mangrove by tying leaves to prop roots or stems in each of the 250 m^2 sub areas to account for any spatial effect at each shore level. After 24 h, 48 h and 8 d from the beginning of the experiment, leaf remains were collected and processed. The amount of green, yellow and brown leaves consumed in the high shore mangrove (HS) was compared with the amount of green, yellow and brown leaves consumed in the low shore mangrove (LS) during the winter experiments. Each of these experiments was repeated three times (Mfilinge, 2004).

2.3. Statistical analyses

The mean original dry weight of the leaves was not the same for each species so results were expressed as percentage of original dry weight consumed. For experiment 1, a multifactorial ANOVA was used to test the effect on the percentage of leaves consumed by crabs due to the factors temperature (levels: low winter, high summer), time in season, i.e. temporal replicates (levels: 1, 2, 3), leaf species (levels: *B. gymnorrhiza* and *K. obovata*), leaf type (levels: green, yellow, brown, 2 weeks, 4 weeks) and duration of leaf deployment on the forest floor (levels: 24 h, 48 h, 8 d). For experiment 2, a multifactorial ANOVA was used to test the effect on the percentage of leaves consumed by crabs due to the factors shore level (levels: high, low), temporal replicates (levels: 1, 2, 3), Sub area (levels: 1, 2, 3, 4, 5), leaf species (levels: *B. gymnorrhiza* and *K. obovata*), leaf type (levels: green, yellow, brown) and duration of leaf deployment on the forest floor (levels: 24 h, 48 h, 8 d). A 2-way ANOVA was used to evaluate differences in the mean concentrations of C, N and the C:N ratio of mangrove surface sediments between the seasons. Post-hoc comparisons were done using Student-Newman-Keuls (SNK) test. All statistical analyses were performed using Stat View software (SAS Institute Inc.). A criterion of $p<0.05$ was used to determine statistical significance.

3. Results

3.1. Experiment 1: Effect of temperature on leaf litter consumption

Each independent factor by itself is likely to influence leaf consumption by crabs. During the low winter season temperatures there were significant differences in the mean percentages of leaves consumed among the three temporal replicates (ANOVA: $F=3.74$, $p<0.024$). SNK

Table 1
Experiment 1 — winter: Summary of multifactorial ANOVAs testing the effect of time within season (treatment), species, leaf type and exposure time on the percentage of leaf material consumed by crabs during winter

Source of variance	% consumed			
	df	SS	F-Value	P-Value
Treatment	2	2651.20	3.74	0.0239
Species	1	376017.34	1061.69	0.0001
Leaf type	4	41993.08	29.64	0.0001
Time	2	483895.18	683.14	0.0001
Species × Leaf type	4	12344.52	8.71	0.0001
Species × Time	2	71130.32	100.42	0.0001
Leaf types × Time	8	41090.42	14.50	0.0001
Species × Leaf type × Time	8	6352.12	2.24	0.0222
Residual	1710	605627.79		

df: degrees of freedom; SS: sum of squares. Statistical significance at $p<0.05$.

Table 2
Experiment 1 — summer: Summary of multifactorial ANOVAs testing the effect of time within season (treatment), species, leaf type and time (duration of exposure in the field) on the percentage of leaf material consumed by crabs during summer

Source of variance	% consumed			
	df	SS	F-Value	P-Value
Species	1	23553.83	195.68	0.0001
Leaf type	4	473964.60	984.40	0.0001
Time	2	43867.18	182.22	0.0001
Species × Leaf type	4	116994.31	242.99	0.0001
Species × Time	2	900.94	3.74	0.0239
Leaf type × Time	8	111370.98	115.66	0.0001
Species × Leaf types × Time	8	6336.83	6.58	0.0001
Residual	1710	205831.19		

df: degrees of freedom; SS: sum of squares. Statistical significance at $p<0.05$.

tests showed no significant difference between replicates 1 and 2, but both replicates 1 and 2 differed significantly from replicate 3, (at $p<0.05$). Significantly more leaves were consumed during replicates 1 and 2 than during replicate 3 (SNK: replicate $1=2>3$, at $p<0.05$). However, there was no significant interaction involving treatments with species, leaf type and the duration of exposure in the field in ANOVAs tests performed separately for each season (Table 1).

Table 3
Experiment 1: Summary of multifactorial ANOVAs testing the effect of temperature, time within season (treatment), species, leaf type and exposure time on the percentage of leaf material consumed by crabs

Source of variance	% consumed			
	df	SS	F-value	P-value
Temperature	1	365813.08	1541.77	0.0001
Treatment	2	2837.31	5.98	0.0026
Species	1	293895.36	1238.66	0.0001
Leaf type	4	371366.09	391.29	0.0001
Time	2	390431.49	822.76	0.0001
Temperature × Species	1	105675.81	445.39	0.0001
Temperature × Leaf type	4	144591.59	152.35	0.0001
Temperature × Time	2	137330.88	289.40	0.0001
Species × Leaf type	4	486107.287	90.73	0.0001
Species × Time	2	40482.17	85.31	0.0001
Leaf type × Time	8	125327.68	66.08	0.0001
Temperature × Species × Leaf type	4	43331.54	45.55	0.0001
Temperature × Species × Time	2	31549.09	66.48	0.0001
Temperature × Leaf type × Time	8	27033.72	14.24	0.0001
Species × Leaf type × Time	8	8297.13	4.37	0.0001
Temperature × Species × Leaf type × Time	8	4391.83	2.31	0.0179
Residual	3420	811458.98		

df: degrees of freedom; SS: sum of squares. Statistical significance at $p<0.05$.

Whereas during summer there was no significant difference in the mean percentages of leaves consumed among the three temporal replicates in ANOVAs (ANOVA: $F=2.37$, $p<0.094$), no significant treatment main effect or interaction involving treatments (mangrove species, leaf types and time) was recorded in the ANOVAs performed separately for each season (Table 2).

There were significant differences in the mean percentages of leaves consumed between seasons (winter and summer) with significant season main effects or interactions involving season with species, leaf type and exposure time, except temporal replicates in ANOVAs (Table 3). Significantly more leaves were consumed during summer than winter (SNK: summer > winter, at $p<0.05$). During both seasons crabs consumed significantly more *K. obovata* than *B. gymnorrhiza* leaves (SNK: *K. obovata* > *B. gymnorrhiza*, at $p<0.05$) with preference for aged leaves (SNK: 2 and 4 wk > brown > yellow > green, at $p<0.05$). In most cases during summer all leaves, particularly the yellow, brown and 2 and 4 wk samples of both species were consumed within 24 h. The preference for aged leaves for both species within the 24 h observation period was significant (SNK: 2 weeks = 4 weeks = brown > yellow > green, at $p<0.05$). Although crabs showed preference for aged leaves in summer, during the winter season crabs consumed significantly more green leaves of *K. obovata* than aged leaves of *B. gymnorrhiza* within 24 h and 48 h of observation.

There were significant differences in the mean concentrations of C (ANOVA, $p<0.0001$), and the C/N ratios (ANOVA, $p<0.0001$) in the mangrove surface sediments

Table 4
Experiment 2 — Low shore mangrove: Summary of multifactorial ANOVAs testing the effect of sub area (small areas within a shore level), time within season (treatment), species, leaf type and exposure time on the percentage of leaf material consumed by crabs in the lower shore level

Source of variance	% consumed			
	df	SS	F-Value	P-Value
Treatment	2	5296.030	7.754	0.0005
Sub area	4	13239.385	9.693	0.0001
Species	1	293214.147	858.651	0.0001
Leaf type	2	19327.329	28.299	0.0001
Time	2	342144.456	500.97	0.0001
Sub area × Species	4	8449.811	6.1686	0.0001
Sub area × Leaf type	8	17604.350	6.444	0.0001
Species × Time	2	48543.382	71.077	0.0001
Leaf type × Time	4	33444.643	24.485	0.0001
Sub area × Species × Leaf type	8	14929.266	5.465	0.0001
Residual	810	276600.677		

(All other interactions involving treatment and sub area were not significant, and therefore were not included in this table). df: degrees of freedom; SS: sum of squares. Statistical significance at $p<0.05$.

Table 5
Experiment 2—High shore mangrove: Summary of multifactorial ANOVAs testing the effect of sub area (small areas within a shore level), time within season (treatment), species, leaf type and exposure time on the percentage of leaf material consumed by crabs in the high shore level

Source of variance	% consumed			
	df	SS	F-Value	P-Value
Sub area	4	8794.52	7.345	0.0001
Species	1	249521.906	833.588	0.0001
Leaf type	2	23763.036	39.693	0.0001
Time	2	295668.339	493.876	0.0001
Sub area × Species	4	6811.841	5.689	0.0002
Sub area × Leaf type	8	24480.96	10.223	0.0001
Sub area × Time	8	7711.968	3.22	0.0013
Species × Leaf type	2	3200.092	5.345	0.0049
Species × Time	2	90384.079	150.975	0.0001
Leaf type × Time	4	50728.593	42.368	0.0001
Sub area × Species × Leaf type	8	18973.175	7.923	0.0001
Sub area × Leaf type × Time	16	8985.691	1.876	0.0195
Species × Leaf type × Time	4	8523.973	7.119	0.0001
Residual	810	242461.142		

(All other interactions involving treatment and sub area were not significant, and therefore were not included in this table). df: degrees of freedom; SS: sum of squares. Statistical significance at $p<0.05$.

between winter and summer seasons. There were significantly lower C (means, 20.8 vs 26.9 mg g^{-1} dry wt) and significantly lower C/N ratios (means, 12.1 vs 15.1) in the sediments during winter than during summer. N concentrations did not differ significantly between the seasons (means, 1.722 vs 1.790 mg g^{-1} dry wt; ANOVA, $p=0.293$).

3.2. Experiment 2: Effect of shore level on leaf litter consumption

3.2.1. Temporal and spatial variations at each shore level

There were significant temporal replicate and sub areas (spatial) effects in the mean percentages of leaves consumed in the low shore mangrove, with no significant interaction between the two factors. In addition, at this shore level there were no significant interactions involving treatments with either of the other factors. But there were significant interaction involving sub area, species and leaf type in ANOVAs (Table 4). On the high shore mangrove there were no significant temporal and spatial effects in the mean percentages of leaves consumed, with no significant interaction between the two factors. Time within season did not have any significant interaction with either of the other factors species, leaf type and exposure time in ANOVAs (Table 5).

3.2.2. Overall variations at both shore levels

There were significant differences in the mean percentages of leaves consumed between shore levels, temporal replicates, sub areas (spatial), species, leaf type and exposure time, with no significant shore level main effect or interaction involving shore level with temporal and spatial factors in ANOVAs (Table 6). Results also indicated a significant shore level, species and exposure time interaction in ANOVAs, suggesting that crabs had consumed different amounts of leaves of each species at different times. Significantly more leaves were consumed in the high shore than in the low shore mangrove (SNK, at $p<0.05$). At both shore levels crabs consumed significantly more *K. obovata* leaves than *B. gymnorrhiza* leaves (SNK, at $p<0.05$) with preference for aged leaves at both shore levels (SNK: brown > yellow > green, $p<0.05$). For *K. obovata* a great proportion of leaves was consumed within the first 24 h (SNK: 24 h > 48 h > 8 d, $p<0.05$), while for *B. gymnorrhiza* it was after 48 h (SNK: 48 h > 8 d > 24 h, $p<0.05$). There was no significant interaction involving shore level, species, leaf type and exposure time in ANOVAs (Table 6), suggesting that crabs chose the same leaf species, leaf type at both shore levels.

Table 6
Experiment 2: Summary of multifactorial ANOVAs testing the effect of shore level, sub area (area within a shore level), time within season (treatment), species, leaf type and exposure time on the percentage of leaf material consumed by crabs

Source of variance	% consumed			
	df	SS	F-value	P-value
Shore level	1	42833.38	133.68	0.0001
Treatment	2	5102.72	7.96	0.0004
Sub area	4	21767.26	16.98	0.0001
Species	1	541855.28	1691.14	0.0001
Leaf type	2	42975.83	67.06	0.0001
Time	2	635128.44	991.12	0.0001
Shore level × Time	2	2684.36	4.19	0.0153
Sub area × Species	4	14858.78	11.59	0.0001
Sub area × Leaf type	8	41347.39	16.13	0.0001
Sub area × Time	8	11841.56	4.62	0.0001
Species × Leaf type	2	4190.76	6.54	0.0015
Species × Time	2	135623.36	211.64	0.0001
Leaf type × Time	4	82699.13	64.53	0.0001
Shore level × Species × Time	2	3304.10	5.16	0.0059
Sub area × Species × Leaf type	8	33632.89	13.12	0.0001
Sub area × Species × Time	8	4519.39	1.76	0.08
Sub area × Leaf type × Time	16	13140.07	2.56	0.0006
Species × Leaf type × Time	4	9870.52	7.70	0.0001
Sub area × Species × Leaf type × Time	16	11077.37	2.16	0.0049
Residual	1620	519061.82		

df: degrees of freedom; SS: sum of squares. Statistical significance was at $p=0.05$.

4. Discussion

4.1. Effect of temperature on leaf litter consumption

This study was carried out to assess the effect of temperature on leaf litter consumption by grapsid crabs in the mangrove forest of Oura Bay. No significant time within temperature effects or interaction involving this factor with species, leaf type and exposure time were found, suggesting that there were no temporal differences within the seasons themselves, and thus the detected differences were seasonal. The lowest percentage of leaves consumed occurred in replicate 3 during the low winter temperatures. These experiments were performed in December through January. Since the third replicate was carried out between mid January and late January, when mean temperatures are the lowest in Okinawa (Mfilinge et al., 2005), the low percentage of leaves consumed could possibly be explained by the reduced crab activity during the period of low temperatures.

Crabs consumed more leaves during summer than winter during the study period. For invertebrates in general, increased temperature leads to acceleration of metabolic demands through increased activity, hence increased food requirement. For example Camilleri (1989) demonstrated in a laboratory experiment that crabs consume more leaf material at 30 °C than at 20 °C. In another investigation, Nakasone et al. (1982) reported that the sesarmid crab *Chasmagnathus convexus* ceased activity outside burrows when air temperature dropped below 13.8 °C. The average surface sediment temperature during our study was 12.9 °C. Such a low temperature would possibly force crabs to remain inside burrows, thus greatly reducing the consumption of surface mangrove leaves. Further evidence suggests that lower temperatures affect the rate of gastric evacuation and enzyme secretion, resulting in decreased desire for food (Mia et al., 2001).

Apart from temperature, the effect of season seems to be even more complex as it also relates to a number of factors: leaf species, leaf type and time, the duration of exposure in the field. Leaf quality varies between species, for example *K. obovata* leaves are nutritionally of higher quality than *B. gymnorrhiza* (Mfilinge et al., 2002), and possibly also seasonally within species, due to changes in photosynthetic production rates. Studies show that crabs prefer leaves with lower tannin content or lower C/N ratio and higher nutritional value (Ashton, 2002; Skov and Hartnoll, 2002). Tannin content was not measured in this study. During both seasons crabs consumed significantly more *K. obovata* leaves than *B. gymnorrhiza* leaves. *K. obovata* leaves have considerably lower C/N ratios than *B. gymnorrhiza* leaves (Mfilinge et al., 2002, 2003), and are therefore of higher nutritional quality than those of *B. gymnorrhiza*. This suggests that the preference for *K. obovata* leaves was related to their higher nutritional values. In addition, leaves with lower C/N ratios are known to support rapid fungal colonisation (Mfilinge et al., 2003), which may affect leaf palatability and possibly provide shredders with feeding cues.

With regard to the duration of exposure, during summer crabs consumed most, especially the aged, leaves in the first 24 h. This is because crabs are more active at this time of the year due to higher temperatures. The higher consumption of aged leaves during summer than winter could also be related to their higher nutritional quality (Giddins et al., 1986; Lee, 1989; Micheli, 1993b). Aged leaves of both species were consumed faster than fresh leaves. This preference for aged leaves could also be related to leaf availability on the ground. Green leaves are normally only available after storms, unless a crab has an arboreal habit (Vannini and Ruwa, 1994; Sivasothi et al., 1996).

The large difference in C/N ratio of green *K. obovata* between winter and summer is probably due to lower photosynthetic production during winter than summer, as well as to the increase in nitrogen in the leaves. The consumption of more green leaves of *K. obovata* than aged leaves of *B. gymnorrhiza* during winter was unexpected, considering that at this time of year forest productivity (in terms of leaf litter production) was the lowest (Mfilinge et al., 2005). Crabs were expected to be more opportunistic during this time of the year when food was scarce, which should predict a preference for higher quality leaves such as the green leaves of *K. obovata* during the winter season.

Based on leaf litter production data in Oura Bay, this study found that leaf consumption was 0.07 g m^{-2} d^{-1} (~ 5% of the leaf fall) and 1.076 g m^{-2} d^{-1} (~ 37% of the leaf fall) in winter and summer, respectively, in Oura Bay mangrove forest. A comparison with another study carried out during the summer season in South Africa in an *Avicennia marina* forest showed that *Sesarma meinerti* consumed 43.58% of the leaf fall (Emmerson and McGwynne, 1992).

The consumption and burial of litter within the mangrove forest by benthic animals help to retain organic matter and increase nutrient turnover within mangroves (Robertson, 1986; Lee, 1989; Emmerson and McGwynne, 1992). Mangrove litter is often characterised by high C/N ratios and poor nutrient contents (Robertson, 1988; Mfilinge et al., 2002). Thus high C/N ratios in estuarine sediments have since been related to increases of mangrove outwelling (Boto and Bunt, 1981; Mfilinge et al., 2005). Likewise, in freshwater wetlands, Wetzel (1983) reported an increase in the C/N ratio due to input of a greater proportion of organic content from vascular plant material produced in the wetland and littoral marsh areas. This also suggests that a low C/N ratio would indicate a relatively lower input of organic material from mangroves (Mfilinge et al., 2005).

The lower contents of organic C and N (20.82±0.89 and 1.72±0.11 mg g^{-1} dwt, respectively) and the lower C/N ratio (12.11±0.30) found in the surface sediments during winter is consistent with the lower leaf consumption, signifying that reduced crab consumption as well as reduced leaf fall in winter leads to reduced sediment organic matter. Whereas the higher organic C (26.91± 2.16) and N (1.79±0.18) mg g^{-1} dw, and the higher C/N ratio (15.05±0.67) found in the surface sediments during summer signify high input of organic matter in the sediments. These results suggest that crab feeding activities play an important role in the retention of organic matter within the mangrove forest of Oura Bay.

4.2. Effect of shore level on leaf consumption

Spatial variability rather than temporal changes had more effect on leaf consumption in each of the shore levels. In this mangrove forest, sediment characteristics especially in terms of grain size distribution of the top 2 mm, did not differ significantly, except for the higher proportions of fine sand and coarse sand in the high and low shore mangrove, respectively. Differences in leaf consumption among sub areas could be explained by aggregation of crabs under tree trunks where there is more water, plenty of decomposing leaves to feed on and abundant refuge (pers. obs.). The deployed leaves were not confined to tree trunks, so leaves far from trunks were probably less likely to be consumed as fast as those nearer to tree trunks. However, there was no significant spatial effects (shore level, sub area, species, leaf type and duration of exposure) on the percent of leaves consumed and spatial variability was similar across the high and low shore levels.

Crabs consumed similar leaf types and quality in the high and low shore mangrove, as there was no significant interaction between shore levels, species and leaf types. However, significantly more leaves were consumed in the high- than in the low-shore mangrove. Previous reports show that sesarmids are zoned across the intertidal area, with small-sized species generally occupying the lower levels and larger species the high intertidal forests (Sasekumar, 1984; Jones, 1984). Emmerson and McGwynne (1992) also found a significant correlation between crab size and mass of leaf consumed; that larger crabs consumed higher dry litter mass per day and exerted a major influence on the turnover of leaf litter than the smaller crabs. This suggests that the difference in leaf consumption between the high and low intertidal mangrove in Oura Bay could be related to differences in crab size composition between the high and low shore mangroves.

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References

Ashton, E.C., 2002. Mangrove sesarmid crab feeding experiments in Peninsular Malaysia. J. Exp. Mar. Biol. Ecol. 273, 97–119.

Boto, K.G., Bunt, J.S., 1981. Tidal export of particulate organic matter from a northern Australian mangrove system. Estuar. Coast. Shelf Sci. 13, 247–255.

Camilleri, J., 1989. Leaf choice by crustaceans in a mangrove forest in Qeensland. Mar. Biol. 102, 453–459.

Chale, F.M.M., 1996. Litter production in an *Avicennia geminans* (L.) Stearn forest in Guyana, South America. Hydrobiologia 330, 47–53.

Emmerson, W.D., McGwynne, L.E., 1992. Feeding and assimilation of mangrove leaves by the crab *Sesarma meinerti* de Man in relation to leaf-litter production in Mgazana, a warm temperate southern African mangrove swamp. J. Exp. Mar. Biol. Ecol. 157, 41–53.

Giddins, R.L., Lucas, J.S., Neilson, M.J., Richards, G.N., 1986. Feeding ecology of the mangrove crab *Neosarmatium smithi* (Crustacea: Decapoda: Sesarmidae). Mar. Ecol., Prog. Ser. 33, 147–155.

Jones, D.A., 1984. Crabs of the mangal ecosystem. Dtsch. Hydrobiol. 20, 89–109.

Lee, S.Y., 1989. The importance of sesarminae crabs *Chiromanthes* spp. and inundation frequency on mangrove (*Kandelia candel* (L.) Druce) leaf litter turnover in a Hong Kong tidal shrimp pond. J. Exp. Mar. Biol. Ecol. 131, 23–43.

Lee, S.Y., 1998. Ecological role of grapsid crabs in mangrove ecosystems: a review. Mar. Freshw. Res. 49, 335–343.

Lee, S.Y., 1999. Tropical mangrove ecology: physical and biotic factors influencing ecosystem structure and function. Aust. J. Ecol. 24, 355–366.

McGuinness, K.A., 1997. Tests for artifacts in some methods used to study herbivory and predation in mangrove forests. Mar. Ecol., Prog. Ser. 153, 37–44.

Mfilinge, P.L., 2004. Fatty acids and nutrients in decomposing mangrove leaves. Ph.D. Thesis, University of the Ryukyus, Okinawa, 133 pp.

Mfilinge, P.L., Atta, N., Tsuchiya, M., 2002. Nutrient dynamics and leaf litter decomposition in a subtropical mangrove at Oura Bay Okinawa Japan. Trees Struct. Funct. 16, 172–180.

Mfilinge, P.L., Meziane, T., Bachok, Z., Tsuchiya, M., 2003. Fatty acids in decomposing mangrove leaves: microbial activity, decay and nutritional quality. Mar. Ecol., Prog. Ser. 265, 97–105.

Mfilinge, P.L., Meziane, T., Bachok, Z., Tsuchiya, M., 2005. Litter dynamics and particulate organic matter outwelling from a subtropical mangrove in Okinawa Island, South Japan. Estuar. Coast. Shelf Sci. 63, 301–313.

Mia, Y., Shokita, S., Watanabe, S., 2001. Stomach content of two grapsid crabs, *Helice formosensis* and *Helice leachi*. Fish. Sci. 67, 173–175.

Micheli, F., 1993a. Feeding ecology of mangrove crabs in North Eastern Australia: mangrove litter consumption by *Sesarma messa* and *Sesarma smithii*. J. Exp. Mar. Biol. Ecol. 171, 165–186.

Micheli, F., 1993b. Effect of mangrove litter species and availability on survival, moulting and reproduction of the mangrove crab *Sesarma messa*. J. Exp. Mar. Biol. Ecol. 171, 149–163.

Nakasone, Y., Ono, Y., Goshima, S., 1982. Daily activity and food consumption of the sesarmid crab, *Chasmagnathus convexus* (Decapoda, Brachyura). Bull. Coll. Educ. Univ. Ryukyus 26, 37–53.

Nordhaus, I., Wolff, M., Diele, K., 2006. Litter processing and population food intake of the mangrove crab *Ucides cordatus* in a high intertidal forest in northern Brazil. Estuar. Coast. Shelf Sci. 67, 239–250.

Robertson, A.I., 1986. Leaf-burying crabs: their influence on energy flow and export from mixed mangrove forests (*Rhizhophora* spp.) in northeastern Australia. J. Exp. Mar. Biol. Ecol. 102, 237–248.

Robertson, A.I., 1988. Decomposition of mangrove leaf litter in tropical Australia. J. Exp. Mar. Biol. Ecol. 116, 235–247.

Robertson, A.I., Daniel, P.A., 1989. The influence of crabs on litter processing in high intertidal mangrove forests in tropical Australia. Oecologia 78, 191–198.

Salgado Kent, C.P., McGuinness, K.A., 2006. A comparison of methods for estimating relative abundance of grapsid crabs. Wetlands Ecol. Manag. 14, 1–9.

Sasekumar, A., 1984. Secondary productivity in mangrove forests. In: Ong, J.E., Gong, W.K. (Eds.), Proc. Workshop on Productivity of the Mangrove Ecosystem: Management Implications. University Sains Malaysia, Penang, pp. 20–28.

Sivasothi, N., Murphy, D.H., Ng, P.K.L., 1996. Tree-climbing and herbivory of crabs in the Singapore mangroves. In: Sasekumar, A. (Ed.), Proc. Workshop on Mangrove Fisheries Connections. Living Coastal Resources, Kuala Lumpur, pp. 220–237.

Skov, M.W., Hartnoll, R.G., 2002. Paradoxical selective feeding on a low-nutrient diet: why do mangrove crabs eat leaves? Oecologia 131, 1–7.

Steinke, T.D., Ward, C.J., 1988. Litter production by mangrove, II: St. Lucia and Richards Bay. S. Afr. J. Bot. 54, 445–454.

Twilley, R.R., Pozo, M., Garcia, V.H., 1997. Litter dynamics in riverine mangrove forests in the Guyas River estuary, Ecuador. Oecologia 111, 109–122.

Vannini, M., Ruwa, R.K., 1994. Vertical migrations in the tree crab *Sesarma leptosoma* (Decapoda: Grapsidae). Mar. Biol. 118, 271–278.

Wetzel, R.G., 1983. Limnology, 2nd ed. Saunders College Publishing, Philadelphia, USA. 767 pp.

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Nutrient dynamics in mangrove crab burrow sediments subjected to anthropogenic input

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Abstract

Bioturbation by burrowing macroinvertebrates has a major impact on sediment properties, pollutant redistribution, and biogeochemical cycling. We assessed the impact of bioturbation on the nutrient dynamics and organic matter of sediments receiving anthropogenic inputs in the Manko wetland, located in southern Okinawa, Japan. We compared sediments that were and were not subjected to the activities of the tidal-flat crab *Helice formosensis*. The fatty acid composition of sediments indicated that different sources contributed to the organic matter profile. Agricultural and domestic waste discharge seemed to induce a high amount of green macroalgae and bacteria in the tidal flat. Sediments without crabs exhibited 2.1–2.4× more NH_4-N release, which was associated with a low C/N ratio during the summer. In the crab burrow sediments, NO_3-N concentrations were 1.4–1.9× more pronounced during winter. A significant correlation existed between NO_3-N and NO_2-N concentrations in sediments of the burrow chamber ($r=0.837$, $p<0.02$) and the mixed zone of burrow opening shaft and chamber ($r=0.885$, $p<0.01$). We suggest that burrow wall sediments provide ideal conditions for nitrate reduction (denitrification). *H. formosensis* thus contributes to balancing the effects of anthropogenic inputs by removing nitrogen loads in sediments.

Keywords: Bioturbation; Fatty acid composition; *Helice formosensis*; Nutrient dynamics

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1. Introduction

Bioturbation processes by macrofauna are important in controlling nutrient cycling within sediments. Activities such as feeding, burrowing, and ventilation strongly influence organic matter decomposition and nutrient exchange in sediments (Aller, 1994; Hansen and Kristensen, 1997). Although their activities may be limited to a narrow sediment layer, invertebrate species at high densities can significantly affect benthic microbial processes and nutrient dynamics up to the ecosystem level (Stief and De Beer, 2004). In addition, growing evidence suggests that benthic sediment processes have the potential to counteract the effects of eutrophication (Hansen and Kristensen, 1997).

Eutrophication and urban pollution have a major influence on the environmental quality of coastal areas. Sediments usually receive organic matter from autochthonous sources originating from diatoms, bacteria (Mfilinge et al., 2005), green macroalgae (Meziane and Tsuchiya, 2000), and fresh and decomposed litter (Tam et al., 1990). Anthropogenic inputs, however, originate from agricultural run-off, fertilisation, or livestock waste from sewage and domestic waste discharge (Cloern, 2001). Consequently, the natural balance between production and

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decomposition of organic matter has been disturbed in many coastal areas (Ferguson, 2002). Understanding the sources of anthropogenic inputs and their impacts on ecosystems is therefore a major environmental concern.

Discrimination of organic matter sources in marine ecosystems has been carried out using fatty acids as biomarkers (Meziane and Tsuchiya, 2000). Because of their structural diversity and high biological specificity (Parkers, 1987), fatty acids can assist in determining the source and fate of organic materials in sediments (Meziane and Tsuchiya, 2002). They can be used as tracers to identify the origin of organic matter and nutrient dynamics (Dittmar et al., 2001), to determine microbial biomass and community structure in sediments (Findlay et al., 1995), and to characterise polluted sediments (Parkers and Taylor, 1985).

The primary aim of this study was to assess the influence of bioturbation on the nutrient dynamics of sediments receiving anthropogenic inputs. We compared sediments without crabs and sediments subjected to the activities of the tidal-flat crab *Helice formosensis*, a dominant species in the upper mangrove swamp at Manko estuary, Okinawa, Japan (Islam et al., 2002; Mchenga et al., 2007). We further investigated changes in autochthonous sources and anthropogenic inputs of organic matter to the tidal flat during summer and winter by comparing concentrations of fatty acid (FA) biomarkers of organic sources in: (i) sediments between burrow components; and (ii) sediments that were or were not inhabited by the crabs. We hypothesised that sediments surrounding crab burrows and bulk surface sediments would differ in nutrients (NO_3-N, NO_2-N, NH_4-N and PO_4-P) and organic matter content.

2. Material and methods

2.1. Area studied

The study was conducted in the 58-ha Manko wetland, which is characterised by a mudflat, mangrove forest, and a mild subtropical climate, and is located in the southern part of Okinawa Island, Japan (26°N and 128°E; Fig. 1). The average annual temperature is 23.2 °C. The lowest monthly mean occurs in February (16.8 °C) and the highest monthly mean temperature occurs in July (28.8 °C). Precipitation is over 100 mm mo^{-1} throughout the year and the average rainfall is 2086 mm y^{-1}. The tidal flat is located at the confluence of the Kokuba and Noha Rivers and serves as a natural breeding reserve for species of crabs, fishes, and various migratory water birds. The mangrove forest found on both banks in the lower course is dominated by *Kandelia obovata*. The most common crabs are the grapsid (*H. formosensis, Perisesarma bidens,*

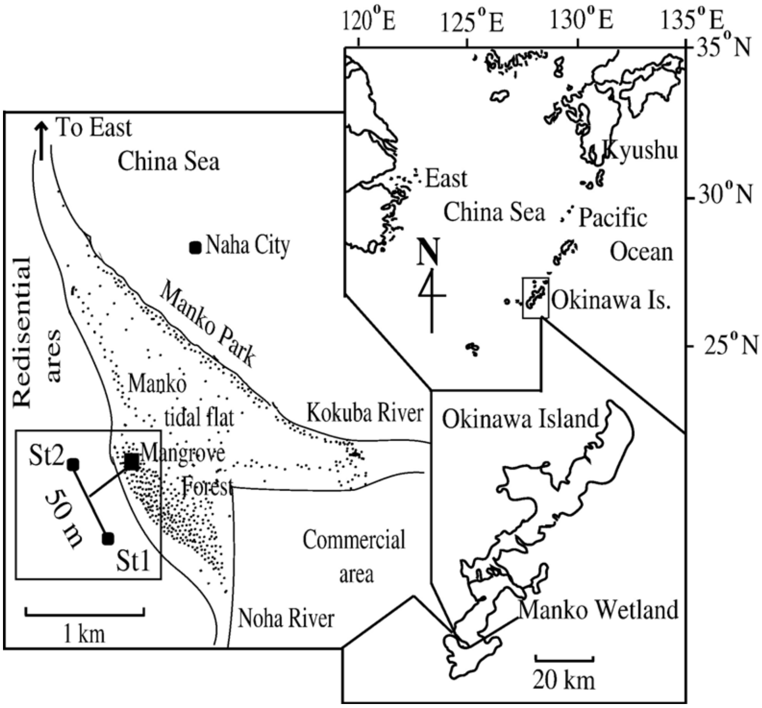

Fig. 1. Manko tidal flat, Okinawa Island. Study sites (St) 1 and 2 are indicated.

Table 1
Sediment characteristics of the surface with and without crab, burrow opening and burrow chamber

	Surface without crabs	Surface with crabs	Burrow opening	Burrow chamberC
% Granules	6.3±1.3	11.8±2.0	4.4±0.9	4.7±2.8
% Very coarse sand	15.9±3.0	25.7±2.6	14.8±2.2	15.9±2.5
% Coarse sand	25.2±2.2	24.9±3.1	25.4±1.4	28.8±2.1
% Medium sand	33.9±2.0	24.1±2.8	35.2±3.5	34.3±4.1
% Fine sand	8.0±1.7	4.4±0.8	10.3±0.9	7.6±0.6
% Very fine sand	4.4±1.5	2.3±0.5	5.3±0.6	3.6±0.5
% Silt mud	2.0±0.9	0.6±0.2	3.2±1.3	1.2±0.2
% Clay mud	0.2±0.2	0.0±0.0	0.1±0.1	0.1±0.1
% Water	19.2±0.9	18.1±2.3	20.7±1.1	17.4±0.3
TN (mg g^{-1})	1.3±0.0	2.1±0.1	1.4±0.1	1.2±0.0
TC (mg g^{-1})	24.3±0.3	20.5±0.3	12.9±0.7	13.1±0.2
C/N ratio	18.6±0.4	9.6±0.5	9.4±0.0	11.0±0.1

Values are means and standard deviation. TC: total carbon, TN: total nitrogen and C/N: carbon: nitrogen ratio.

Chasmagnathus convexus, Neosarmatium smithi, and *Sesarmops intermedium)* and ocypopid (*Uca lactea perplexa, U. dussumieri dussumieri,* and *U. chlorophthalmus crassipes*). The Manko basin does not support any major industrial activity, although agriculture, livestock, and domestic waste discharge have been reported (Tashiro et al., 2003) and may affect the water quality and benthic processes in the tidal-flat sediments. Thus, the site is useful in elucidating the impact of human activity on the nutrient dynamics and organic matter processes in the tidal flat ecosystem.

2.2. Sample collection

Sampling was performed during the summer (July 2005) and winter (January 2006) seasons. Sediments were collected from two stations located ~50 m apart (Fig. 1). The first station had a high grapsid crab burrow density, particularly of *H. formosensis*, whereas the second station had no crab burrows. Triplicate sediment samples were randomly collected from surfaces (~1 cm in depth) inhabited by crabs and from those without crabs and burrow compartments. For burrow sampling, a thin layer of the burrow wall opening was carefully scraped from the opening shafts (to ~10 cm depth) using sterile spatulas. Sediment samples were pooled from two openings of the same burrow. For the burrow chamber sample, similar burrows were filled with a polyester resin to determine its morphology. After 24 h, the cast was carefully removed (casting method of Dworschak, 1983) and a 1-cm slice of sediment was collected from the bottom of the burrow chamber (Mchenga et al., 2007). Sediment samples were then taken to evaluate organic matter, grain size, nutrient and fatty acid composition.

2.3. Analytical methods

Sediments were first dried at 80 °C to a constant weight and then used to determine water content. The total organic carbon (TC) and nitrogen (TN) contents of the sediments were analysed using a high-sensitivity C/N analyser (Shimadzu NC 80). Prior to analysis, 1 g of each sediment sample was treated with 20 ml of a 1 N HCl solution for 24 h to remove carbonates and bicarbonate. A subsample was ignited in an electrical muffle furnace (FUL 220FA) at 550 °C for 3 h to obtain the percentage loss on ignition (% LOI) as a measure of total organic matter (TOM). Grain size distribution was evaluated by sieve and sedimentation analysis following Ingram (1971).

Dissolved organic carbon (DOC) extractions were performed in triplicate for each sediment category using Milli-Q Millipore water (Jone and Willett, 2005). Oven-dried sediment samples (2.5 g; <1 mm) were shaken with

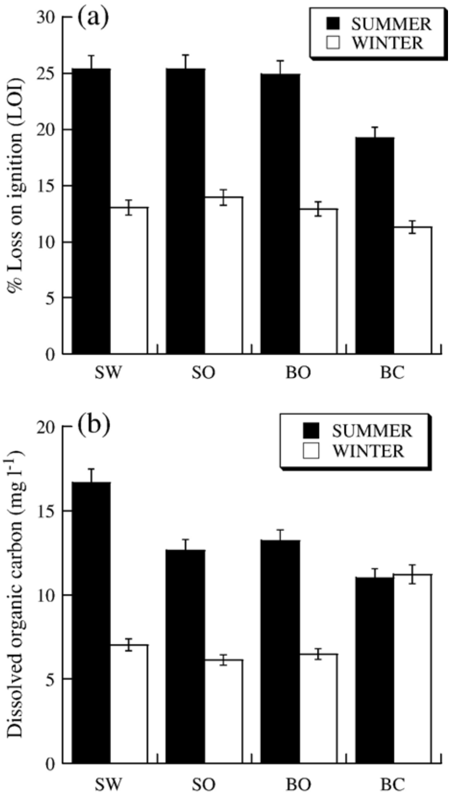

Fig. 2. Seasonal variation in: (a) total organic matter, and (b) dissolved organic carbon. SW: surface with crabs; SO: surface without crabs; BO: burrow opening; and BC: burrow chamber. Values are means and standard deviations.

25 ml of Milli-Q water solution (1:10 w/v soil to solution ratio) for 1 h in 50-ml bottles on a reciprocating shaker at 200 rev min^{-1}. The soil extracts were then centrifuged at 2500 rpm for 15 min to obtain a clear supernatant liquid before filtering with Whatman filter paper. The filtrate was stored in small glass bottles in a −40 °C freezer prior to analysis. DOC concentrations were analysed by a DOC HITACHI TOC-$\mathrm{V_{CSH}}$ auto analyser.

Measurement of NO_3-N, NO_2-N, and NH_4-N was conducted using the alkaline reagent 2 M KCl to extract sediments (Jone and Willett, 2005), and PO_4-P levels were determined after the extraction of air-dried sediments using a solution of 0.01 M $CaCl_2$ (Kuo, 1996). All extracts were treated following the above-mentioned procedures and analysed using a QuAAtro automatic water analyser (Bran + Luebbe GmbH, Norderstedt, Germany).

Table 2
FA concentrations (μg g^{-1} dry wt) in surface sediments with crabs (SW), without crabs (SO), burrow opening (BO) and burrow chamber (BC)

	Summer				Winter			
	SW	SO	BO	BC	SW	SO	BO	BC
Saturated								
14:0	2.6±1.1	2.5±0.6	0.5±0.1	2.7±2.0	4.8±0.5	1.4±0.3	2.0±0.7	4.1±2.7
15:0	0.6±0.2	1.0±0.2	–	3.6±1.6	0.9±0.1	–	0.7±0.1	1.5±0.9
16:0	27±0.7	35.1±4.9	13.4±0.4	99.4±13	56.4±11	22.4±4.3	25±4.2	60.8±20.0
17:0	0.8±0.4	0.9±0.3	0.6±0.1	5.3±0.9	0.7±0.0	1.4±0.7	1.1±0.3	2.5±1.1
18:0	3.3±0.2	7.4±0.9	4.9±0.5	40.7±8.9	4.3±1.4	2.7±0.5	6.4±0.9	24.3±4.4
20:0	0.5±0.3	0.5±0.2	–	–	–	–	–	0.7±1.2
22:0	–	0.8±0.1	0.5±0.1	3.4±3.0	0.5±0.5	–	1.0±0.0	1.3±2.2
24:0	0.6±0.2	1.8±0.8	0.9±0.1	9.1±5.6	3.0±1.8	1.6±0.3	2.3±0.7	1.3±2.2
26:0	0.9±0.4	0.8±0.1	0.5±0.1	20.8±5.4	–	–	1.6±0.8	1.0±1.7
28:0	2.4±0.2	0.8±0.2	1.4±0.6	3.6±3.2	0.5±0.7	0.7±0.5	4.3±2.7	13.9±4.1
30:0	–	6.3±3.8	–	–	–	–	–	–
Total	38.6±3.8	58.4±12	23.8±1.9	188.6±43	71±16.6	30.2±6.7	44.3±10	111.4±40.5
Branched								
15:0i	1.3±0.5	2.4±0.6	1.1±0.1	7.0±1.0	1.7±0.3	1.3±0.3	3.2±0.2	8.5±4.6
15:0a	0.6±0.3	1.2±0.3	0.6±0.1	3.4±0.6	1.0±0.2	0.8±0.2	1.8±0.1	4.5±2.6
17:0i	1.9±0.4	1.6±0.9	0.9±0.1	6.1±1.2	1.6±0.4	1.2±0.5	1.9±1.0	3.6±2.2
17:0a	0.8±0.3	1.0±0.2	0.8±0.2	5.6±1.2	1.6±0.6	1.2±0.2	2.0±0.9	3.4±1.7
Total	4.6±1.5	6.1±2	3.4±0.5	22.1±4.1	5.9±1.5	4.5±1.2	8.9±2.2	20.1±11.0
Monounsaturated								
16:1ω7	2.8±0.2	7.1±1.3	2.6±0.2	18.7±3.5	3.7±0.1	2.1±0.4	5.1±0.2	11.6±2.2
17:01	0.6±0.6	1.7±0.6	–	–	0.9±1.5	–	1.0±0.9	1.2±2.1
18:1ω9	3.9±0.5	7.2±1.1	2.4±0.2	37.4±14	7.5±1.9	4.2±1.0	8.5±4.5	21.3±6.8
18:1ω7	4.7±0.3	10.9±1.4	3.1±0.2	37.1±3.3	7.0±3.4	6.0±1.0	6.1±7.5	33.0±16.5
Total	11.9±1.6	26.9±4.4	8.1±0.7	93.1±21	19.1±6.9	12.2±2.5	20.7±13	67.1±27.6
Polyunsaturated								
18:2ω6	1.6±0.2	2.8±0.1	0.5±0.1	14.4±4.0	3.2±1.1	1.3±0.2	0.6±1.0	3.4±1.2
18:3ω6	–	0.6±0.1	–	1.1±2.0	–	–	–	–
18:3ω3	0.8±0.3	1.9±0.6	–	4.4±4.1	2.0±0.7	0.5±0.1	–	–
18:4ω3	0.6±0.2	0.8±0.1	–	0.9±1.5	1.1±0.4	–	–	–
20:02	–	–	–	2.0±3.5	–	–	–	4.1±2.0
20:3ω6	0.8±0.9	–	–	–	2.5±1.6	–	0.6±0.8	–
20:4ω6	–	–	–	4.4±7.7	–	1.5±0.3	–	2.2±3.8
20:3ω3	–	–	–	9.5±2.4	–	–	–	6.9±6.6
20:4ω3	–	4.6±1.7	–	5.4±5.3	–	–	0.8±1.4	3.2±0.9
20:5ω3	4.2±0.4	9.3±1.8	–	–	9.6±4.4	5.4±0.9	–	–
Total	8.1±1.9	20±4.3	0.5±0.1	42.1±35	18.4±8.1	8.7±1.5	2±3.1	19.9±14.4
LCFAs	3.9±0.9	10.2±4.9	3.9±0.8	33.5±14.2	3.5±2.6	2.3±0.8	8.2±4.2	16.2±8.1
18:2ω6+18:3ω3	2.4±0.5	4.7±0.6	0.5±0.1	18.8±3.3	5.2±1.8	1.8±0.3	1.0±1.6	3.4±1.2
Others*	2.2±2.4	5.0±2.8	1.9±2.0	25.6±19.5	4.9±5.1	4.6±2.3	6.1±5.9	16.0±16.9

*includes fatty acids not indicated in this table, –: not detected or traces.
Values are mean±SD; LCFAs: long chain fatty acids.

2.4. Lipid extraction and fatty acid (FA) analysis

Sediment samples (10 g wet weight) were extracted using a modified method of Bligh and Dyer (1959). Sediments were ultrasonically extracted for 20 min with a mixture of chloroform:methanol:distilled water (1:2:1; 20 cm^3; v:v:v). Two aqueous-organic layers were formed by the addition of a distilled water:chloroform mixture (1:1; 10 cm^3; v:v). The lipids were transferred into a lower chloroform phase and improved by centrifugation (2000 rpm for 5 min). After evaporation of the solvent, lipid extracts were saponified under reflux (2 h, 100 °C) with a 2 mol dm^{-3} NaOH solution in methanol and distilled water (2:1; v:v). After acidification with an ultra-pure HCl solution (37.5%), 2 × 2 cm^3 of chloroform were successively added to recover the lipid. The solvent was then evaporated under a nitrogen stream, and FAs were converted to methyl esters under reflux using 1 ml of 14% BF3-methanol for 10 min. Saponification and methylation were performed to obtain total FAs (Meziane and Tsuchiya, 2002; Mchenga et al., 2007).

The FAMEs were separated and quantified by a gas chromatograph (GC 14.B, Shimadzu) equipped with a flame ionisation detector. Separation was performed with a free fatty acid phase (FFAP)-polar capillary column (30 m × 0.32 mm internal diameter, 0.25 µm film thickness) using helium as a carrier gas. After injection at 60 °C, the oven temperature was raised to 150 °C at a rate of 40 °C min^{-1}, then to 230 °C at 3 °C min^{-1}, and finally held constant for 30 min. The flame ionisation was held at 240 °C. FAME peaks were identified by comparison of their retention times to those of authentic standards (Supelco Inc., Bellefonte, PA, USA).

2.5. Data analysis

Data were analysed using a one-way ANOVA with habitats (burrow opening, burrow chamber, and sediments with and without crabs) as a fixed factor and nutrient concentrations, TN, TC, DOC, and individual/groups of FAs as dependent variables. Test for honestly significant difference (HSD) was applied post hoc to detect differences between treatments once significant differences were found. Results were considered significant if $p < 0.05$.

A two-tailed paired Student's *t*-test was used to compare seasonal variation in nutrients and individual or groups of FA in sediments. Linear regression and Pearson's correlation coefficient test were used to test correlations between nutrients and individual/groups of FA markers in sediments. The significant level for the correlation tests was adjusted using a Bonferroni correction ($\alpha_{new} = \alpha/$ number of correlation tests applied).

3. Results

3.1. Sediment characteristics

Surface sediments with and without crabs were sandy > 250 µm (Table 1). Sediments of the burrow

Table 3
Results of Pearson coefficient correlation (r-value) test among the fatty acid markers, organic matter and nutrient profiles in sediment (combined data) during the summer

	15i	15a	17i	17a	18:1ω7	18:2ω6	18:3ω3	20:5ω3	16:1ω7	22:6ω3	18:1ω9	LCFA	TOM	TN	TC	DOC	NO$_3$	NH$_4$
15i																		
15a	**1.0**																	
17i	**0.9**	**0.9**																
17a	**0.9**	**0.9**	**1.0**															
18:1ω7	**1.0**	**1.0**	**1.0**	**1.0**														
18:2ω6	**0.9**	**0.9**	**0.9**	**0.9**	**0.9**													
18:3ω3	**0.7**	**0.7**	0.5	0.5	0.6	0.5												
20:5ω3	−0.4	−0.4	−0.3	−0.5	−0.3	−0.4	−0.1											
16:1ω7	**1.0**	**1.0**	**0.9**	**1.0**	**1.0**	**0.9**	0.6	−0.3										
22:6ω3	−0.3	−0.3	−0.2	−0.3	−0.3	−0.2	−0.1	0.1	−0.3									
18:1ω9	**0.9**	**0.9**	**0.9**	**0.9**	**0.9**	**0.9**	0.4	−0.4	**0.9**	−0.3								
LCFA	**0.9**	**0.9**	**0.9**	**0.9**	**1.0**	**1.0**	0.6	−0.4	**0.9**	−0.3	**−1.0**							
TOM	**−0.9**	**−0.9**	**−0.9**	**−0.9**	**−0.9**	**−0.9**	−0.6	0.4	**−0.9**	0.0	**−0.9**	**−0.9**						
TN	−0.3	−0.3	−0.4	−0.4	−0.3	−0.4	−0.1	**0.9**	−0.3	−0.2	−0.4	−0.3	0.5					
TC	−0.5	−0.5	−0.4	−0.5	−0.5	−0.4	−0.2	0.7	−0.5	0.6	−0.5	−0.5	0.3	0.4				
DOC	−0.7	−0.7	−0.6	−0.7	−0.7	−0.6	−0.5	0.3	**−0.7**	**0.8**	−0.63	−0.7	0.5	−0.1	0.8			
NO$_3$	−0.7	−0.7	−0.6	−0.7	−0.6	−0.7	−0.4	0.7	−0.7	0.0	−0.7	−0.7	0.8	0.7	0.5	0.3		
NH$_4$	−0.2	−0.2	−0.1	−0.2	−0.1	−0.2	0.1	**0.9**	−0.1	−0.2	−0.2	−0.1	0.2	**1.0**	0.4	−0.2	0.6	

LCFAs: long chain fatty acids; TOM: total organic matter; TN: total nitrogen; TC: total carbon, and DOC: dissolved organic carbon. Significant values are shown in bold characters (Bonferroni's adjustment, $\alpha_{new} = 0.002$).

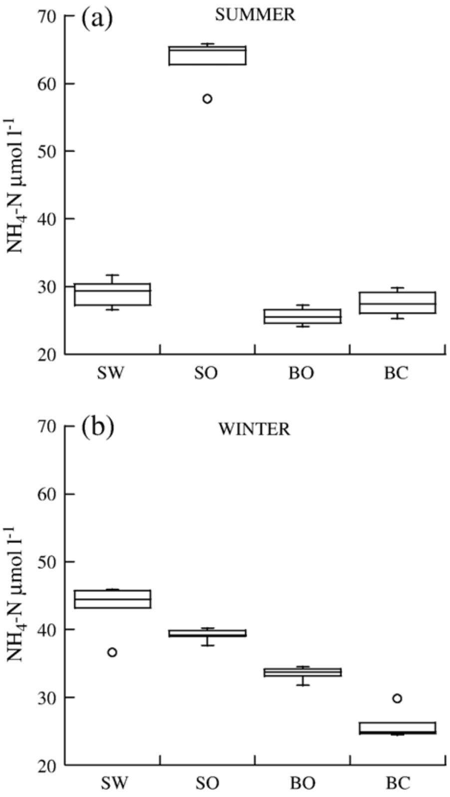

Fig. 3. Seasonal variation in sediment NH_4-N concentrations. Boxes represent the 75th and 25th percentiles; whiskers indicate the 10th and 90th percentiles; the lines inside the boxes are the medians; o represents an outlier. Sample abbreviations as in Fig. 2.

opening and chamber contained much less fine sand (250–125 µm, 10.3% and 7.6% respectively), very fine sand (125–63 µm, 5.6% and 3.6% respectively) and a small fraction of silt and mud (<63 µm). The sediment water contents in the burrow opening (20.7%) and the surface area (19.2%) were higher in locations with crabs than in those without crabs (18.1%).

The total carbon (TC) in sediments with crabs was significantly higher (24.3 mg g^{-1} dry wt; ANOVA, $F=588.8$, df=3, 8; $p<0.001$) than in sediments without crabs and burrow chamber sediment. However, total nitrogen (TN) values were higher in sediments without crabs (2.1 mg g^{-1} dry wt; ANOVA, $F=79.1$, df=3, 8; $p<0.001$). The C/N ratios in burrow opening sediments and surface sediments without crabs were relatively lower (9.4 and 9.6, respectively) than in surface sediments with crabs (18.6; Table 1). TOM was significantly higher in summer than in winter, ranging from 19.3 to 25.3% and 10 to 15%, respectively (t-test, $t=-22.6$, df=23; $p<0.001$) However, no significant difference was found between sediments types, except that lower values were recorded in sediments of the burrow chamber (Fig. 2a). A significant difference in DOC was observed between sediments sampled during the summer and winter seasons (t-test, $t=5.1$, df=11; $p<0.001$), but DOC was not different in the burrow chamber sediments (Fig. 2b).

3.2. FA composition in sediments

The mean percentage compositions of identified individual FAs (≥14:0) that accounted for >0.2% of the total FAMEs in the profiles for all sediment samples were used. The FA results are given in absolute dry weight (μg g^{-1}) following the conversion of initial sediment wet weight to dry weight and estimation of the contribution of individual FAs in the total lipids.

Significant seasonal variation was found among the sediment FA profiles. The FA composition of all sediment types was dominated by palmitic acid (16:0), with the highest concentration recorded in the burrow chamber (99.4 and 60.8 µg g^{-1} dry wt in summer and winter, respectively). Additionally, the second and third most dominant FAs were the monounsaturated fatty acids (MUFAs) 18:1ω9 and 18:1ω7 in sediments of the

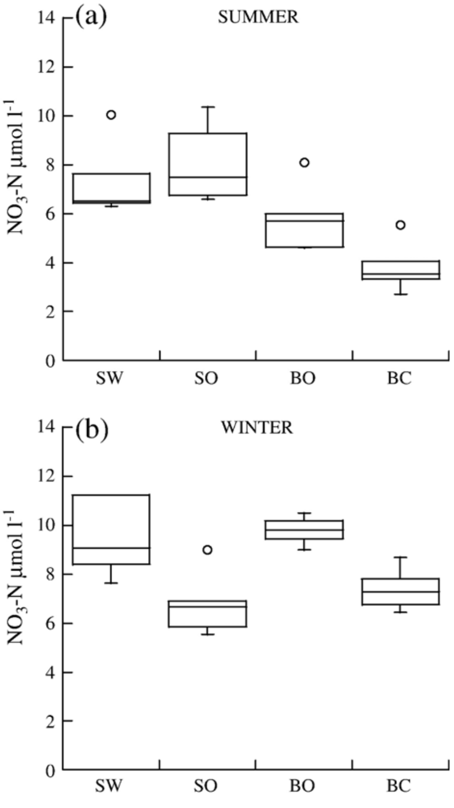

Fig. 4. Seasonal variation in sediment NO_3-N^- concentrations recorded during summer and winter seasons. Sample abbreviations as in Fig. 2.

burrow chamber (37.4 and 37.1 μg g^{-1} dry wt, respectively) during summer (Table 2).

In all sediment types, vaccenic acid (18:1ω7) and the odd-branched C_{15}-C_{17} (iso and anteiso; FA markers of bacteria) were found in relatively high amounts in both the summer and winter periods. Seasonally, individual bacteria markers were not significantly different when analysed according to the sediment types (*t*-test, $t=0.1$, df=11; $p>0.05$), except for C_{15} (iso and anteiso) in the burrow opening and sediments without crabs (*t*-test, $t=12.7$, df=2; $p<0.01$ and $t=-4.4$, df=2; $p<0.05$ respectively). A Pearson's correlation coefficient test from combined sediments types showed a significant correlation between individual and groups of FA bacteria markers with green macroalgae markers, particularly 18:2ω6 and 18:3ω3 during summer (Table 3). However, no significant correlation was found between bacteria and green macroalgae FA markers in winter (table of winter results not shown).

Polyunsaturated fatty acids (PUFAs), 18:2ω6 and 18:3ω3 in particular, were detected in sediments during both seasons. Linoleic acid (18:2ω6) was found in significantly higher amounts, particularly in the burrow chamber during summer (14.4 μg g^{-1} dry wt; ANOVA, $F=31.2$, df=3, 8; $p<0.001$). When analysed according to sediment types, 18:2ω6 was significantly correlated with LCFAs in the burrow chamber and surface sediments with crabs. However, 18:2ω6 showed a negative correlation with TOM. The surface sediments with and without crabs had a moderate concentration of eicosapentaenoic acid (20:5ω3) in both seasons. FA 20:5ω3 was correlated with TN and NH_4-N during summer (Table 3).

Concentrations of long-chain fatty acids (LCFAs) of length $\geq C_{24}$ were relatively higher in burrow chamber sediments and surface sediments without crabs during summer (33.5 and 10.2 μg g^{-1} dry wt, respectively). Both seasons showed a significant difference in LCFAs between sediment types (ANOVA, $F=39.1$, df=3,8; $p<0.001$; $F=18.7$, df=3, 8; $p<0.001$, summer and winter respectively). A significant correlation was found between LCFAs and the fatty acid 18:2ω6 in summer and bacteria markers in both seasons.

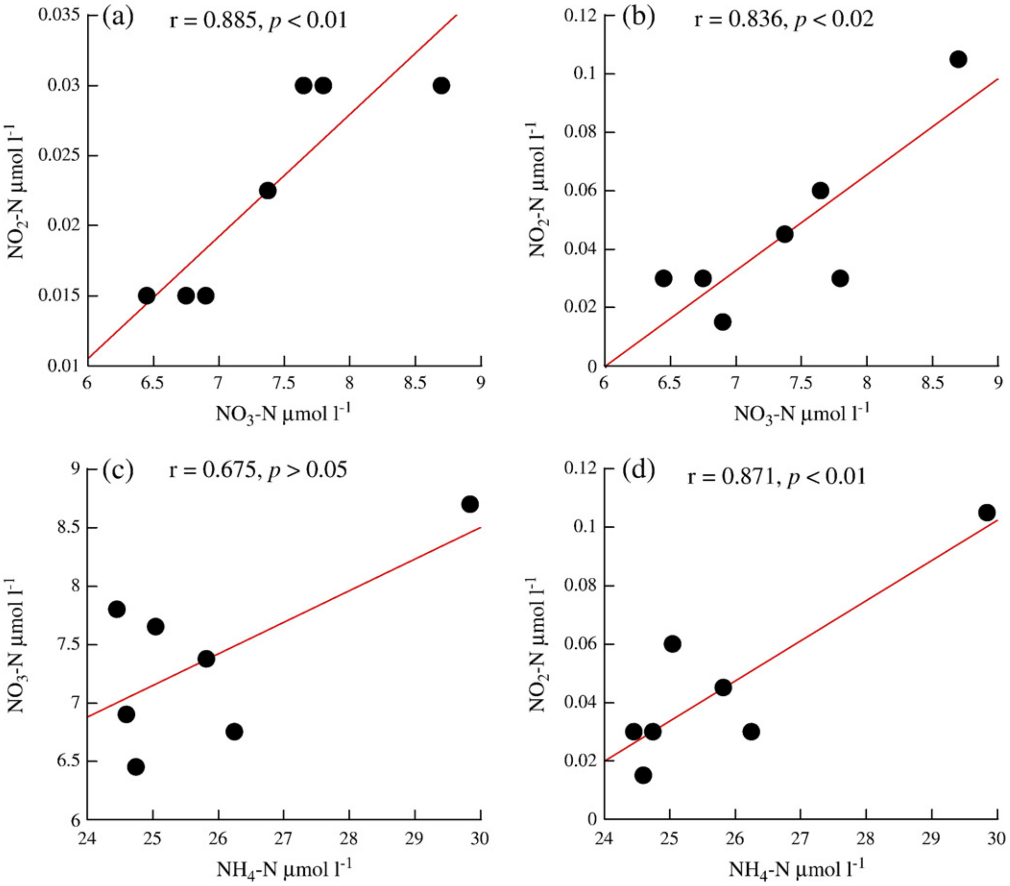

Fig. 5. Correlations among different nitrogen forms in sediments of the mixed zone of burrow opening shaft and chamber (a) and burrow chamber sediments (b, c, and d) during winter. The line is based on simple linear regression (n=7).

3.3. Inorganic nitrogen and phosphate

NH_4-N was the dominant form of inorganic nitrogen with a significantly higher concentration (63.6 µmol l^{-1}) in the surface sediments without crabs during summer (ANOVA, $F=453.6$, df=3, 20; $p<0.001$). However, the NH_4-N concentration decreased in winter (39.2 µmol l^{-1}). In contrast, sediments of the burrow opening, chamber and surface with crabs had a lower concentration of NH_4-N (25.6, 27.5 and 29.1 µmol l^{-1}) during summer. However, NH_4-N concentration increased significantly in the surface sediments with crabs during the winter period (43.4 µmol l^{-1}; ANOVA, $F=76.3$, df=3, 20; $p<0.001$; Fig. 3). A statistically significant correlation was found between NH_4-N and TN contents during summer (Table 3). In addition, results showed a seasonal difference for NO_3-N and NO_2-N concentrations in various sediment types (t-test, $t=3.8$, df=23; $p<0.001$ and $t=-10.7$, df=23; $p<0.001$ respectively). A significantly higher concentration of NO_3-N (ANOVA, $F=6.1$, df=3, 20; $p<0.01$) was recorded in surface sediments with crabs during winter (10.2 µmol l^{-1}, Fig. 4). The change in NO_2-N concentrations was strongly correlated with NO_3-N in sediments of the burrow chamber (r=0.837, $p<0.02$) and the mixed zone of the burrow opening shaft and chamber (r=0.885, $p<0.01$; Fig. 5a, b), particularly during winter. In contrast, no significant correlation was found between NO_3-N and NH_4-N in different sediment types and seasons (Fig. 5c). Overall, PO_4-P concentrations were higher in summer than in winter (t-test, $t=-7.1$, df=23; $p<0.01$). The highest concentrations were recorded in sediments without crabs (1.8 µmol l^{-1}) during summer, while the lowest concentrations were found in sediments with crabs during winter (0.4 µmol l^{-1}; Fig. 6).

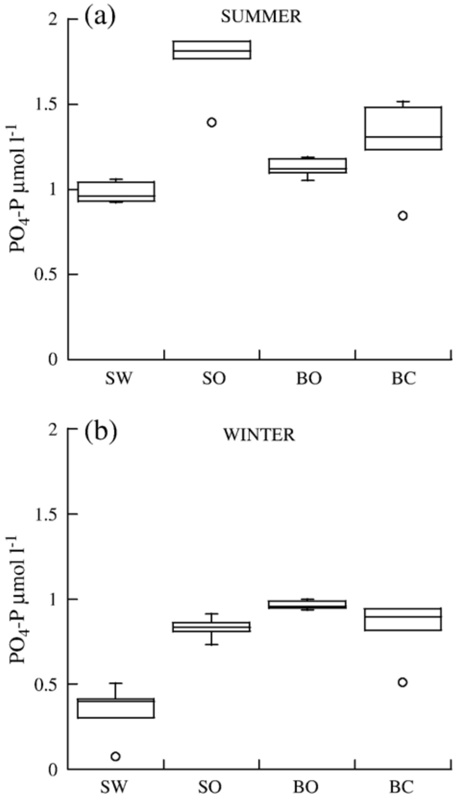

Fig. 6. Seasonal variation in sediment PO_4^+ concentrations recorded during summer and winter seasons. Sample abbreviations as in Fig. 2.

4. Discussion

4.1. Sources of sediment organic matter

In this study, we observed a significant variation in FA composition between the summer and winter seasons. A higher amount of LCFAs, markers of vascular plant (Meziane and Tsuchiya, 2000) is related to the peak mangrove litter fall, which occurred during the summer (Mfilinge et al., 2005). The significant negative correlations between LCFAs and TOM (r=−0.904, $p<0.001$) in both seasons suggest that sources other than mangrove detritus are entering the tidal flat sediments, probably from a nearby agricultural field and waste water discharge (Meziane and Tsuchiya, 2002; Tashiro et al., 2003). However, the low concentrations of LCFAs detected at the burrow opening and in surface sediments with crabs could be associated with high feeding activity by crabs during this period (Mchenga et al., 2007), and/or passive deposition of mangrove detritus into the burrow (Botto et al., 2006).

Considerable amounts of 18:2ω6 and 18:3ω3, green macroalgae biomarkers (Mfilinge et al., 2005) were found either together or alternately during the summer and winter seasons, indicating fresh algal input (Carrie et al., 1998). However, these markers should have occurred more in winter when green macroalgae (*Ulva pertusa* and *Enteromorpha interstinalis*) are the main contributors to sedimentary organic matter in subtropical mangroves, particularly in Okinawa (Mfilinge et al., 2005). The presence of these biomarkers in high amounts during summer indicates over-enrichment (Fong et al., 1998) in the Manko wetland. PUFAs (Σ18:2ω6+18:3ω3) have been used as an indicator of the relative importance of terrestrial material in marine sediments (Budge and Parrish, 1998). Therefore, the detection of high levels of these two PUFAs in burrow chamber sediments and surface sediments with and without crabs in both seasons implies some terrestrial inputs to the

Manko estuary. For instance, the presence of 18:2ω6 reinforces the possibility of input from agricultural products (Meziane and Tsuchiya, 2002) and domestic waste water (Quemeneur and Marty, 1994).

The PUFA 20:5ω3, in association with 16:0 and 16:1ω7, is the most common diatom marker in aquatic environments (Canuel et al., 1995; Carrie et al., 1998; Meziane and Tsuchiya, 2002). The contribution of 20:5ω3 in surface sediments is related to higher concentrations of microalgae in the water column, particularly in summer (Meziane et al., 2006). Moreover, in both seasons, 20:5ω3 may be associated with the colonisation of fresh and decomposed plant materials rich in nitrogen by epiphytic diatoms and protozoans (Mfilinge et al., 2003), an idea supported by the significant correlation of the 20:5ω3 with TN and NH_4-N in both the summer and winter seasons. A low amount of 20:5ω3 in surface sediments with crabs during summer could be related to microalgae consumption by crabs. *Helice formosensis* is omnivorous; however, other deposit feeders have been reported to ingest diatoms (Meziane and Tsuchiya, 2002). FA 16:1ω7 is another signature of diverse algae taxa including diatoms (Napolitano, 1999). This FA, however, was not correlated with either 20:5ω3 (microalgae marker) or 22:6ω3 (dinoflagellate marker), but was significantly correlated with bacteria markers (18:1ω7, C_{15}-C_{17} iso and anteiso). Consequently, it appeared to reflect bacterial input of organic matter (Perry et al., 1979).

The MUFA 18:1ω7 and odd-branched FAs (C_{15}-C_{17} iso and anteiso) are usually synthesised by bacteria (Volkman et al., 1980). Vaccenic acid (18:1ω7) is a signature of bacteria living under both aerobic and anaerobic conditions, while odd-branched FAs (C_{15}-C_{17} iso and anteiso) are an indicator of sulfate-reducing bacteria (Pinture-Geiss et al., 2002). The relative increase of these markers in all sediment types and seasons indicates an increased level of bacteria in the environment (Carrie et al., 1998; Mfilinge et al., 2005). These FAs were significantly correlated with LCFAs, vascular plant marker and 18:2ω6 green macroalgae marker (Meziane and Tsuchiya, 2002; Mfilinge et al., 2005), particularly in surface sediments, indicating high levels of organic matter degradation by bacteria during high summer temperatures. In addition, during the summer and winter seasons, bacterial FAs were correlated with 18:1ω9. A combined high amount of 18:1ω9 and 18:2ω6 is a signature of some fungal strains (Chen et al., 2001) and has been used as an indicator of microbial sources in a terrestrial environment (Frostegård and Bååth, 1996; Chen et al., 2001) and as a domestic waste water indicator (Quemeneur and Marty, 1994), thus reinforcing the implied contributions of pollutants to the Manko tidal flat sediments.

4.2. Impact of crab activities on nutrients

Our findings revealed seasonal variations in TOM and DOC. An overall increase in organic matter input at the study site in summer may enhance community metabolism and stimulate the recycling of nutrients (Andersen and Hargrave, 1984; Van Duyl et al., 1992). The higher amounts of PO_4-P recorded in sediments without crabs during summer may therefore be associated with high litter decomposition (Nielsen and Andersen, 2003). In the burrow sediments, accumulations of detritus may enhance the release of PO_4-P through the decomposition process. The variation in C/N ratio between sediment types is associated with different sources of sediment organic matter. The low C/N ratio is therefore attributed to the presence of green macroalgae (as indicated by FA markers), which could explain the higher release of NH_4-N (2.1–2.4×) in sediments without crabs, particularly in summer (Schlesinger, 1997). In a mangrove forest, the ammonium concentrations were significantly higher in plots without crabs (Smith et al., 1991). Sediment oxygen consumption increases in summer because of the higher temperatures, leading to a low redox condition. Consequently, reduction of NH_4-N through the oxygen-dependent process of nitrification becomes considerably low, particularly in sediments without crabs. In contrast, crab activities may improve sediment aeration (Mchenga et al., 2007), thus creating a more favourable environment for the nitrification process. A significant correlation between NO_2-N and NH_4-N (Fig. 5d), particularly in burrow chamber sediments, indicates that some NO_3-N was recycled to NH_4-N via the dissimilatory pathway of NO_3-N reduction to NH_4-N. However, in well-vegetated wetland sediments, dissimilatory NO_3-N reduction to NH_4-N is not a major mechanism for generating NH_4-N (Matheson et al., 2002). In comparison, a relative increase of NH_4-N (1.3 x) in sediments used by crabs in winter was due to crab inactivity.

A 1.9-, 1.7-, and 1.4-fold increase in NO_3-N concentration during winter in the sediments of the burrow chamber, the opening shaft, and the surface with crabs, respectively, indicates that NH_4-N was converted to NO_3-N via nitrification. Although NO_3-N increased, its level never surpassed that of NH_4-N, indicating that nitrification was minimal. These results can be attributed to a higher quality carbon (algae) providing a better substrate (NH_4^+) for heterotrophic bacteria, which would outcompete the less abundant and slower-growing nitrifying bacteria and reduce nitrification (Strauss and Lamberti, 2002). This suggestion is supported by the occurrence of a significantly higher concentration of total FA bacteria markers in crab burrow and surface sediments without crabs. These were also significantly correlated with green macroalgae markers. Alternatively, NO_3-N could have been reduced via the denitrification that occurs under anoxic environments, particularly inside the burrow chamber of *H. formosensis* (Mchenga et al., 2007). Interestingly, there is a strong correlation between NO_3-N and NO_2-N^- concentrations in sediments of the burrow during winter, indicating that denitrification occurred. The denitrification process is most pronounced at lower temperatures (winter) during which nitrate concentrations increase (Sørensen et al., 1979). The burrow chamber is probably the only place sampled that continuously receives organic material; thus, it may serve as a dietary source for microbial growth (Mchenga et al., 2007) and provide an aerobic-anaerobic area where both nitrification and denitrification processes can continuously occur. Through this interaction, crab burrows can effectively contribute to the removal of nitrogen loading from the sediments. These results contribute to our understanding of the nutrient dynamics of subtropical mangrove ecosystems and the role of bioturbation in processing elevated nutrients in mangrove sediments.

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References

Aller, R.C., 1994. Bioturbation and remineralization of sedimentary organic matter: effects of redox oscillation. Chem. Geol. 114, 331–345.

Andersen, F.Ø., Hargrave, B.T., 1984. Effects of *Spartina* detritus enrichment on aerobic/ anaerobic benthic metabolism in an intertidal sediment. Mar. Ecol. Prog. Ser. 16, 161–171.

Bligh, E.G., Dyer, W.J., 1959. A rapid method of total lipid extraction and purification. Can. J. Biochem. Physiol. 37, 911–917.

Botto, F., Iribarne, O., Gutiérrez, J., Bava, J., Gagliardini, A., Valiela, I., 2006. Ecological importance of passive deposition of organic matter into burrows of the SW Atlantic crab *Chasmagnathus granulatus*. Mar. Ecol. Prog. Ser. 312, 201–210.

Budge, S.M., Parrish, C.C., 1998. Lipid biochemistry of plankton setting matter and sediments in Trinity Bay, New-foundland. II. Fatty acids. Org. Geochem. 29, 1547–1559.

Canuel, E.A., Cloern, J.E., Ringelberg, D.B., Guckert, J.B., Rau, G.H., 1995. Molecular and isotopic tracers used to examine source of organic matter and its incorporation into the food webs on San Francisco Bay. Limnol. Oceanogr. 40, 67–81.

Carrie, R.H., Mitchell, L., Black, K.D., 1998. Fatty acids in surface sediment at Hebridean shelf edge, west of Scottland. Org. Geochem. 29, 1583–1593.

Chen, J., Ferris, H., Scow, K.M., Graham, K.J., 2001. Fatty acid composition and dynamics of selected fungal-feeding nematodes and fungi. Comp. Biochem. Physiol. 130, 135–144.

Cloern, J.E., 2001. Our evolving conceptual model of the coastal eutrophication problem. Mar. Ecol. Prog. Ser. 210, 235–265.

Dittmar, T., Lara, R.J., Kattner, G., 2001. River or mangrove? Tracing major organic matter sources in tropical Brazilian coastal waters. Mar. Chem. 73, 253–271.

Dworschak, P.C., 1983. The biology of *Upogebia pusila* (Petagna) (Decapoda, Thalassinidea). I. The burrows. P.S.Z.N. I: Mar. Ecol. 4, pp. 19–43.

Ferguson, A.J., 2002. A comparison of benthic nutrient cycling in the sub-tropical Sandon and Brunswick Estuaries. Environmental Science and Management Department, Ph.D. Thesis, Sourthern Cross University, Lismore, unpublished.

Findlay, R.H., Watling, L., Mayer, L.M., 1995. Environmental impact of salmon net-pen culture on marine benthic communities in Maine: a case study. Estuaries 18, 145–179.

Fong, P., Boyer, K.E., Zedler, J.B., 1998. Developing an indicator of nutrient enrichment in coastal estuaries and lagoon using tissue nitrogen content of the opportunistic alga: *Enteromorpha intestinalis* (L. Link). J. Exp. Mar. Biol. Ecol. 231, 63–67.

Frostegård, A., Bååth, E., 1996. The use of phospholipids fatty acid analysis to estimate bacteria and fungal biomass in soil. Biol. Fertil. Soils 22, 59–65.

Hansen, K., Kristensen, E., 1997. Impact of macrofaunal recolonization on benthic metabolism and nutrient fluxes in shallow marine sediment previously overgrown with macroalgae mats. Estuar. Coast. Shelf Sci. 45, 613–628.

Ingram, R.L., 1971. Sieve analysis. In: Carver, R.E. (Ed.), Procedures in Sedimentary Petrology. Wiley-Interscience, New York, pp. 49–67.

Islam, M.S., Shokita, S., Nagai, T., Nasure, T., Yogi, A., Oshiro, T., 2002. Distribution and abundance of macrobenthos in the Nuha River mangrove swamp in Manko Estuary of Okinawa Island, Japan. Biol. Mag. Okinawa 40, 15–31.

Jone, D.L., Willett, V.B., 2005. Experimental evaluation of methods to quantify dissolved organic nitrogen (DON) and dissolved organic carbon (DOC) in soil. Soil Biol. Biochem. 38, 991–999.

Kuo, S., 1996. Phosphorus. In: Sparks, D.L. (Ed.), Methods of Soil Analysis. Part 3—Chemical Methods. Soil Science of America, Inc., USA, pp. 869–919.

Matheson, F.E., Nguyen, M.L., Cooper, A.B., Burt, T.P., Bul, D.C., 2002. Fate of ^{15}N-Nitrate in unplanted, planted and harvested riparian wetland soil microcosm. Ecol. Eng. 19, 249–264.

Mchenga, I.S.S., Mfilinge, P.L., Tsuchiya, M., 2007. Bioturbation activity by the grapsid crab *Helice formosensis* and its effects on mangrove sedimentary organic matter. Estuar. Coast. Shelf Sci. 73, 316–324.

Meziane, T., Tsuchiya, M., 2000. Fatty acids as tracers of organic matter in the sediment and food web of a mangrove/intertidal flat ecosystem, Okinawa, Japan. Mar. Ecol. Prog. Ser. 200, 49–57.

Meziane, T., Tsuchiya, M., 2002. Organic matter in a subtropical mangrove-estuary subjected to wastewater discharged: origin and utilization by two macrozoobenthic species. J. Sea Res. 47, 1–11.

Meziane, T., d'Agata, F., Lee, S.Y., 2006. Fate of mangrove organic matter along subtropical estuary: small-scale exportation and contribution to the food of crab communities. Mar. Ecol. Prog. Ser. 312, 15–27.

Mfilinge, P.L., Meziane, T., Bachok, Z., Tsuchiya, M., 2003. Fatty acids in decomposing mangrove leaves: microbial activity, decay and nutritional quality. Mar. Ecol. Prog. Ser. 265, 97–105.

Mfilinge, P.L., Meziane, T., Bachok, Z., Tsuchiya, M., 2005. Litter dynamics and particulate organic matter outwelling from a subtropical mangrove in Okinawa Island, South Japan. Estuar. Coast. Shelf Sci. 63, 301–313.

Napolitano, G.E., 1999. Fatty acids as trophic and chemical markers in Freshwater Ecosystems. In: Arts, M.T., Wainman, B.C. (Eds.), Lipids in Freshwater Ecosystems. Springer-Verlag, New York, pp. 21–44.

Nielsen, T., Andersen, F.Ø., 2003. Phosphorus dynamics during decomposition of mangrove (*Rhizophora apiculata*) leaves in sediments. J. Exp. Mar. Biol. Ecol. 293, 73–88.

Parkers, R.J., 1987. Analysis of microbial communities within sediments using biomarkers. Ecology of Microbial Communities. SGM, vol. 41. Cambridge University Press, pp. 147–177.

Parkers, R.J., Taylor, J., 1985. Characterisation of microbial populations in polluted marine sediments. J. Appl. Bacteriol. Sympos. 14, pp. 155–175.

Perry, G.J., Volkman, J.K., Johns, R.B., Bavor, H.J., 1979. Fatty acids bacteria origin in contemporary marine sediments. Geochim. Cosmochim. Acta 43, 715–1725.

Pinture-Geiss, L., Méjanelle, L., Dale, B., Karlsen, D.A., 2002. Lipids as indicator of eutrophication in marine coastal sediments. J. Microbiol. Methods 48, 239–257.

Quemeneur, M., Marty, Y., 1994. Fatty acid and sterol in domestic waste water. Water Res. 28, 1217–1226.

Schlesinger, W.H., 1997. Biogeochemistry: an Analysis of Global Change. Academic Press, San Diego, CA.

Smith III, T.J., Chan, H.T., Frusher, S.D., Giddens, R.L., 1991. Keystone species and mangrove forest dynamics: the influence of burrowing by crabs on soil nutrient status and forest productivity. Estuar. Coast. Shelf Sci. 33, 419–432.

Sørensen, J., Jørgensen, B.B., Revsbech, N.P., 1979. A comparison of oxygen, nitrate and sulphate respiration in marine sediments. Microb. Ecol. 5, 105–115.

Stief, P., De Beer, D., 2004. Small-scale bioturbation/bioirrigation by midge larvae in freshwater sediments: implication for the benthic N-cycle. First Nereis Park Conf. Carry-Le-Rouet, France, p. 22.

Strauss, E.A., Lamberti, G.A., 2002. Effect of dissolved organic carbon quality on microbial decomposition and nitrification rates in stream sediments. Freshw. Biol. 47, 65–74.

Tam, N.F.Y., Vrijmoed, L.L.P., Wong, S.Y., 1990. Nutrient dynamics associated leaf decomposition in a small subtropical mangrove community in Hong Kong. Bull. Mar. Sci. 47, 68–78.

Tashiro, Y., Takemura, A., Fujii, H., Takahira, K., Nakanishi, Y., 2003. Livestock waste as a source of estrogens and their effects on wildlife of Manko tidal flat, Okinawa. Mar. Pollut. Bull. 47, 143–147.

Van Duyl, F.C., Kop, A.J., Kok, A., Sandee, A.J.J., 1992. The impact of organic matter and macrobenthos on bacterial and oxygen variables in marine sediments boxcosms. Neth. J. Sea Res. 29, 343–355.

Volkman, J.K., Johns, R.B., Gillian, F.T., Perry, G.J., Bavour, H.J., 1980. Microbial lipids of an intertidal sediment—1. Fatty acids and hydrocarbons. Geochim. Cosmochim. Acta 44, 1133–1143.

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Mangrove crab (*Scylla serrata*) populations may sometimes be best managed locally

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Abstract

Mangrove crabs (*Scylla serrata*) were trapped in summer and fall 2004 at four sites, each in a separate municipality on the Pacific island of Kosrae, Federated States of Micronesia. Carapace width (CW) of the 219 crabs averaged 15.1 ± 0.13 cm (SE), slightly larger than the mean size of 221 crabs trapped from the same sites 4 y earlier. Mean CW of the 56 crabs in the upper quartile was 17.5 ± 0.17 cm (SE). In the current study, both sizes of crabs as well as degree and direction of change in size from summer to winter varied among the municipalities. The average CW of crabs from one municipality was significantly larger than from any of the other municipalities. Average CW of crabs from another municipality decreased from summer to fall. These results suggest that although the island-wide crab population appears to be stable, some municipalities may wish to enact site-specific management policies to obtain a harvest regimen that will meet local needs.
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Keywords: *Scylla serrata*; Mangrove crab; Mangrove forests; Catch per unit effort; Micronesia; Kosrae

1. Introduction

Mangrove crabs (*Scylla* spp., also called mud crabs) are large, tasty, and relatively easy to capture, making them an increasingly scarce resource throughout the Indo-Pacific region (Brown, 1993; Marichamy and Rajapackiam, 2001). In spite of continued harvest pressure, these crabs are managed in only a few parts of their range, most notably in northern Australia (e.g., Pillans et al., 2005). Consequently, they have become smaller and harder to catch in many places, especially in developing countries. Appropriate harvest policies for these large crabs (carapace width, or CW, of males can reach 25–28 cm: Carpenter and Niem, 1998, reported by Williams and Primavera, 2001) might sustain a source of protein and cash for many communities. The purpose of this study was to analyse local differences in crab populations both spatially and temporally in order to suggest simple but meaningful management practices.

Although four species of mangrove crab are now recognised (Keenan et al., 1998), only one species (*Scylla serrata*, the most widespread) is found on the island of Kosrae, Federated States of Micronesia, where it is one of the most valuable products harvested from the island's mangrove forests (Naylor and Drew, 1998). On Kosrae, mangrove crabs are prized for family feasts, sold to local tourist hotels, and exported primarily as gifts to

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family members in Guam, Hawaii, and elsewhere in the Pacific islands. The crabs may be either trapped in small estuaries and tidal creeks or collected by hand in mangrove forests. Household surveys suggest that catch per unit effort (CPUE) declined from 1990 to 2000, the number of households participating in crab harvesting also decreased, and fewer harvesting trips were made each month (Naylor et al., 2002). Nevertheless, the number of crabs exported from Kosrae for sale and for gifts increased from 1997 to 2000.

A sample of 368 crabs caught from 1999–2001 primarily by traps set along interior and fringe mangrove channels and by hand along randomly selected transects in Kosrae averaged 15.2±2.4 cm (SD) in CW (Bonine et al., 2008); the largest was 21.0 cm. In April 2000, in response to the growing sense documented above that crabs were getting smaller and harder to catch, a new law passed by the Kosrae State Legislature established a minimum harvestable size limit of 6 in (15.2 cm) “measured along the largest diameter across the outside of the shell” (Kosrae State Legislature, 2006). The law also prohibited export of mangrove crabs and declared a closed season from 1 August through 31 December. This law was unpopular, and the portions prohibiting export and declaring a closed season were repealed the following year. During the time the law was in effect, people may have continued to harvest crabs for family consumption, but none were sold to hotels on the island or exported during the 5-mo ban.

The objectives of this study were to determine how the mean CW of crabs and CPUE in Kosrae might have changed since the earlier study, as well as how variable they might be both around the island and over shorter periods of time. I also wanted to determine whether different locations on the island might benefit from different regulations.

2. Materials and methods

2.1. Study sites

Kosrae (5°19′N, 163°E) is a high volcanic island in the eastern Caroline Islands in the Pacific Ocean and is one of four island-states in the Federated States of Micronesia. It is ~104 km^2 in area with a narrow coastal plain and a mountainous interior. With rainfall of ~4–5 m y^{-1} and no distinct dry season, several small rivers traverse the coastal plain and flow through mangrove forests that vary from narrow strips to belts as wide as 800 m.

Most of Kosrae’s ~ 7800 people live on the coastal plain. The island is divided into four municipalities: Lelu, Malem, Utwe, and Tafunsak (Fig. 1), each with at least one village as a population centre. In spite of Kosrae’s small size, these municipalities differ socio-economically (Table 1).

Lelu contains the government offices for the State of Kosrae. It has a number of wealthy and influential families, an active harbour, and many small businesses, and in most households at least one member has a salary. The Pukusrik Tidal Channel, the trapping location for Lelu, is lined by narrow strips of mangrove forest and terminates in a large stand of mangroves. Many Lelu households are located along the landward edge of the mangroves; many of these residents own boats, and they harvest crabs and fish.

At the other socioeconomic extreme, the municipality of Utwe contains many subsistence-level households, especially in the underpopulated southwestern part of the island. Trapping was conducted in the Utwe-Walung Tidal Channel, which provides boat access during high tide to some of the most remote, extensive, uninterrupted mangrove forests on the island. In Utwe, several women earn money by catching crabs by hand. Crabs were exported commercially from Utwe before 2000, but those were harvested on the other side of the municipality, distant from the Utwe-Walung Tidal Channel and closer to the remote village of Walung (which is part of Tafunsak municipality).

Malem, with a moderate income level, is located on a high-energy coastline where boat access is difficult. Few people in Malem have fishing boats, and the only place where they can harvest crabs is along the Inya River, which is actually part of Utwe.

The fourth municipality, Tafunsak, is the location of another major harbour and the airport, so it has several small businesses and a moderately high standard of living. The trapping location for Tafunsak was the Okat River, which is beyond the harbour and the main concentration of households. Most of the mangroves in this municipality are found in a belt several hundred metres wide and stretching from north of the Okat River south to Walung. Before 2000, crabs were harvested from the Okat River for commercial export to other Micronesian islands, especially Guam, but this enterprise did not resume after the law was repealed.

Little is known about the life history of the mangrove crabs from spawning through the larval stages. However, once the crabs have matured enough to migrate from the reef into a mangrove forest, their long-shore movements are known to be limited (Hill, 1975; Perrine, 1978; Hyland et al., 1984; Bonine et al., 2008). The area of mangrove forest within 0.5 km around each channel where traps were set was measured on a vegetation map

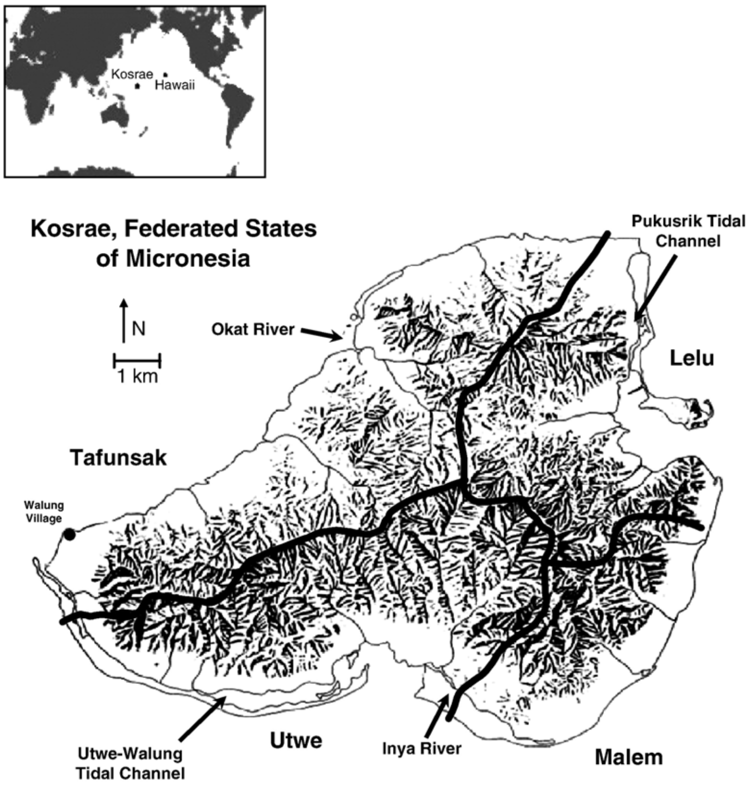

Fig. 1. Location of municipalities and study sites in Kosrae, Federated States of Micronesia.

(Whitesell et al., 1986) (Table 1). Except for extent of mangroves and degree of harvesting, primarily for firewood (Table 1), there are no known differences among the mangrove forests surrounding the sites where traps were set for this study.

2.2. Trapping protocol

I sampled crabs on a more systematic basis than in the earlier study, trapping at four sites before and after an interval ranging from 4.5 to 5.5 mo. Recruitment for mangrove crabs appears to be aseasonal in many tropical environments (Brown, 1993), and Kosrae's climate has little seasonality (Krauss et al., 2006), indicating that the actual time of year when trapping occurs is not likely to be important. Because mean size of a population sample may be biased by entry of a new cohort of crabs, the mean size of the largest quartile from each sample was also calculated. Decreases in the largest quartile could reflect over-harvesting, because individuals do not have an opportunity to grow into larger size classes.

Crabs were sampled from the four sites in mid-June to mid-July 2004 (summer) and again from mid-

Table 1
Characteristics of municipalities (FSM Dept. Econ. Affairs, 2000) and sites where crabs were sampled

Municipality	Population density (persons km^{-2})	Median household income (US$)	Percent of adults living at subsistence level	Sampling site	Extent of mangroves around channel (ha)	Percent area harvested annually between 1996–2000 (Hauff et al., 2006)
Lelu	124	$9155	2.9	Pukusrik Tidal Channel	49	1.7
Malem	93	$7156	11.8	Inya River	61	1.1
Tafunsak	58	$7626	10.6	Okat River	61	1.9
Utwe	37	$5833	12.6	Utwe-Walung Tidal Channel	185	1.2

Table 2
Trapping schedule in 2004 and numbers of mangrove crabs trapped

Municipality	Site sampled	Summer dates of trapping	Number of crabs trapped	Summer CPUE	Fall dates of trapping	Number of crabs trapped	Fall CPUE
Lelu	Pukusrik Tidal Channel	15 – 19 June	29	0.73	30 November – 4 December	30	0.75
Malem	Inya River	6 – 10 July	43	1.08	23 – 27 November	25	0.63
Tafunsak	Okat River	22 – 26 June	34	0.85	7 – 11 December	22	0.55
Utwe	Utwe-Walung Tidal Channel	29 June – 3 July	20	0.50	16 – 20 November	16	0,40
OVERALL			126	0.79		93	0.58

November to mid-December (fall) (Table 2). Eight crab traps ~ 1.2×0.6×0.3 m were constructed of 2.5-cm mesh wire. They were baited with fish, set out for five consecutive nights (40 trap nights) at a single site, and checked daily. The sites were trapped in this manner, one after the other, over four consecutive weeks in each season.

2.3. Data analysis

Differences in CW described below were tested using SAS/STAT® software, Version 9.1 of the SAS System for Windows (SAS Institute Inc., 2000–2004). Student's t-test was used to determine significance ($p<0.05$) of the seasonal difference between mean CW and between mean CW of the upper quartile of the crabs. The sample sizes of the two populations were pooled to determine the degrees of freedom for the t-test when the folded F statistic (Steele and Torrie, 1980) indicated that the variances of the two populations were equal. The Satterthwaite method (Satterthwaite, 1946) was used to determine the degrees of freedom for the t-test when the folded F statistic indicated the two populations had unequal variances. The t values calculated using these two methods are designated as t_{pooled} and t_{Sat}, respectively. Differences between CWs for municipalities within seasons were tested for homogeneity of variance using Levene's test. The data were natural-log-transformed when Levene's test indicated the variances were unequal. Tukey's Studentized Range Test at the 5% significance level was used to determine differences among municipalities for transformed and untransformed means. Means of the upper quartile were calculated and compared in the same manner. A paired Student's t-test in Excel was used to determine whether a significant difference ($p<0.05$) existed in CPUE at all sites between the two seasons.

3. Results

CW of the 219 crabs that were trapped in summer and fall in the four municipalities averaged 15.1 cm (Table 3). Mean CW of the crabs trapped in fall was not significantly ($t_{Sat.}=1.61$, df=156, $p=0.109$) larger than for those trapped in summer, but the mean CW in the upper quartile was significantly larger in fall than in summer ($t_{pooled}=3.42$, df=54, $p=0.001$).

In summer 2004, mean CW of crabs from Utwe was significantly ($F=13.4$; df=3,122; $p<0.0001$) larger than for crabs from the other municipalities. By fall 2004, Utwe crabs were still significantly wider, but Malem crabs were then significantly smaller than in the other municipalities ($F=28.6$; df=3,89; $p<0.0001$). Mean width of crab carapaces in the upper quartile was significantly larger in Utwe than in the other municipalities in

Table 3
Average CWs of all crabs trapped in 2004 in this study and of crabs in upper quartile

	All crabs			Upper quartile		
Island-wide	Overall	Summer	Fall	Overall	Summer	Fall
Mean (cm)	15.1	14.9	15.4	17.5	17.0a	18.1b
SE (cm)	0.13	0.15	0.24	0.17	0.20	0.27
N	219	126	93	56	32	24
Utwe						
Mean (cm)	17.6	16.9	18.5	19.6	19.3	20.1
SE (cm)	0.33	0.46	0.39	0.44	0.24	0.97
N	36	20	16	9	5	4
Lelu						
Mean (cm)	15.0	14.3a	15.5b	16.5	16.0a	17.1b
SE (cm)	0.20	0.25	0.27	0.18	0.17	0.13
N	59	29	30	16	8	8
Tafunsak						
Mean (cm)	14.8	14.6	15.0	16.3	16.1a	16.7b
SE (cm)	0.18	0.22	0.32	0.13	0.11	0.22
N	56	34	22	15	9	6
Malem						
Mean (cm)	14.2	14.6b	13.5a	15.9	15.8	16.0
SE (cm)	0.20	0.17	0.42	0.11	0.15	0.19
N	68	43	25	18	11	7

Different lower case letters indicate a significant difference ($p<0.05$) between seasons.

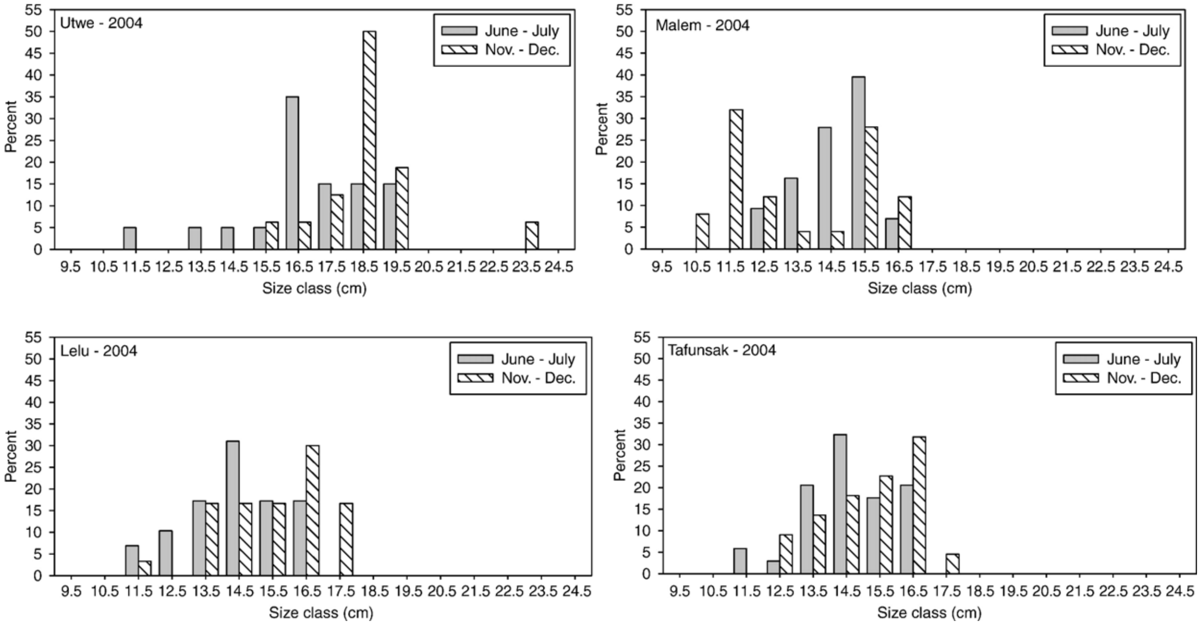

Fig. 2. Age-class distributions of mangrove crabs trapped in summer and fall 2004 in four municipalities in Kosrae, Federated States of Micronesia.

both summer and fall (summer: $F=64.9$; $df=3,29$; $p<0.0001$; fall: $F=20.9$; $df=3,21$; $p<0.0001$).

Mean CW was significantly larger in fall than in summer for Lelu ($t_{pooled}=3.22$, $df=57$, $p=0.002$), Malem ($t_{Sat.}=2.54$, $df=31.8$, $p=0.016$), and Utwe ($t_{pooled}=2.49$, $df=34$, $p=0.018$), but there was no significant seasonal difference for crabs in Tafunsak ($t_{pooled}=1.18$, $df=54$, $p=0.242$). Mean CW of the upper quartile was significantly larger in fall than in summer in Lelu ($t_{pooled}=5.32$, $df=14$, $p=0.0001$) and Tafunsak ($t_{pooled}=2.29$, $df=13$, $p=0.039$), but there was no significant seasonal difference in either Malem ($t_{pooled}=0.81$, $df=16$, $p=0.430$) or Utwe ($t_{Sat.}=0.84$, $df=3.38$, $p=0.456$).

Size-class histograms suggest that a crab in Kosrae is not captured in a trap until its CW reaches ~ 10.5 cm (Fig. 2). The largest crab trapped in this study was from Utwe and had a CW of 23.0 cm. In Malem, the smallest size classes were trapped only in fall, and no larger size classes were present in fall than in summer. In the other three sites, the largest size class was in the fall.

CW of 221 crabs that were trapped from the same sites in the earlier study as in this study averaged 14.7 ± 0.14 (SE), and the mean of the upper quartile was 17.1 ± 0.13 (SE).

CPUE did not differ significantly from summer to fall among the four sites ($t=0.898$, $df=3$, $p=0.14$). The overall CPUE, including data from both seasons and all municipalities, was 0.685 crab per trap night.

4. Discussion

Significant differences among populations of *Scylla serrata* at four sites around Kosrae and across a time span of 4 mo demonstrate the importance of local environmental conditions and management practices to this species. Crabs from the Utwe-Walung Tidal Channel in the municipality of Utwe included the largest individuals of all four municipalities, and neither overall mean size nor mean size of the upper quartile changed from summer to fall (Fig. 2). Human population density is lowest on this part of the island, mangroves are the most extensive among the four sites, and subsistence life styles are most common, so more trips are made to collect crabs, and more crabs are collected (Tables 1 and 2; Naylor and Drew, 1998; Naylor et al., 2002). Perhaps the large, remote mangrove forest beyond the area trapped acts as a reserve, so that crabs have more opportunity to grow to large sizes than on other parts of the island. With the recent construction of a new road to the remote village of Walung, access to these mangrove forests and ease of getting to a market may increase pressure on this population.

Harvest pressure on mangrove crabs has traditionally been lowest in the municipality of Malem (Naylor et al., 2002). Nevertheless, CW of the Inya River population, both overall and in the upper quartile, decreased during this study (Table 3, Fig. 2), suggesting that the population at this site cannot support even a relatively modest harvest level. Mean CW in the upper quartile increased in both the Pukusrik Tidal Channel (Lelu) and the Okat River (Tafunsak), and overall mean CW of Pukusrik crabs also increased (Table 3, Fig. 2). The Resource Management Committee in Lelu considered several management options during this project and is now establishing a marine protected area in part of Lelu Harbour, which is adjacent to Pukusrik (although the mangrove forests are not contiguous). The crab population in Tafunsak's Okat River may still be recovering from extensive trapping for commercial use before 2000.

The presence of significant differences in CW among mangrove crabs on different parts of the island reinforces earlier observations in Kosrae (Bonine et al., 2008) and is consistent with other studies describing restricted movement from one mangrove stand to another elsewhere in Micronesia (Pohnpei, Federated States of Micronesia: Perrine, 1978) and in the Indo-Pacific, including Australia (Hyland et al., 1984; Pillans et al., 2005) and for *S. paramamosain* in Vietnam: Le Vay et al., 2007). Because of a high degree of site fidelity and likely differences in harvest pressures arising from socio-economic differences, site-specific harvest regulations could be an effective way of managing mangrove crab populations to meet local needs in many places.

However, the degree of genetic isolation of each population is still not understood for any of the species of mangrove crabs, because of the difficulty of tracking larval stages before they settle in mud flats and mangrove forests as juveniles. Understanding the nature of dispersal of mangrove crabs during their larval stages is still important to understanding the long-term implications of management or mismanagement of adjacent populations along a shoreline.

Trends in CW and CPUE from 1999 to 2004 suggest that the overall population on Kosrae may be stable. Harvest pressure may have decreased since the earlier study (Bonine et al., 2008), perhaps because of heightened awareness of the species' vulnerability. The existing regulation that no crab of CW<6 in (15.2 cm) may be taken appears to be protecting the overall population adequately.

Further study to examine such environmental characteristics as spatial variation in food sources for crabs and effects of waste disposal in mangrove forests may help achieve a better understanding of differences in size characteristics among different sites on Kosrae, justifying additional restrictions such as prohibiting the harvest of females, establishing marine protected areas, or suspending harvest occasionally for a few months where appropriate. Regular monitoring of the crab populations at the same sites, perhaps at yearly intervals, should enable island resource managers to determine if additional regulation is needed.

This study demonstrated that populations of *S. serrata* can develop distinctive size distributions because of differing environmental conditions and harvest patterns. Even size at maturity for a related species can vary from one population to another (*S. paramamosain*: Walton et al., 2006). The existence of site fidelity and local variations in growth patterns not only in *S. serrata* but in other species of mangrove crabs as well suggests that local regulations in addition to regional restrictions may be appropriate for many sites in the Indo-Pacific. Monitoring populations on a regular basis may increase the ability of small, remote communities to manage an important resource sustainably.

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References

Bonine, K.M., Bjorkstedt, E.P., Ewel, K.C., Palik, M., 2008. Population characteristics of the mangrove crab *Scylla serrata* in Kosrae, Federated States of Micronesia: effects of harvest and implications for management. Pac. Sci. 62.

Brown, I.W., 1993. Mangrove crabs. In: Wright, A., Hill, L. (Eds.), Nearshore Marine Resources of the South Pacific: Information for Fisheries Management and Development. Forum Fisheries Agency, Honiara, Solomon Islands, pp. 611–642.

Carpenter, K.E., Niem, V.H., 1998. The Living Marine Resources of the Western Central Pacific. Cephalopods, Crustaceans, Holothurians and Sharks. FAO Species Identification Guide for Fishery Purposes, vol. 2. FAO, Rome.

FSM Dept. Econ. Affairs, 2000. Kosrae State Census Report. Palikir, Pohnpei, FSM.

Hauff, R.D., Ewel, K.C., Jack, J., 2006. Tracking human disturbance in mangroves: estimating harvest rates on a Micronesian island. Wetlands Ecol. Manag. 14, 95–105.

Hill, B.J., 1975. Abundance, breeding and growth of the crab *Scylla serrata* in two South African estuaries. Mar. Biol. 32, 119–126.

Hyland, S.J., Hill, B.J., Lee, C.P., 1984. Movement within and between habitats by the portunid crab *Scylla serrata*. Mar. Biol. 80, 57–61.

Keenan, C.P., Davie, P.J.F., Mann, D.L., 1998. A revision of the genus *Scylla* de Haan, 1833 (Crustacea: Decapoda: Brachyura: Portunidae). Raffles Bull. Zool. 46, 217–245.

Kosrae State Legislature, 2006. Kosrae State Code. Section 19.417.2.h. p. 297.

Krauss, K.W., Keeland, B.D., Allen, J.A., Ewel, K.C., Johnson, D.J., 2006. Effects of season, rainfall, and hydrogeomorphic setting on mangrove tree growth in Micronesia. Biotropica 39, 161–170.

Le Vay, L., Ut, V.N., Walton, M., 2007. Population ecology of the mud crab *Scylla paramamosain* (Estampador) in an estuarine mangrove system: a mark-recapture study. Mar. Biol. 151, 1127–1135.

Marichamy, R., Rajapackiam, S., 2001. The aquaculture of *Scylla* species in India. Asian Fish. Sci. 14, 231–238.

Naylor, R., Drew, M., 1998. Valuing mangrove resources in Kosrae, Micronesia. Environ. Dev. Econ. 3, 471–490.

Naylor, R.L., Bonine, K.M., Ewel, K.C., Waguk, E., 2002. Migration, markets, and mangrove resource use on Kosrae, Federated States of Micronesia. Ambio 31, 340–350.

Perrine, D., 1978. The mangrove crab on Ponape. Technical Report, Marine Resources Division, Ponape, Trust Territories of the Pacific Islands.

Pillans, S., Pillans, R.D., Johnstone, R.W., Kraft, P.G., Haywood, M.D.E., Possingham, H.P., 2005. Effects of marine reserve protection on the mud crab *Scylla serrata* in a sex-biased fishery in subtropical Australia. Mar. Ecol., Prog. Ser. 295, 201–213.

SAS Institute Inc., 2000–2004. SAS 9.1.3 Help and Documentation. Cary, NC.

Satterthwaite, F.E., 1946. An approximate distribution of estimates of variance components. Biometeorol. Bull. 2, 110–114.

Steele, R.G.D., Torrie, J.H., 1980. Principles and Procedures of Statistics. McGraw-Hill, New York.

Walton, M.E., Le Vay, L., Truong, L.M., Ut, V.N., 2006. Significance of mangrove-mudflat boundaries as nursery grounds for the mud crab, *Scylla paramamosain*. Mar. Biol. 149, 1199–1207.

Whitesell, C.D., MacLean, C.D., Falanruw, M.C., Cole, T., Ambacher, A., 1986. Vegetation survey of Kosrae, Federated States of Micronesia. USDA Forest Service PSW-17, Berkeley, CA.

Williams, M.J., Primavera, J.H., 2001. Choosing tropical portunid species for culture, domestication and stock enhancement in the Indo-Pacific. Asian Fish. Sci. 14, 121–142.