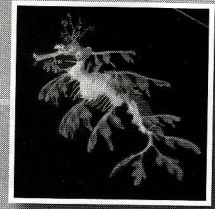# Mangroves and Saltmarsh

<div style="text-align: right">18</div>

Rod M. Connolly and Shing Yip Lee

CHAPTER OVERVIEW

Mangroves and saltmarsh are the ubiquitous, high intertidal habitats of undisturbed, soft-sediment shorelines around the world. In this chapter we describe the current ecological understanding of mangrove and saltmarsh habitats, beginning with brief descriptions of the flora and fauna, and discuss links between plants and animals. We then consider ecological theories about the two habitats from a global perspective, and discuss these in more detail with an emphasis on Australasian examples. One of the key concepts is how animals such as grapsid crabs affect processes that influence mangrove structure and function, and more broadly how biotic (e.g. propagule predation, adult-sapling competition) and abiotic (e.g. light gap, propagule dispersal) factors interact to determine local mangrove species distributions. We also examine in detail how saltmarsh and mangrove habitats are used by fish when inundated. Another emphasis is the role of mangroves and saltmarsh in the provision of organic matter that supports coastal secondary production. Finally, we examine the ecological responses of mangroves and saltmarsh to human activities, and discuss how research can help to provide solutions for managing those activities.

Introduction

Mangroves are typically considered to be characteristic of the warmer seas of low latitudes, and saltmarsh of cooler seas at high latitudes, particularly in the northern hemisphere (Adam 1990). Their distributions can have major overlap, however, and in places such as Australia, mangroves and saltmarsh occur together in the same estuaries along the majority of the coastline (Adam 1990), and they are therefore covered together in this chapter.

The vegetation of mangroves and saltmarsh is in many respects similar to that of the fully terrestrial habitats on their landward boundary, but mangrove and saltmarsh plants exhibit a suite

KEY CONCEPTS

- Outwelling of organic material to support coastal secondary production
- Role of animals in mangrove structure and function
- Interplay between biotic and abiotic factors in determining local mangrove/saltmarsh distribution

of adaptations to the physiological stresses of high and variable salinity and fluctuating sediment levels (Hutchings & Saenger 1987; Pennings & Bertness 2001). The habitats typically have high rates of primary and secondary productivity despite the extremely variable abiotic characteristics of their environment (Saenger 1994), and this has led to theories about very high levels of importance of mangroves and saltmarsh in food webs within the habitats and in adjacent waters.

Mangroves and saltmarsh occur predominantly, albeit not exclusively, in estuaries, which are the site for so many of the world's major urban centres. Both habitats have thus suffered the detrimental effects of being exposed to a wide range of human activities (Adam 2002). As knowledge of mangrove and saltmarsh systems has increased, so has the recognition that these habitats need to be actively preserved.

Mangroves

The term mangroves collectively refers to trees and shrubs dominating the intertidal zone of sheltered coastlines in the tropics and subtropics, mainly between 25°N and 25°S, where the winter seawater temperature is ≥20°C. Extension of mangrove distribution beyond these latitudinal limits is usually associated with the influence of warm oceanic currents; for example, on the east coast of Australia, where *Avicennia marina* occurs at ~38.5°S in Corner Inlet, Victoria. Dominance by mangroves declines gradually with increasing latitude. In Australia, species richness decreases rapidly south of the Queensland–New South Wales border (Hutchings & Saenger 1987). Saltmarshes dominate in the cooler latitudes, but there are recent signs that mangroves are intruding into saltmarsh areas on the eastern Australian coastline (Saintilan & Williams 1999).

Because of their association with soft, often smelly, mud, and difficulties of access, mangrove ecosystems have been studied less extensively than some other major coastal ecosystems, such as coral reefs. Historically, ecological studies of mangroves have lagged behind those of their temperate counterpart, saltmarsh, where most of the theories in estuarine ecology originated. However, their geographical extent and potential importance as a contributor to tropical estuarine productivity has prompted more research on mangroves in the past few decades (Ellison et al. 1999).

Earlier studies of mangroves described the flora and fauna, with relatively little advance on ecological processes in this structurally complex and dynamic environment. The need to concentrate on the animal and plant life associated with mangrove habitat is understandable in populous tropical countries, where mangroves are expected to contribute significantly to the economy through the provision of food (e.g. fish and crustaceans, fruits and seeds of certain mangroves) and raw materials for construction (e.g. timber) and crafts (e.g. tannins as dye). Heavy reliance on consumptive uses has resulted in significant reduction in the area of mangroves in the tropics, with most countries having lost more than half of their mangrove areas over the past 50 years (Spalding et al. 1997) (see Box 18.1).

Mangrove flora

Mangroves are an 'artificial assemblage' (i.e. species are not taxonomically related) of about 55 extant species of trees and shrubs that demonstrate special adaptations for life in the intertidal zone (Tomlinson 1986). Another 80 species of plants, both herbaceous and woody, have been recorded as mangrove associates, and bear no special adaptations to living in the intertidal environment. Mangrove associates usually occur in the upper littoral zone, at the border between true mangroves and terrestrial vegetation. The population genetics of the main mangrove species have only been analysed in the past decade or so (Duke 1995; Ellison et al. 1999). Recently, many species of hybrid mangroves have been reported, for example *Rhizophora* (Duke et al. 2002), potentially shedding new light on the pattern of

mangrove radiation and the route of colonisation of the tropical shores.

Mangrove fauna

Practical difficulties in sampling fauna in the spatially complex mangrove habitat (Hindell & Jenkins 2005; Salgado Kent & McGuinness 2006) have restricted the number of studies of mangrove fauna. Individual elements of the mangrove fauna have, however, been studied because of their functional roles and potential commercial significance. Decapod crustaceans such as prawns and crabs, commercially important species of fish, and gastropod molluscs have received most attention. Other elements of the mangrove fauna, such as the insect herbivore assemblage, are poorly documented.

Mangrove animals have been studied mostly for their trophic and bioturbating roles, and their capacity for commercial fisheries production. Grapsid crabs (family Grapsidae) are the most important bioturbators in tropical, especially 'eastern', mangroves (*sensu* Tomlinson 1986; boundaries at east Africa and the mid Pacific islands, longitude 30° to 180°E). High levels of species richness and abundance have been reported from African, Asian and Australian mangroves (Macintosh 1984; Tan & Ng 1994; Davie 2002), and there is a general positive correlation between crab and mangrove species richness (Lee 1998). This relationship has further been demonstrated by the difference in the population biology of species associated with different mangroves (Lee & Kwok 2002), a reflection of the importance of mangroves in shaping the environment available to their associated fauna (e.g. Wilson 1989; Tanaka & Maia 2006). Grapsid crabs typically dominate the mobile epifauna of tropical mangrove forests, with most species exhibiting a burrowing habit. These crabs consume and process large amounts of mangrove leaf litter (Lee 1998; Nordhaus et al. 2006), with a trophic role similar to the shredders of low-order freshwater streams. The significance of this pathway increases with tidal height, provid-

ing a sink that operates in the opposite direction to tidal export.

Grapsid crabs also shape the structure and function of tropical mangrove forests through their bioturbation of the sediment. Studies in the crab species-rich 'eastern' mangroves have prompted Smith et al. (1991) to accord 'keystone species' status to these crabs. Grapsid crabs are not indispensable to all mangroves, however, since the 'western' mangroves (15° to 130°W) have an impoverished crab fauna. Since one of the main driving forces on protected sediment shores is the limited oxygen penetration into sediment, bioturbation through burrowing by crabs is expected to result in significant changes in sediment biogeochemistry. Crab burrowing activities can result in increased flux of material between sediment and tidal water by providing increased surfaces for material exchange (e.g. Ridd 1996). More importantly, crab bioturbation can alter the redox condition of the sediment to influence biogeochemical pathways that control the production of substances like ammonia and sulphide, which are known phytotoxins (Smith et al. 1991). Such effects could, however, be subtle and indirect, as has been demonstrated by the effect of the polychaete *Nereis diversicolor* on *Spartina anglica* saltmarsh geochemistry (Gribsholt & Kristensen 2002). *Nereis diversicolor* removes the epibenthic algal mat from the sediment, thus modifying the redox condition of the substrate to influence biogeochemical processes. Removal of phytotoxins by tidal flushing is one mechanism by which 'tidal subsidy', that is, increased productivity of coastal wetlands with increase in tidal energy (Odum 1980), may occur.

The benthos of mangrove forests has not been well documented, but data obtained to date suggest that species richness, diversity and abundance are low, and are usually lower than those of other estuarine habitats (e.g. Koch & Wolff 2002; Morrisey et al. 2003; Alfaro 2006). Dominance by a small number of species, usually gastropods or decapod crustaceans in the epifauna, and polychaetes in the infauna, is common.

The link between macrobenthos assemblages and mangrove sediment characteristics is unclear. While Morrisey et al. (2003) were able to detect differences in species richness between mangrove stands of different ages, and relate the difference to sediment characteristics (e.g. degree of compaction, organic content) arising from the age difference, Chapman and Tolhurst (2004) failed to detect a significant dependence of assemblage structure on selected sediment properties (water content, chlorophyll and carbohydrate concentrations). The latter study was conducted in forests affected by urban impact, which arguably could have had an overwhelming effect (e.g. due to toxic pollutants) on assemblage structure. A study by Lindegarth and Hoskin (2001), however, found no difference in macrobenthic assemblages between mangrove forests in urban and non-urban sites in the Port Hacking estuary in New South Wales.

The influence of mangroves on physical and chemical characteristics of the habitat also seems to affect the abundance of meio- and microfauna. Nematodes, harpacticoid copepods and micro-gastropods dominate the mangrove meiofauna, and there is evidence to support their trophic importance to fish and crustaceans (Coull 1998). Nematodes are particularly associated with decaying mangrove leaf litter (Gwyther 2003). Although mangrove leaf litter provides the nutrient source supporting the nematodes, Alongi and Christoffersen (1992) recorded a general negative effect of mangrove detritus amount on nematode abundance, an effect attributed to the high tannin content and poor nutritional quality of mangrove detritus. Meiofaunal assemblages are shaped more by sediment characteristics such as grain size and organic content (Ólafsson et al. 2000) than by the mangrove species present (Gee & Somerfield 1997). Mangrove colonisation of estuarine sediment seems to increase the abundance of some microfauna (e.g. foraminiferans) and larvae of macrofauna through the provision of shade and a buffer from extreme environmental conditions (Debenay et al. 2002), or chemical cues from mangrove organic matter (Fleck & Fitt 1999).

The role of mangrove trees in providing substrates for colonisation by sessile and mobile invertebrates has also attracted considerable attention, and has been used as a model for studying forces determining assemblage structure (e.g. Farnsworth & Ellison 1996; Satumanatpan et al. 1999; Brooks & Bell 2001; Satumanatpan & Keough 2001). Many of these studies concluded that post-settlement processes (such as predation) do not determine recruitment as effectively as do pre-settlement processes (such as larvae availability and substrate selection) (see also Chapter 2, Early Life Histories of Marine Invertebrates and Fishes).

Mangroves seem to provide an important habitat to many estuarine and reef fishes. Earlier studies of mangrove fish assemblages suggest that mangroves support higher juvenile fish abundances than neighbouring habitats, and most of the species supported do not spawn in mangroves (Robertson & Blaber 1992). Robertson and Blaber (1992) summarised and compared the fish fauna of four estuaries in tropical arid Australia, recording between 38 and 197 species. Even higher species richness has been recorded from tropical mangrove estuaries in Asia (260 to 400 fish species in the mangroves of Vietnam and Bangladesh, respectively; Hong & San 1993 and Hussain & Acharya 1994). Robertson and Blaber (1992) indicate that habitat diversity (linked to tidal amplitude), water turbidity, and the proximal presence of seagrass beds all favour high fish diversity and abundance. Sampling in subtropical water at high tide, Laegdsgaard and Johnson (1995) found that juveniles of seven out of the ten commercially harvested fishes recorded were most abundant in mangroves among the estuarine habitats. In temperate Australian waters, large stands of mangroves in Victoria have been shown to support more fish than adjacent mud-flats (Hindell & Jenkins 2005), but no such difference was found for small mangrove stands in Sydney Harbour (Clynick & Chapman 2002). Detailed analyses are still necessary to assess the importance of habitat mosaics and their connectivity in determining the faunal assemblages

of estuarine habitats including mangrove forests (Sheaves 2005).

Theories of mangrove ecology

Early research on mangrove ecosystems focused on documenting their biotic assemblages ('what lives where'), but in the last few decades attention has gradually shifted towards understanding the processes behind the observed patterns ('how and why'). The most influential recent questions being asked in mangrove ecology include the mechanism leading to local mangrove species distribution, the trophic contribution of mangroves to estuarine food webs (Figure 18.1), and the role played by key animal species in ecosystem structure and function. These components of mangrove ecology are obviously inter-related. For example, the activities (feeding, bioturbation) of animals influence local mangrove community structure and productivity, thus moderating the capacity of mangroves to contribute to estuarine food webs.

Local distribution of mangroves: zonation, succession, and forest structure

On a geographical scale, the global occurrence of mangroves is influenced by temperature, the availability of suitable substratum, and to a lesser extent, freshwater supply. Mangroves thrive on protected shorelines where penetrable but relatively stable sand or mud is available, and are most productive where soil salinity is ameliorated by freshwater influx (see Chapter 11, Linking

Figure 18.1 Three mechanisms of transfer of organic matter from marsh/mangroves to food webs in deeper water.

Detrital Transport

Ontogenetic Migration
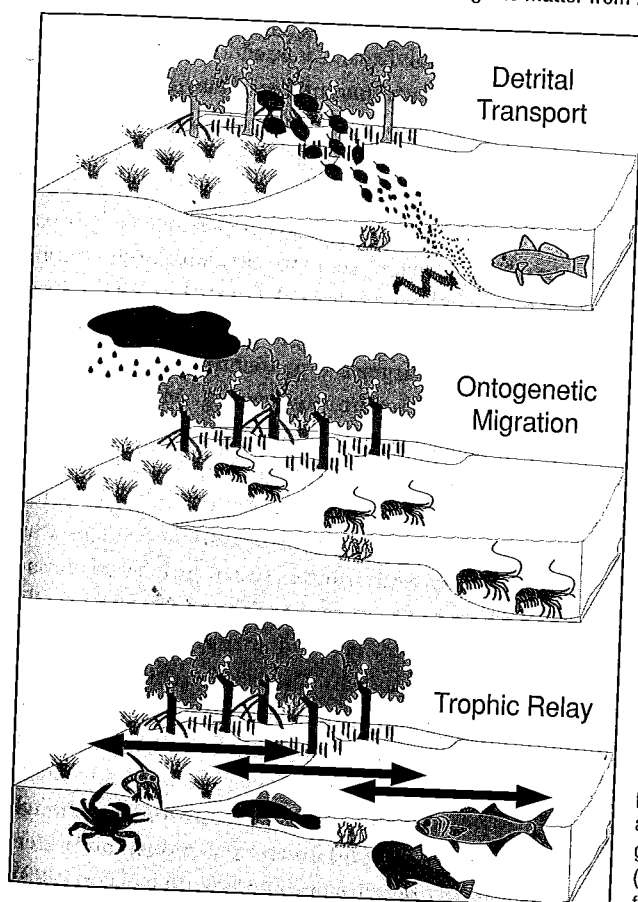
Trophic Relay

Detrital transport includes movement of particulate and dissolved organic matter. Ontogenetic migration is movement in migrating animals such as banana prawns (*Fenneropenaeus merguiensis*). Trophic relay (Kneib 1997) involves a series of predator–prey interactions; in Australia, for example, crabs and their larvae high on the shore, eaten by fish such as glassfish (Ambassidae), gobies (Gobiidae) and juvenile mullet (Mugilidae), which in turn are preyed upon by fish such as flathead (Platycephalidae) and tailor (Pomatomidae).

Terrestrial-Freshwater and Marine Environments). These general factors of influence on mangrove growth have underpinned the early recognition of different types of mangrove forests based on forest structure (Lugo & Snedaker 1974).

Species assemblages of mangroves demonstrate distinct biogeographical differences. Slightly more than forty species of mangroves are known in the 'eastern' hemisphere (longitude 30° to 180°E), while fewer than ten species are found in the 'western' hemisphere (15° to 130°W; Tomlinson 1986). Peak diversity is found between 90° and 150°E, where more than thirty species may be found at locations favourable for mangrove growth.

Species distribution of mangroves on a local scale is also expected to be affected by the same factors, but the pattern is complicated by the varying abilities of different species to cope with these environmental influences. Early studies of mangrove floristics focused on the documentation of 'zonation', and many explanations have been suggested (Watson 1928; MacNae 1968; Hutchings & Saenger 1987). The notion of different species of mangroves apparently occupying different 'zones' on the shore is a common observation, as species often seem to occur in monotypic patches in sequence. Bunt (1996) examined 'zonation' of mangroves in 17 north Australian estuaries and noted a high variability in the sequence of occurrence of species. True zonation, defined as particular suites of co-occurring species occupying the intertidal zone according to a definite sequence, has rarely been demonstrated (see also Chapter 15, Intertidal Temperate Rocky Shores). Sometimes it is confused with patchy distribution due to, for example, poor dispersal, which is common in mangroves (e.g. McGuinness 1997a).

Smith (1992) reviewed factors and mechanisms that may determine local forest structure of mangroves: (1) land building processes driving autogenic succession of mangroves; (2) response of species to geomorphologic influences such as sea level rise; (3) physiological adaptations to stress gradients such as soil salinity in the intertidal zone; (4) dispersal patterns of mangrove propagules in accordance with size and rooting time; and (5) post-dispersal processes determining propagule establishment, such as predation and competition.

The experimental evidence for processes influencing mangrove zonation is disproportionately small compared with the effort in documenting species distribution patterns (Smith 1992). Of the five broad mechanisms proposed, physiological adaptations to local gradients and post-settlement processes seem to be supported to various extents by experimental evidence, while anecdotal evidence is available to support the notion that mangroves respond to geomorphic and climatic factors. Different mangrove species have different optimal requirements in salinity, nutrient abundance and soil characteristics (Hutchings & Saenger 1987), translating to correlations between soil properties and species recruitment, establishment and dominance (e.g. McKee 1995a; Lovelock et al. 2005). Availability (e.g. proximity to parent trees, tidal dispersal) and retention of propagules also influence the initial community structure (McKee 1995a; Patterson et al. 1997).

Many species of mangrove produce viviparous propagules that develop to substantial sizes before dispersal, a behaviour that has been hypothesised as an adaptation to their intertidal habit (Tomlinson 1986). The large, energy-rich propagules attract grazers both before (insects, e.g. Murphy 1990) and after (grapsid crabs, e.g. Smith 1987) abscission. Smith (1987) investigated propagule predation by crabs experimentally and noted that for four species of mangrove examined, there was an inverse relationship between propagule predation rate and dominance by conspecifics in the same area. This is now known as the *dominance-predation hypothesis* (Sousa & Mitchell 1999), however recent tests of this hypothesis have failed to support its generality in determining mangrove forest structure (McKee 1995b; McGuinness 1997b; Clarke & Kerrigan 2002). Although grapsid crabs are known to demonstrate preferences in their mangrove leaf diet (Lee 1998),

whether these preferences are strong enough to act as a differentiating force affecting forest structure through propagule predation is yet to be evaluated under a wide range of mangrove–crab associations. Experiments in Australia demonstrate that propagule survival and establishment are influenced by the interaction of a complex suite of factors including light, soil condition, local topography and predation intensity (McGuinness 1997a; Minchinton 2001; Clarke 2004).

Mangroves may affect their physical environment (Lacerda et al. 1995). Geochemical processes and organic matter dynamics are influenced by the mangroves and their associated fauna through differences in aeration efficiency and bioturbation activities (e.g. Smith et al. 1991; Lee & Kwok 2002; Marchard et al. 2004). Such interdependency tends to cloud analysis of processes such as mangrove zonation and succession, as cause and effect are not easily separable. Recent evidence suggests, however, that although mangroves can shape their environment, their influence is usually weak compared with physical (e.g. geomorphologic changes, Thom 1982) or anthropogenic (e.g. changes in sedimentation and pollution regimes) forces. Autogenic mangrove succession (Chapman 1970) is rarely effective in determining mangrove forest structure, as many other more powerful influences, including severe climatic events such as cyclonic storms, would interrupt successional processes that occur only over long time spans and under relatively stable environmental conditions (Lugo 1980; Thom 1982; Smith 1992; Duke 2001).

Notwithstanding the dense stilt roots of *Rhizophora* or the almost impenetrable shrubby growth of *Aegiceras*, mangrove forests tend to have relatively simple vertical structure. One characteristic of mangrove forests is the absence of an understorey layer (Janzen 1985). Corlett (1986) proposed that the understorey environment in mangrove forests presents significant challenges to establishing saplings because of a combination of low light availability and salinity stress. Ball (2002) evaluated this model experimentally on *Ceriops* spp. and showed that juvenile trees could survive the combined low light/salinity stress if below-ground competition with adult trees was eliminated.

The mangrove–fisheries connection

One of the most controversial theories in estuarine wetland ecology has been that nearshore secondary production depends on tidal export of wetland organic matter (Figure 18.1). This outwelling hypothesis (Odum 1980) is based on observations of saltmarsh systems on the Atlantic coast of North America. The dependency, if applicable to mangroves, would have strong implications for the management and conservation of mangroves worldwide.

Because of the spatial scale of the export process, direct experimental tests of outwelling are extremely difficult. Early studies used correlation analysis of the extent of coastal wetland and fishery production in the adjacent waters. Most of these analyses have resulted in positive correlations, taken by researchers to represent a dependency of nearshore production on wetlands (e.g. Martosubroto & Naamin 1977; Turner 1977; Pauly & Ingles 1986). There are, however, many methodological issues affecting the conclusions drawn from such correlative analyses (Lee 2004). Many predictors used in the regression models are themselves strongly correlated, and catch statistics are often not well delineated. In a detailed analysis of fishery species with different degrees of assumed mangrove dependence, Manson et al. (2005) found a significant influence of mangrove forest characteristics (e.g. perimeter and area) on mangrove-related and estuarine fishery species, while latitude was the only variable influencing catch of offshore species along the north-eastern Australian coast.

Lee (1995) reviewed the results of >20 studies on material exchange between mangroves and nearshore waters and concluded that although most systems seem to be exporting, both the spatial extent and magnitude of export were variable and generally restricted. Two broad approaches, mass balance and chemical tracing, have been

employed to measure exchange of materials between coastal wetlands and nearshore waters. The mass balance approach uses measurements from estimates of material movement based on water movement and time-series changes in concentration of materials in flumes (e.g. Childers 1994; Davis et al. 2003) or small natural water bodies with well-defined boundaries and channels of flow (e.g. Woodwell et al. 1977). Common chemical tracers include the stable isotopes of biologically important elements such as carbon, sulphur and nitrogen, and chemicals unique to specific producers such as fatty acid biomarkers (see Boxes 4.1 and 9.2). Studies using stable isotope tracers to track the movement of material of mangrove origin in coastal waters have largely concluded that mangrove trophic contribution to nearshore secondary production is limited (Table 18.1). This conclusion is supported by recent studies using stable isotope analysis demonstrating that carbon movement and assimilation by animals can be limited to a spatial scale of just a few metres (Guest et al. 2004; 2006).

There are many missing links in the mangrove–fishery connection. Indirect export pathways such as export through movement of animal biomass have not been well studied. Export of animal biomass may be in the form of transport of species that spawn in mangroves, such as grapsid and ocypodid crabs, or through a series of predator–prey interactions known as trophic relay (Kneib 1997). These indirect transfer pathways are poorly documented and their significance is yet to be demonstrated.

The importance of forms of organic matter that are more difficult to measure and analyse than macro-detritus is also obscure. Mangrove-derived dissolved organic matter (DOM) often dominates tropical estuaries (Jaffé et al. 2005). Although most of DOM in mangrove waterways and nearshore waters is thought to be refractory and thus of little direct value to consumers, the nature and transport dynamics of mangrove DOM is yet to be clarified. Boto et al. (1989) demonstrated through incubation experiments that tropical Australian mangrove sediments provide on average 35% of

bacterial productivity requirements in dissolved organic carbon (DOC). This strong uptake by bacteria suggests that mangrove sediments are a sink for DOC. Labile fractions of macrophyte DOM have been demonstrated to contribute to macrofauna nutrient intake (e.g. Alber & Valiela 1995), but this pathway has not been given much attention in mangroves. The role of small pieces of particulate organic matter (POM), or micro-POM, in food chains in mangrove-dominated estuaries also deserves attention. Robertson et al. (1992) highlighted the significance of micro-POM in terms of its abundance in a mass balance model for north-eastern Australian mangroves, but such assessments are rare.

The major source of micro-POM is fragmented and decomposed mangrove leaves and wood. Both sources are of poor nutritional quality, with C/N ratios of 100 or more. Microbial decomposition, considered the main process leading to mineralisation of mangrove organic matter in early trophic models, requires long periods (months) to produce micro-POM of sufficient nutritional quality for macrofaunal utilisation (Robertson 1986). Microbial colonisation alone is too low to provide substantial nutrition to macrofaunal consumers. Grapsid crabs act as shredders of mangrove leaf organic matter in most mangrove forests, consuming a large proportion of leaf litter (Lee 1998). Werry and Lee (2005) compared the rate of change in C/N ratio and the density of surface bacteria on microbe- and crab-processed leaf litter of *Avicennia marina*. Grapsid crabs, through breaking whole leaf litter into particles of ~200 µm, greatly accelerated bacterial colonisation of the faecal material and consequently, enrichment in N, compared to decomposition mediated by microbes alone. The enriched faecal material deposited on the forest floor could then become part of the micro-POM pool upon re-suspension. The importance of this indirect export process mediated by grapsid crabs is yet to be assessed.

The contribution by mangroves to coastal fisheries is not limited to the supply of nutrients and organic matter. The complex spatial environment provided by mangroves acts as habitat for larvae

Table 18.1 Results of selected stable isotope tracer studies investigating the mangrove–offshore trophic connection to nekton.

Nekton species analysed	Isotope tracers used	Signature of nekton (‰)	Signature of mangroves (‰)	Difference (consumer–mangrove) (‰)	Reference/ notes
Penaeus spp., Metapenaeus spp. Parapenaeopsis spp. Fish	$\delta^{13}C$	$\delta^{13}C$: −14.9 to −17.9 $\delta^{13}C$: −13.1 to −18.6	$\delta^{13}C$: −24.5 to −28.5	$\Delta\delta^{13}C$: 6.6 to 13.6 $\Delta\delta^{13}C$: 5.9 to 15.4	Rodelli et al. 1984/ samples from the 'offshore station'
Penaeus spp. Parapeneopsis spp.	$\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$	$\delta^{13}C$: −15.3 to −17.8 $\delta^{15}N$: 11.1 to 12.1 $\delta^{34}S$: 10.1 to 12.4	$\delta^{13}C$: −26.7 to −29.8 $\delta^{15}N$: 2.2 to 6.3 $\delta^{34}S$: −1.4 to 5.1	$\Delta\delta^{13}C$: 8.9 to 14.5 $\Delta\delta^{15}N$: 4.8 to 9.9 $\Delta\delta^{34}S$: −5.0 to −13.8	Newell et al. (1995)/ samples collected 3.5 km from mangroves
Penaeus spp. Metapenaeus spp.	$\delta^{13}C$, $\delta^{15}N$	$\delta^{13}C$: −15.5 to −19.6 $\delta^{15}N$: 8.4 to 11.3	$\delta^{13}C$: −26.9 to −30.0 $\delta^{15}N$: 6.3 to 8.0	$\Delta\delta^{13}C$: 7.3 to 14.5 $\Delta\delta^{15}N$: −0.4 to 5.0	Primavera (1996)
Penaeus spp. Metapenaeus spp.	$\delta^{13}C$, $\delta^{15}N$	$\delta^{13}C$: −14 to −17 $\delta^{15}N$: 5.2 to 10.0	$\delta^{13}C$: −27.0 to −28.8 $\delta^{15}N$: 1.3 to 3.7	$\Delta\delta^{13}C$: 10 to 15 $\Delta\delta^{15}N$: −1.5 to 8.7	Loneragan et al. (1997)
Parapeneopsis sp. Metapenaeus spp. Stomatopods	$\delta^{13}C$, $\delta^{15}N$	$\delta^{13}C$: −18.2 to −20.2 $\delta^{15}N$: 10.0 to 12.6	$\delta^{13}C$: −24.4 to −28.1 $\delta^{15}N$: 4.0 to 12.6	$\Delta\delta^{13}C$: 4.2 to 9.9 $\Delta\delta^{15}N$: 0 to 8.6	Lee (2000)
Penaeus spp. Metapenaeus spp.	$\delta^{13}C$, $\delta^{15}N$	$\delta^{13}C$: −17.0 to −25.1 $\delta^{15}N$: 8.4 to 11.3	$\delta^{13}C$: −28.7 to −26.7 $\delta^{15}N$: 4.4 to 6.3	$\Delta\delta^{13}C$: 1.6 to 11.7 $\Delta\delta^{15}N$: 2.1 to 6.9	Chong et al. (2001)
Decapod larvae	$\delta^{13}C$, $\delta^{15}N$	$\delta^{13}C$: −17 to −23 $\delta^{15}N$: 6.2 to 7.7	$\delta^{13}C$: −25.5 to −26.8 $\delta^{15}N$: 4.4	$\Delta\delta^{13}C$: 2.5 to 9.8 $\Delta\delta^{15}N$: 1.8 to 3.3	Schwamborn et al. (2002)
Mean		$\delta^{13}C$: −15.6 to −19.9		$\Delta\delta^{13}C$: 5.9±3.0 to 13.1±2.3	

The typically large difference (>5‰) between consumer and mangrove signatures indicates a relatively minor contribution of mangrove material in nekton diets (from Lee 2005).

and juveniles of estuarine nekton. The value of mangroves to larval and juvenile fish is thought to be related to reduced predation risk, increased food availability and, for some species, refuge from physical stress (Laegdsgaard & Johnson 2001; Meager et al. 2005). Quantitative sampling of larval or juvenile nekton abundances in spatially complex intertidal wetland habitats such as mangroves and saltmarshes presents many challenges (Rozas & Minello 1997; Connolly 1999). Perhaps because of this, it is only recently that studies have begun to examine the nursery role of mangroves fully, by comparing the contributions of juveniles from adjacent habitats to adult stocks (Beck et al. 2001).

Recent studies in the Caribbean have demonstrated some degree of dependence of coral reef and non-mangrove fishes on mangroves and seagrass habitats as nursery grounds (Nagelkerken et al. 2000; Mumby et al. 2003; Dorenbosch et al. 2004), although the dependency may vary according to species, spatial scale of the analysis (Halpern 2004) and characteristics of the mangroves (Ley et al. 1999). The main benefits of the mangrove association to fish are increased food supply (e.g. epiphytic algae on mangrove

structures), combined with reduced predation risk (Laegdsgaard & Johnson 2001; Cocheret de la Morinière et al. 2004). The effects of mangrove structure are complex, however, as the benefit is species- and size-specific. Nocturnal species seem to respond to shade provided by mangroves in different ways from diurnal species (Cocheret de la Morinière et al. 2004), while larger individuals are less dependent on mangrove structures in the presence of predators (Laegdsgaard & Johnson 2001). Stands of very short mangroves in southern Australia (Figure 18.2) support fish assemblages of lower diversity and abundance than more tropical mangroves (Hindell & Jenkins 2005).

Herbivory as an ecological process

Consumption of live producer biomass has been considered to be a relatively minor pathway for energy flow in coastal wetlands (see also Chapter 4, Negative Interactions: the Influence of Predators and Herbivores on Prey and Ecological Systems). Although specifically addressed as an energy sink by Smalley (1960) in his analysis of the Sapelo Island saltmarsh ecosystem, insect

Figure 18.2 Stands of very short mangroves (*Avicennia marina*) occur in New Zealand and southern Australia, generally supporting assemblages of fish with low species diversity and low abundance.

Photo: R. Connolly.

herbivory on producers in saltmarshes and mangroves has generally been documented at <10% standing biomass based on the proportion of leaf area missing (e.g. Lee 1991). Interspecific variation in herbivory attack can be highly variable, however, as has been demonstrated for species in north-eastern Australia (Robertson & Duke 1987). Recent detailed studies have recorded large numbers of insect species grazing mangroves (e.g. twenty-four on *Kandelia obovata*, Tong et al. 2006; thirty-one and thirty-three species respectively for *Avicennia marina* and *Rhizophora stylosa* and sixty-one in total, Burrows 2003).

Measuring missing areas on leaves is, however, not the optimal method for assessing the importance of herbivory as an ecological process in mangroves. Apart from errors due to change in the size of the missing areas with leaf growth (Reichle et al. 1973), discrete one-off measurements of missing area may also underestimate herbivory damage by three to six times (Burrows 2003). Simple missing area measurements do not consider the more subtle effects of herbivory damage. Effects include the reduction of leaf longevity and thus turnover by herbivory (Lee 1991; Ellison & Farnsworth 1996; Burrows 2003)

Box 18.1 Threats to mangroves

The global extent of mangroves is estimated to be between 1.7 and 1.8 million hectares (Spalding et al. 1997), while a loss of 1% per annum has been suggested by some researchers (Ong 1982). Locations conducive to mangrove development also are prime locations for human settlement. Most of the major tropical cities in the world are centred at the estuaries of the largest rivers, such as the Mekong (Ho Chi Minh City), the Pearl (Hong Kong), and the Chao Phraya (Bangkok) in Asia. Urban development and other anthropogenic activities such as agriculture that support human settlement have great impacts on coastal wetlands (Farnsworth & Ellison 1997; Salm et al. 2000; Lee et al. 2006), especially in developing countries, which historically support the most luxurious mangrove resources. It is estimated that these anthropogenic threats have destroyed >50% of mangrove forests in most of the South-East Asian countries (Wilkinson et al. 1994; Spalding et al. 1997). Two of the most significant threats are intensive aquaculture of crustaceans (particularly prawns) and finfish (e.g. Islam & Haque 2004), and harvesting mangroves for woodchip production (Ong 1995). Regrettably, such operations are environmentally unsustainable (e.g. Primavera 1997; Gunawardena & Rowan 2005) and, if allowed to proliferate, would result in long-term destruction of tropical mangrove resources.

There are, however, examples of sustainable use of mangrove resources. The Matang mangrove forest in peninsular Malaysia has been managed for many decades, based on simple thinning techniques, for charcoal and timber production, and is probably the best-managed and one of the best-studied mangrove forests in the world (Ong 1995). The management success of the Matang forest is an example of how tropical mangrove resources may provide long-term sustainable ecosystem and economic services to society.

While mangroves are being destroyed, recently there has been increasing attention given to their restoration and rehabilitation. There is some debate over how easily mangrove ecosystems can be restored or rehabilitated (e.g. Ellison et al. 1999), as most efforts are directed towards, and evaluated for, establishing the structure rather than the functional attributes of mangrove forests (e.g. Field 1996).

and changes in reproductive output and leaf chemistry (Tong et al. 2003).

The impact of herbivory on mangroves is also mediated through consumption of propagules both before and after abscission (Murphy 1990; Smith 1987). Herbivore preference for propagules of different species may result in significant effects on seedling establishment and stand structure (Robertson et al. 1990; Minchinton 2001, 2006).

Saltmarsh

Saltmarsh occurs on the same types of unconsolidated, sheltered shorelines as mangroves, but consists of grasses, herbs and shrubs rather than trees. Saltmarsh occurs in elevations from about mean tidal to upper astronomical tidal height. Saltmarshes are widespread on all inhabited continents. In the temperate waters of North America, Europe (with exceptions, see Dame & Allen 1996) and parts of South Africa, saltmarshes extend from the very top of the intertidal zone down to mean water level. The marshes of much of temperate North America are dominated by grasses, particularly *Spartina alterniflora* cordgrass, which is typically 0.5 to 1.5 m high, but can grow to over 2 m along the edge of creeks (Adam 1990). Vegetation is often shorter at higher elevations, in what is termed 'high marsh' in the USA (although not, for example, where stands of tall *Phragmites* grass occur). In the warmer waters of North America, South Africa, Australia, and Asia, mangroves dominate the mid intertidal zone and saltmarshes are restricted to the very highest part of the intertidal zone (Adam 1990), except where on occasion *Spartina* also occurs seaward of the mangroves. The vegetation in these regions is similar to that on high marshes in the USA, and consists of a combination of shorter grasses, turf-forming succulent herbs and woody shrubs (Adam 1990). There are thus important differences between the better-studied saltmarshes of east coast USA and marshes in other regions, including Australia (Adam 2002), and considerable effort is needed to test the generality of our current understanding of ecological processes on saltmarshes.

Saltmarshes in arid or strongly seasonal tropical regions often include extensive unvegetated pans. High evaporation rates render the porewater in sediment hypersaline, preventing growth of even the salt-tolerant vegetation that occurs elsewhere on the marshes (Adam 1990). These pans are little studied, but might prove to be an ecologically important extension to vegetated marsh habitats in regions such as the Middle East, where they are known as sabkha (Adam 2002), and in tropical and perhaps arid parts of temperate Australia. Key early texts ignored the presence of saltmarsh in tropical regions (e.g. Chapman 1960). The relatively recent inclusion of the whole saltmarsh, vegetated and unvegetated, in coastal resource inventories, shows that saltmarsh habitat is very widespread in tropical and subtropical regions. In Australia, the area of saltmarsh is much greater in the tropical north (Queensland, Northern Territory and northern Western Australia) than in the rest of the country (Zann 1995).

The degree of understanding and focus in scientific and conservation efforts differs for mangroves and saltmarsh in Australia. Australian research on mangroves has been central to the development of ecological concepts in this habitat (Robertson & Alongi 1992), and mangrove habitat is prevalent in ecological studies in Australia (10% of marine ecological papers at the time of a review by Fairweather 1990). Saltmarsh models, on the other hand, have been formulated, tested and advanced predominantly on northern hemisphere marshes. Our understanding of key processes such as plant productivity, grazing rates and use of inundated marshes by fish and shrimp comes from northern hemisphere marshes. Literature about marsh nekton (fish, prawns and shrimps), for example, is predominantly from North America (90% of all papers), with 7% from Europe and 3% from Australia (Connolly 1999). Given that Australian marshes are different from the better studied marshes of the Atlantic and Gulf coasts of the USA, they might well function differently. Fairweather (1990) singled out saltmarsh habitat as being in particular need of scientific and conservation attention in Australia. The

lack of saltmarsh research in Australia has begun to be rectified, prompted partly by wetland studies done during the Homebush site development for the 2000 Olympic Games in Sydney, New South Wales. This also contributed to the 2004 declaration of coastal saltmarsh as an Endangered Ecological Community under the New South Wales Threatened Species Conservation Act.

Saltmarsh flora

The ecology of saltmarsh plants has been studied mainly on the Atlantic and Gulf coasts of the USA and in Europe. *Spartina alterniflora* marshes are among the most productive habitats in the world (Adam 1990). Dense aggregations of closely spaced plants minimise energy allocated to structural support (Pennings & Bertness 2001). Plants on Australian marshes are usually less dense, perhaps because nutrients are scarcer (Adam 1990), but structural support is presumably less important in any case, since the plants are relatively short. The exception is the dense stands of introduced *Spartina anglica* in southern Australian estuaries (Kriwoken & Hedge 2000). Productivity of the two plants common on Australian marshes, *Sporobolus virginicus* and *Sarcocornia quinqueflora*, is considerably below rates measured for *Spartina* in the USA (Clarke & Jacoby 1994). Australian measurements have been made only on temperate marshes, however, and productivity of these and other plants on subtropical and tropical saltmarshes are unknown and require further investigation.

High porewater salinities arising from high rates of evapo-transpiration result in the formation of unvegetated pans on marshes at low latitudes (Pennings & Bertness 2001). These pans are semi-permanent features of the marsh. At high latitudes, unvegetated areas result from different types of disturbances, and typically last only until recolonisation during warmer months (Pennings & Bertness 2001). Some bare areas occur seasonally where plants die back. The rapid growth during warmer months can eventually also lead to the collapse of above-ground portions

of plants, which are then deposited on adjacent marshes where they form bare areas by smothering existing plants (Valiela & Rietsma 1995). In Australia, growth of marsh plants in the warmer waters is less seasonal, wrack formation is less pronounced and smothering has not been recorded. Deposition of mangrove and seagrass wrack from adjacent habitats is more pronounced, and the consequences for marsh plants, energy budgets and detritivorous animals is only just beginning to be considered (Chapman & Roberts 2004).

Microalgae and cyanobacteria living in and on saltmarsh sediment, collectively known as microphytobenthos, are very productive autotrophs on marshes of the east coast of the USA (Currin et al. 1995). It is not known whether productivity of microphytobenthos is as high on the less frequently inundated marshes of places such as Australia, although a relatively high rate of nitrogen fixation by cyanobacteria has been demonstrated on the saltpans of northern Western Australia (Paling et al. 1989).

Saltmarsh fauna

The level of herbivory by animals on saltmarsh vegetation is considered to be low (Pennings & Bertness 2001), although grazing by large mammals is widespread, particularly in Europe, and can be locally important (Adam 1990). Large grazing mammals including cattle and kangaroos are conspicuous on certain Australian marshes, but any effects on plant assemblages are unrecorded. Invertebrate grazers play a role in the provision of detritus on the east coast of the USA. Standing, senescent *Spartina* grass is colonised by fungi, and grazing on the plant/fungi complex results in detrital fragments falling to the sediment where they are colonised by bacteria and consumed by detritivores (Graca et al. 2000). It has been shown that the rate of supply of this detritus can regulate growth rates of detritivores such as marsh crabs (Genoni 1985).

In Australia, ecological work on marsh macrofauna has been mainly on gastropods and crustaceans. Perhaps because of the infrequency of

inundation of Australian marshes, invertebrates alter their behaviour after the marsh becomes wet. Grapsid crabs burrow more actively under moist conditions (Richardson et al. 1998), and the pulmonate gastropod, *Salinator solida*, responds to inundation by leaving the shelter of cracks in the sediment to feed on the sediment surface (Kaly 1988; Roach 1998). Experimental work on *S. solida* has also shown an unusual effect of predation on gastropod size distributions. Fish apparently prey more effectively on larger snails, with the result that there are more larger snails higher on the shore where predation pressure is less (Roach 1998).

The relatively small home range of adult grapsid crabs (Guest et al. 2006) has made them an ideal organism for testing theories about energy flow in estuarine food webs. The early emphasis on outwelling of carbon from estuarine habitats provided the framework for numerous subsequent empirical studies of estuarine systems (Kneib 2000), based around the concept that animals can be spatially segregated from the ultimate autotrophic source on which they rely. The most common technique for examining energy flows became carbon stable isotope analysis (Peterson & Fry 1987). In some estuaries, large-scale movement of carbon proved to be negligible (e.g. Loneragan et al. 1997; Dittel et al. 2000), and the focus shifted to carbon movement between areas within estuaries. Results of studies that examined the within-estuary movement of carbon indicated that animals were ultimately deriving their nutrition from local sources (e.g. Deegan & Garritt 1997; Bouillon et al. 2004). The distances between sampling locations in such studies were typically measured in kilometres, but the work nevertheless pointed towards smaller-scale spatial resolution of food webs. A recent study in a subtropical estuary in Australia analysed carbon isotopes of grapsid crabs collected across the boundary of saltmarsh and mangrove patches to measure the extent of carbon movement and assimilation by invertebrates (Guest et al. 2004). Large differences in crab isotope values were found between individuals collected in the two adjacent habitats, showing that animals derived their carbon predominantly from sources in their immediate surrounds (within 15 m). Subsequent sampling at an even finer scale showed that carbon isotope values of invertebrates changed rapidly across the saltmarsh–mangrove boundary, with carbon isotope values shifting up to 8‰ in a narrow transition zone (Figure 18.3). Carbon movement and

Figure 18.3 Carbon stable isotope values of the grapsid crab, *Parasesarma erythrodactyla*, across the mangrove/saltmarsh interface in a subtropical estuary (averaged, with standard errors, from three sites).

Averaged data
$r^2 = 0.98$
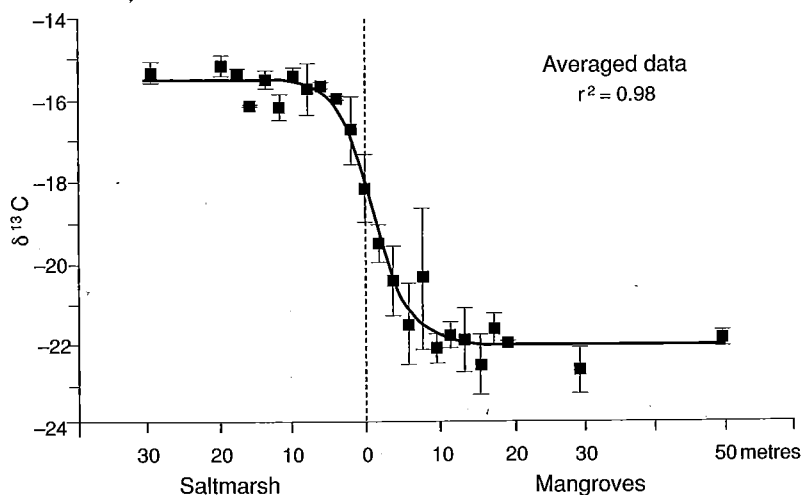
Reprinted from Guest and Connolly, 'Fine-scale movement and assimilation of carbon in saltmarsh and mangrove habitat by resident animals'. Aquatic Ecology 38: 599–609, copyright (2004) with permission from Elsevier.

assimilation by these invertebrates was limited to 5–7 m either side of the habitat boundary (Guest & Connolly 2004).

Fish assemblages on inundated Australian marshes are dominated by adults of one or two small species (60–90% of total abundance, Thomas & Connolly 2001; Bloomfield & Gillanders 2005), occasionally with high densities of commercially important species such as banana prawns, *Fenneropenaeus merguiensis* (Connolly 2005). The remainder of the fauna comprises small numbers of up to about twenty other fish species, including juveniles of many economically important species (Thomas & Connolly 2001). Fish diversity is lower in temperate waters (two to ten species, Connolly et al. 1997; Crinall & Hindell 2004; Bloomfield & Gillanders 2005) than in subtropical waters (twenty-three species, Thomas & Connolly 2001).

Australian marshes have no equivalent to marsh residents such as the killifish found in marshes of the USA. Toadfish (family Tetraodontidae) are a particularly conspicuous and common component of the fish fauna on marshes around Australia, yet are rare on North American marshes. Toadfish move onto the marsh early on the incoming tide, pushing far onto the marsh in very shallow water. This strategy has the effect of increasing the likelihood of finding major prey items such as snails and crabs (Hughes 1984). The abundances of this family on Australian marshes relative to those on North American marshes might result from the different hydroperiods. The short, infrequent inundation periods on Australian marshes that prevent small, resident fish from occurring may create an opportunity for the toadfish to obtain prey relatively easily as they enter the marsh upon inundation.

Sampling of fish at different distances onto inundated marshes in subtropical Australian waters shows that fish are found all over the marsh, as far as 0.5 km from subtidal water. No differences in fish assemblages occur between vegetated and unvegetated areas, perhaps because the short inundation periods prevent fish from selecting habitat (Thomas & Connolly 2001).

The best predictor of fish densities is proximity to small, mangrove-lined intertidal creeks that supply the marsh with water (Connolly 2005). Densities alongside creeks are two to three times higher than those 100 m away. Not all species found in the mangroves venture onto the marsh, however, and the saltmarsh fauna is a subset of the broader suite of species found in adjacent mangroves. The importance of marsh creeks fits with the demonstration in recent innovative work on the east coast of the USA of a strong relationship between nekton production and the amount of intertidal marsh/creek edge within 200 m of a site (Kneib 2003).

The shallowness of saltmarsh habitat when inundated might offer some degree of protection to small fish from predation, but the most common observation is that fish feed while visiting saltmarsh. Several studies have demonstrated feeding on saltmarsh by comparing stomach fullness and prey composition of fish entering and leaving marsh habitat. Studies in the USA (e.g. Nemerson & Able 2004; and in brackish marshes, Rozas & LaSalle 1990) and Europe (e.g. Lefeuvre et al. 1999; Laffaille et al. 2002) have detected higher stomach fullness after fish visit marshes. Diets consist predominantly of marine invertebrates (e.g. polychaete worms, amphipods) with occasional terrestrial (insect) invertebrates.

Fish caught in a small creek draining a subtropical Australian marsh were found to feed on marine invertebrates such as adult shore crabs and planktonic crab larvae and amphipods (Morton et al. 1987). Several fish species also ate terrestrial invertebrates, including adult insects from eight different orders. It cannot be assumed, however, that these stomach contents result from feeding on the marsh itself, since fish can remain in marsh creeks and feed without entering the inundated marsh (Szedlmayer & Able 1993; Le Quesne 2000). Some marshes in subtropical Australian waters have brackish, semi-permanent pools high on the marsh. Fish occurring in these pools feed predominantly on insect larvae that breed there (Morton et al. 1988). Fish visiting temperate Australian marshes have been shown to feed

on amphipods and hemipteran insects (Crinall & Hindell 2004). On a marsh in Sydney, New South Wales, the glassfish, *Ambassis jacksoniensis*, was found to feed on shore crab larvae and insects (Mazumder et al. 2006). This species was also found to eat crab larvae on a subtropical marsh in Queensland, and showed a striking temporal pattern of feeding (Hollingsworth & Connolly 2006). In winter, the marsh is inundated only at night and only on spring tides. Glassfish visiting the marsh on the first night of a tidal cycle feed only lightly, eating a small number of a range of prey types. This inundation, however, apparently acts as a cue for shore crabs to release larvae, and on subsequent nights glassfish eat an average of 100–200 crab larvae per fish (Figure 18.4).

Theories of saltmarsh ecology

Studies of saltmarsh ecology have historically taken an ecosystem approach, and even very early research emphasised links with other habitats.

Two of the most important theories have become paradigms in saltmarsh ecology. These are theories about the ecological role of saltmarsh within estuaries, one relating to the concept of outwelling of organic matter from high intertidal habitats to adjacent estuarine waters, the other about the way fish and crustaceans use inundated saltmarsh. Together, these concepts go a long way towards explaining the importance placed on saltmarsh habitat by coastal managers in Europe and the USA.

Saltmarsh primary production in estuarine food webs

It was on the *Spartina alterniflora* saltmarshes of Sapelo Island, on the Atlantic coast of the USA, that the concept that organic matter from intertidal habitats could sustain high rates of secondary production in adjacent waters was first developed. This outwelling hypothesis (Odum 1980) has been supported by empirical evidence at Sapelo

Figure 18.4 Crab zoea abundances in glassfish (*Ambassis jacksoniensis*) stomachs after feeding on subtropical saltmarsh.
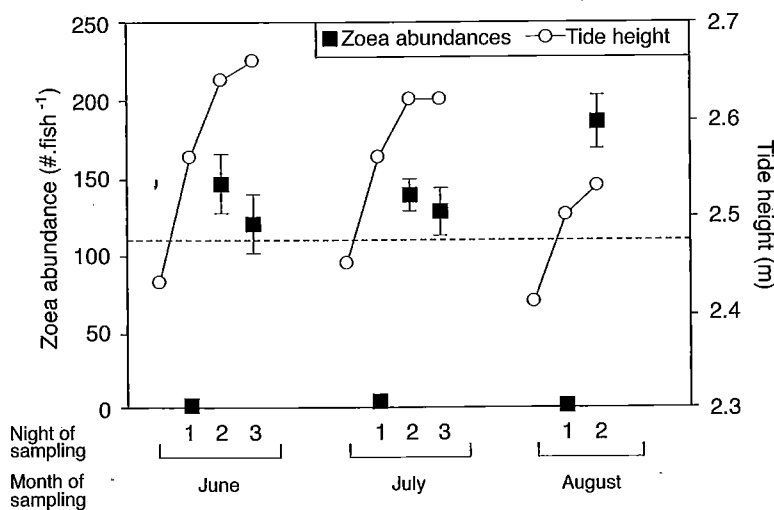
In each monthly cycle, fish do not feed on zoea on the first night a marsh is flooded but do so on subsequent nights (values are means, SE, scale on LHS). Tidal height is shown for each night of sampling and the night before sampling. Tidal height at which marsh is inundated (2.48 m) is shown by dotted line.

Reprinted from Hollingsworth and Connolly, 'Feeding by fish visiting inundated subtropical saltmarsh'. Journal of Experimental Marine Biology and Ecology, 336: 88–98, copyright (2006) with permission from Elsevier.

Island (Hughes & Sherr 1983) and many other places along both the Atlantic and Gulf coasts of the USA (e.g. Currin et al. 1995). For these marsh systems, both on the marsh itself and in adjacent estuarine waters, food webs are based on a mixture of detrital marsh plants and microalgae. Benthic microalgae are important for animals on the marsh itself, whereas phytoplankton is more important for animals in estuarine water (Currin et al. 1995). The transfer of energy from marsh to adjacent waters via particulate and dissolved organic matter was emphasised in early works but, as for mangroves, the alternative mechanism of trophic relay must now be considered (Kneib 1997).

Evidence from saltmarshes from a wider geographical spread shows a good deal of variability in the pattern of nutrient transfer between marsh and adjacent waters (Dame & Allen 1996). Animals in South African estuaries predominantly utilise organic matter from the water column rather than from macrophytes on surrounding saltmarshes (Schlacher & Wooldridge 1996). One study of invertebrates resident on Australian marshes, however, found that they utilised organic matter from marsh macrophytes and, surprisingly, showed little reliance on microalgae (Guest et al. 2004). So, what factors determine whether marshes will be sources or sinks for nutrients? Differences in height of the marsh in the intertidal zone result not only in different rates of plant productivity but also in different levels of export (Taylor & Allanson 1995). Even on the same marsh during a single tidal period there can be fluctuations caused by wind and waves. For example, more turbulent water results in increasing export of particulate nitrogen and phosphorus, but not of dissolved nitrogen and phosphorus (Childers et al. 1993). The type of tidal time–velocity asymmetry is also likely to be important. Marshes in eastern USA typically have a tide characterised by faster flow rates near the ebb point, both on flooding and ebbing tides (ebb-dominated). These marshes tend to export energy and sediment (Dame & Allen 1996). Conversely, European marshes are often characterised by faster flows near the high tide (flood-dominated),

and tend to import carbon and sediment (Dame & Allen 1996). Patterns of energy and nutrient exchange on a particular marsh are not easily made from general geographical overviews, however, since exchange is also influenced by other factors such as the position of the marsh within an estuary, its age (stage of evolution), and plant species composition (Adam 1990).

Use of saltmarsh by nekton

Patterns in the use of saltmarsh by nekton (fish and swimming crustaceans) have been well described for North American marshes (Kneib 1997). Large numbers of certain small species such as killifish (*Fundulus* spp.) and grass shrimp (*Palaemonetes* spp.) are resident on marshes. Numerous other fish and crustacean species visit the inundated marsh as transients (Kneib 1997). A review of the value of saltmarsh as nursery habitat, taking into consideration abundances, growth rates and survival, found that nursery value was greatest for vegetated marsh, particularly at the marsh edge, and lower for unvegetated marsh (Minello et al. 2003). The review pointed out, however, that results were predominantly from the Atlantic and Gulf coasts of the USA, and that fish use of saltmarsh elsewhere in the world might differ because of differences in tidal amplitude and frequency of flooding.

Encroaching human development is resulting in the fragmentation of saltmarshes, which are a critical nursery habitat for brown shrimp, *Penaeus aztecus*, on the Gulf coast of the USA (see Box 18.2). Empirical data and modelling of survival rates demonstrate that brown shrimp productivity increases as saltmarshes decline in extent and fragment into smaller units (Browder et al. 1989; Haas et al. 2004). For a time, these smaller units increase the length of the interface between marsh and water, increasing the linear extent of the preferred marsh edge habitat. Modelling shows that, ultimately, the amount of marsh relative to open water will decrease to the point where shrimp productivity begins to decline again (Browder et al. 1989).

Box 18.2   Threats to saltmarsh

The global threats to saltmarsh are similar to those for mangroves except that saltmarsh is not usually harvested directly for human use, although it is used for grazing of stock in places (Adam 1990; see also Chapter 11, Linking Terrestrial-Freshwater and Marine Environments). The distribution of high intertidal habitats is affected by changes in sediment supply to estuaries, either increases from clearing of catchments for agricultural and urban purposes, or decreases resulting from the building of dams in river catchments (Adam 2002). Reclamation of saltmarsh (or 'land claim', as it has been more accurately termed, Allen 2000) for urban, agricultural or aquaculture purposes remains a major threat. Outside of the USA and western Europe, levels of protection for saltmarsh are low, and loss of marsh areas continues to occur (Connolly & Bass 1996). In southern Moreton Bay in the rapidly urbanising region of south-east Queensland, for example, there was a net loss of 83% of saltmarsh area between 1955 and 1998 (Sinclair Knight Mertz 2001). Even where marshes have not suffered directly at the hand of humans, their area has decreased due to the global threat of sea level rise. In areas where mangroves occur seaward of saltmarsh, sea level rise has resulted in mangroves colonising shoreward at the expense of saltmarsh (Rogers et al. 2005).

Anthropogenic changes to saltmarsh topography affect the frequency and length of inundation (Rozas 1995), and can affect nekton abundances (Rozas & Minello 1999). Marsh plants themselves are affected by erosion, including through the use of off-road vehicles and grazing by stock (Adam 2002). The single most obvious alteration of drainage has been for mosquito control (see Box 18.3). Saltmarsh vegetation has proven vulnerable to invasive species, with substantial areas of change due to invasion by *Phragmites* in the USA (Meyerson et al. 2000) and *Spartina anglica* in numerous places around the world (Adam 1990). Australian marshes in temperate waters have already been altered by *Spartina anglica* colonisation over wide areas, and the invasive *Juncus acutus* has also replaced the native *J. kraussii* in some places (see also Chapter 22, Invasive Marine Species Management and Research).

The restoration of saltmarshes has become an important driver of research into ecological understanding of marshes in the USA, where it has been most thoroughly investigated (e.g. Zedler & Lindig-Cisneros 2001), and more recently in north-eastern Europe (e.g. Wolters et al. 2005). Saltmarsh restoration work in Australia remains in its infancy, although it has been propelled in recent times by work at the Homebush site developed for the 2000 Olympic Games in Sydney, New South Wales.

Conclusions and recommendations for future research

The historical development and emphasis of ecological research differs for mangroves and saltmarsh. For mangroves, a relatively recent but now substantial body of work supports our ecological understanding. The theories have been formed mainly in tropical waters and, in an Australian context where mangroves occur near major cities on temperate sections of coast, there is a need to test them also in temperate mangrove forests. Theories about saltmarsh vegetation, food webs and use by nektonic animals have been developed over many years, particularly in the USA, but also in Europe. The numerous studies at different times and places give the theories a convincing generality. These theories cannot be applied to Australian marshes without further testing, however, because the infrequent and short periods of

Box 18.3 **Control of saltmarsh mosquitoes and effects on non-target biota**

Mosquitoes are a natural and conspicuous component of subtropical and tropical saltmarsh fauna, but their abundances are monitored and controlled in many areas because of the serious arboviruses that they carry. Control of mosquitoes on marshes in the USA has largely been engineered through major structural modifications such as Rotational Impoundment Management, that have also altered densities of fish (Talbot et al. 1986; Poulakis et al. 2002) and invertebrates (Barnby et al. 1985). In Australia, the main form of marsh modification for mosquito control is runneling, particularly in south-east Queensland, northern New South Wales and south-west Western Australia. Runnels are shallow (<30 cm depth), spoon-shaped channels constructed to a maximum gradient of 1:1000 (Hulsman et al. 1989). They provide tidal access to isolated mosquito-breeding pools high on the marsh (Dale & Hulsman 1990). Runnels control mosquitoes by allowing water movement over the marsh during low-amplitude tides that would not normally flood higher regions of the marsh. This water movement is thought to reduce mosquito abundances by reducing the number of oviposition sites, increasing marsh access for predatory fish, and changing water quality, which affects maturation and survival of larvae that are produced (Morton et al. 1987; Dale & Hulsman 1990). Runnels have little effect on some plants (e.g. marsh herbs and grasses, Dale et al. 1993), but increase the frequency at which mangrove propagules are transported to the upper marsh and ultimately increase mangrove colonisation on marshes (Breitfuss et al. 2003). Runnels also increase substrate moisture content and decrease sediment consolidation 5–10 m on either side (Breitfuss & Connolly 2004), subsequently altering densities of shore crabs alongside runnels (Breitfuss et al. 2004). Fish species richness and densities of several individual fish species are lower alongside runnels (0–5 m) than further away (30 m), especially higher on the marsh (Connolly 2005). Runneling does, therefore, affect the distribution and abundance of many organisms other than mosquitoes, but only in narrow bands immediately alongside the runnels.

inundation of Australian marshes quite probably alter ecological processes.

The strong association of mangroves and saltmarsh with estuaries, which are subject to very high rates of human perturbation, has seen these habitats either degraded or reduced in area. Research needs are now largely driven by threats arising from the rapid urbanisation of the coastline. Recent evidence shows that, even where habitats are retained, the likely increase in their recreational use by humans will need careful management. In mangroves, for example, trampling by humans along unofficial paths can lead to short-term reductions in algal abundance and longer-term reductions in recruitment success of macroinvertebrates (Ross 2006).

The issue of freshwater flows to estuaries is likely to be important for mangrove and saltmarsh habitat (see also Chapter 11, Linking Terrestrial-Freshwater and Marine Environments). Freshwater surface and groundwater flow is an important factor, for example, in the distribution of saltmarsh plants (Pennings & Bertness 2001; Adam 2002), and salinity also affects the distribution and species composition of mangroves (Hutchings & Saenger 1987). Freshwater is now in such short supply that a global shortage is looming (Postel 2000), and increased harvesting is a certainty, including in Australia. Increased harvesting of water will affect saltmarsh fauna directly (Gillanders & Kingsford 2002), as well as indirectly through changes wrought on vegetation. Of particular importance

is the potential increase in average salinity in upper estuaries resulting from increased water harvesting. The question arises as to how much freshwater flow from riverine sources is required to sustain a healthy balance of saltmarsh, mangroves and their respective faunas.

Conservation of the extensive areas of saltmarsh and saltpan in tropical Australia has lagged behind even that for saltmarsh in temperate waters. This has occurred because of the lack of such basic information as the distribution of habitats along remote tropical coastlines, where little research effort was expended beyond the narrow fringe of mangroves along the estuarine margins. Now that the existence of vast areas of saltmarsh and saltpan is acknowledged, it is the lack of knowledge about their value that hinders conservation efforts. Research is needed to determine the ecosystem services provided by these habitats, for example in terms of their value to fisheries and their roles in nutrient processing and sediment stabilisation during peak storm conditions.

Global warming and the associated sea-level rise will affect mangrove and saltmarsh regardless of the level of protection offered at a local scale (see also Chapter 23, Climate Change in Marine Ecosystems). The issue that arises is how human uses of estuaries can be best managed to allow mangroves and saltmarsh to cope with sea-level rise. Evidence already exists of the intrusion of mangroves onto saltmarsh along the east coast of Australia (Rogers et al. 2005). This occurs where the distribution of mangroves moves landward onto existing saltmarsh, but the saltmarsh is bounded on its landward edge by urban infrastructure. Research efforts are needed to underpin advice to planners, for example about the potential of leaving green corridors on urban coasts that permit natural progression of saltmarsh inland.

Globally, the large-scale loss of mangrove and saltmarsh habitat has resulted in scientific effort being directed towards restoration projects, something only beginning to be examined fully in Australia. One of the major losses of estuarine habitats along the Australian coastline resulted from the building of barriers to tidal inundation at the time of European settlement. The possibility of removing barriers and restoring what have become agricultural lands to mangrove and saltmarsh habitats is being examined in many places. Research is needed to identify the key factors in successfully re-establishing mangrove and saltmarsh communities when removing artificial barriers to tidal inundation. Collectively, the next decade of research needs to provide coastal managers and planners with realistic options for the conservation and protection of mangrove and saltmarsh habitats.

QUESTIONS AND PROBLEMS

1 How can human uses of estuaries be best managed to allow mangroves and saltmarsh to cope with sea-level rise?

2 How much freshwater flow from riverine sources is required to sustain a healthy balance of saltmarsh, mangroves and their respective faunas?

3 What ecosystem services are provided by tropical saltmarshes and saltpans occurring as extensive habitats behind a mangrove fringe?

4 What are the key factors in successfully re-establishing mangrove and saltmarsh communities when removing artificial barriers to tidal inundation?

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