Oceanography and Marine Biology: An Annual Review, 2010, **48**, 43-160
© R. N. Gibson, R. J. A. Atkinson, and J. D. M. Gordon, Editors
Taylor & Francis

THE ECOLOGY AND MANAGEMENT OF TEMPERATE MANGROVES

DONALD J. MORRISEY[1], ANDREW SWALES[2], SABINE DITTMANN[3],
MARK A. MORRISON[4], CATHERINE E. LOVELOCK[5] & CATHERINE M. BEARD[6]

[1]*National Institute of Water and Atmospheric Research Ltd.,*
P.O. Box 893, Nelson, New Zealand
E-mail: d.morrisey@niwa.co.nz
[2]*National Institute of Water and Atmospheric Research Ltd.,*
P.O. Box 11-115, Hamilton, New Zealand
E-mail: a.swales@niwa.co.nz
[3]*School of Biological Sciences, Flinders University,*
GPO Box 2100, Adelaide, South Australia 5001, Australia
E-mail: sabine.dittmann@flinders.edu.au
[4]*National Institute of Water and Atmospheric Research Ltd.,*
Private Bay 99940, Auckland, New Zealand
E-mail: m.morrison@niwa.co.nz
[5]*Centre for Marine Studies and School of Biological Sciences,*
University of Queensland, St. Lucia, Queensland 4072, Australia
E-mail: c.lovelock@cms.uq.edu.au
[6]*Environment Waikato, P.O. Box 4010, Hamilton East, New Zealand*
E-mail: catherine.beard@ew.govt.nz

Abstract Previous reviews of mangrove biology focused on the more extensive and diverse tropical examples, with those of temperate regions generally relegated to a footnote. Temperate mangroves are distinctive in several ways, most obviously by the lower diversity of tree species. Their occurrence in relatively developed countries has created different issues for mangrove management from those in the tropics. Mangroves in several temperate areas are currently expanding, due to changes in river catchments, in contrast to their worldwide decline. Information derived from the greater body of research from tropical regions has sometimes been applied uncritically to the management of temperate mangroves. The growing body of information on the ecology of temperate mangroves is reviewed, with emphasis on productivity, response to anthropogenically enhanced rates of sediment accumulation, and potential effects of climate change. There is no unique marine or estuarine fauna in temperate mangroves, but the poorly known terrestrial fauna includes mangrove-dependent species. Although productivity generally declines with increasing latitude, there is overlap in the range of reported values between temperate and tropical regions and considerable within-region variation. This, and variation in other ecologically important factors, makes it advisable to consider management of temperate mangroves on a case-by-case basis, for example, when responding to expansion of mangroves at a particular location.

Introduction

Why a review of information on temperate mangroves?

In the preface to his book *The Energetics of Mangrove Forests*, Alongi (2009) asked “Why another mangrove book?” and a similar question could be asked of the present review. While there has been no previous detailed review of the ecological energetics of mangrove forests, what possible need could there be for another general review of mangrove biology and ecology given the numerous previous reviews of this topic (e.g. Macnae 1968, Teas 1983, Hutchings & Saenger 1986, Tomlinson 1986, Kathiresan & Bingham 2001, Saenger 2002, Hogarth 2007)? Our justification is that all of these have focused primarily on mangroves in tropical and subtropical areas, and temperate mangroves have been relatively neglected. Macnae’s (1968) review of Indo-Pacific mangroves, for example, devoted only 3 pages of 168 to “extratropical extensions”. This inequality is not surprising given the larger areas and greater biological diversity of mangroves in warmer regions (Twilley et al. 1992) but has sometimes led to uncritical application of information about tropical mangroves to those in temperate regions or, conversely, to the assumption that, since temperate mangroves are less diverse and slower growing than those in the tropics, they are of relatively little ecological value.

The uncertainty created by the relative lack of information on temperate mangroves provided the impetus for this review in the form of a request by a statutory environmental management agency for a technical review of information on mangroves in New Zealand. The review was intended to inform a proposed change to the conservation status of mangroves in their jurisdiction. That proposal was, in turn, a response to requests from coastal property owners and others for permission to remove mangroves in areas where they are spreading in order to protect access to the coast and maintain open waterways. Low diversity and productivity of these mangrove assemblages, relative to their tropical counterparts and to estuarine habitats that they displace, are sometimes cited as mitigating factors in these proposed removals. Opponents of mangrove removal, on the other hand, may emphasise their potential ecological significance. Both claims have tended to lack supporting evidence or to use information selectively.

These issues identified several characteristics of mangrove assemblages in temperate regions that distinguish them from their tropical or subtropical equivalents. First, the number of mangrove species declines with increasing latitude (Ellison 2002), and temperate regions generally contain between one and three species, as discussed in this review. Whether their productivity and associated biological diversity are comparably lower is less clear. Second, temperate mangroves often occur in relatively developed countries, such as Australia, New Zealand, South Africa, and the United States, where issues relating to their management may be very different from those in tropical regions. For example, statutory protection of mangroves may be stricter, and mangrove conservation groups may have relatively greater influence. The areal extents of mangroves in some temperate areas, including New Zealand and southern Australia, are currently increasing (Saintilan & Williams 1999, Swales et al. 2007b), in contrast to the ongoing decline in mangrove areas worldwide, particularly the tropics (Duke et al. 2007). These changes are often in response to historic changes in terrestrial vegetation cover upstream following European colonisation and create specific management issues of their own.

Scope of the review

The present review expands the original New Zealand study to include mangroves throughout their temperate range. Temperate mangroves are considered in their own right and are not specifically compared with their tropical counterparts. Nevertheless, if comparisons are relevant to management of temperate mangroves (e.g., testing assumed similarities or differences that have been presented as arguments for or against removal of spreading mangroves), these comparisons are discussed.

The review starts with a working definition of *temperate mangroves* and their global distribution, followed by a discussion of their taxonomy and diversity. This discussion leads into a consideration of the physiological tolerances of temperate mangroves and their influence on distribution along latitudinal gradients and among habitats within latitudes.

Biomass and productivity of temperate mangroves are reviewed, with reference to equivalent information on tropical mangroves to address the question of whether they have similar ecological importance in both regions. This discussion also includes the role of other primary producers in mangrove forests, such as microalgae, macroalgae, ferns and vascular plants.

A review of mangrove-associated faunas is followed by discussion of primary consumption of mangrove material. Primary consumption includes direct consumption by herbivores, indirect consumption by detritivores, the uptake of mangrove-derived material within the forest and its export to adjacent habitats, and trophic pathways within mangrove systems.

Discussion of the role of mangroves in trapping sediment and mitigating coastal erosion and their associated role in the natural ageing of estuaries leads into a consideration of patterns and causes of changes in mangrove distribution. Changes include losses due to human activities such as infilling and clearance of coastal areas, effects of increased sediment loads from coastal catchments, and inputs of other anthropogenic contaminants. In some areas, in contrast, anthropogenically enhanced rates of sedimentation have resulted in the spread of mangroves, and the extent of their spread, the influencing factors and the consequences for estuarine habitat diversity are reviewed. Future changes in the distribution of mangroves in temperate areas are also considered, including effects of climate change and sea-level rise (SLR). Management of these changes, both to protect mangrove forests and to protect other coastal habitats, is discussed in relation to legislation and management initiatives in various temperate-zone countries, with New Zealand as a case study of managing conflicts resulting from the spread of mangroves. Management initiatives considered include restoration in addition to removal and the broader ecological effects of each. The review finishes with discussion of directions for future research.

Definition of temperate mangroves

The development of an appropriate working definition of *temperate mangroves* is important to ensure that all relevant areas of mangrove distribution are considered in the study. It is equally important, however, to ensure that the geographical and climatic ranges covered are not so broad that they defeat the object of the exercise, namely, to provide a review of information on this relatively distinct subset of high-latitude, low-diversity mangrove assemblages, and risk straying into subject areas that have been reviewed previously.

There are several relevant factors to consider in deriving the definition, the broadest of which (and the most clearly defined—at least at first glance) is latitude. Climate correlates with latitude in a general sense but with considerable smaller-scale variation at any given latitude. The third major factor for present purposes is the diversity of the mangrove assemblages present.

Latitude and climate

The Tropics of Cancer and Capricorn lie at latitudes of 23°30′N and S 23°30′S, respectively, and, according to classical geographical zonation, define the boundary between the tropical and the temperate zones. The separation of subtropical and temperate regions, however, is much more equivocal. In South Africa, for example, Whitfield (1994) categorised the eastern coast from the border with Mozambique (26°52′S) south to the Mbashe River estuary (32°15′S) as “subtropical”, and the remaining stretch to the southern limit of the continent (34°52′S) as “warm temperate”, based largely on water temperatures. This side of the Cape is subject to the warm, southward-flowing

Table 1 Latitudinal limits of mangroves in the main regions of their range

Region	Northern limit	Southern limit
America, western coast	30°15′N	5°32′S
America, eastern coast/Bermuda	30°02′/32°20′N[a]	28°56′S
Africa, western coast	19°50′N	12°20′S
Africa, eastern coast and Red Sea	28°24′N	33°04′S[b]
Australia, western coast	na	33°16′S
Australia, eastern coast	na	38°45′S
New Zealand	na	38°05′S[c]
Pacific continental Asia	31°22′N[a]	na

Source: Information from Saenger 1998 except as indicated.

Note: na = not applicable because mangroves are present to the northernmost (in the case of northern limits) or the southernmost (in the case of southern limits) limit of the region.

[a] From Spalding et al. 1997.

[b] From Ward and Steinke (1982).

[c] From de Lange and de Lange (1994).

Agulhas Current, whereas the western side is exposed to the cooling influence of the Benguela Current. Consequently, the western coast is generally classified as 'cool temperate', even though it lies within the same latitudes as the warm-temperate region on the eastern side.

Mangroves straddle the tropical-temperate boundary but are generally restricted to latitudes between 30°N and 30°S. Exceptions occur in Bermuda (32°20′N), Japan (31°22′N), Australia (38°45′S), New Zealand (38°05′S) and South Africa (33°04′S) (Table 1; see Ward & Steinke 1982, Hughes & Hughes 1992, de Lange & de Lange 1994, Spalding et al. 1997). They also occur along the 30° parallel in the south-eastern United States (Spalding et al. 1997).

As discussed later (p. 51 et seq.), the main latitude-related factor limiting mangrove distribution appears to be the occurrence of low temperatures (sea surface and air) and, in particular, extremes of temperatures. Patterns of rainfall are also important (Spalding et al. 1997, Saenger 1998). The modifying role of factors other than latitude is demonstrated by the notable absence of mangroves on the western coasts of Africa and America south of 12°20′ and 5°32′, respectively. The most obvious of these modifying factors are local climatic features, including warming or cooling effects of coastal currents and patterns of rainfall.

The limits to the distribution of mangroves on the western coasts of Africa and South America (Table 1) correspond with the limits of arid regions, defined as summer rainfall and winter drought, >30 mm rainfall in any month of the year, and a precipitation to a potential evaporation ratio of <0.03 (Saenger 1998). Aridity is also likely to restrict mangrove distribution in western Asia and the Middle East.

The Köppen-Geiger climate classification scheme, based in part on the distribution of types of vegetation (Peel et al. 2007), has been widely used since its development in the early twentieth century. Despite some criticisms, it is still commonly used and has been modified and updated over time. Recent updates include that of Peel et al. (2007), on which the present discussion is based.

The Köppen-Geiger system divides climates into five main groups (tropical, arid, temperate, cold and polar), each containing several types and subtypes (see, e.g., Peel et al. 2007). The temperate group (group C), defined as regions with the temperature of the hottest month >10°C and temperature of the coldest month >0°C but <18°C, is clearly the most relevant for present purposes. It is subdivided into three types: Cs, dry summer (precipitation in the driest summer month <40 mm and less than a third of the precipitation in the wettest winter month); Cw, dry winter (precipitation in the driest winter month less than a tenth of the precipitation in the wettest summer month); and Cf, without dry season (fitting neither of the previous criteria). Each of these three types (Cs, Cw and Cf) is further divided according to summer temperature: a, hot summer (temperature of the hottest month ≥22°C); b, warm summer [not (a) and the number of months when the temperature is above 10°C ≥ 4]; c, cold summer [not (a) or (b) and the number of months when the temperature is above 10°C ≥ 1 but <4].

Comparison of the Peel et al. (2007) climate map with maps of the global distribution of mangroves (e.g., those in Spalding et al. 1997) suggests that the Cs and Cf climate types are most relevant for the present study (particularly the a and b subtypes of both). In some parts of the world, these climate types extend into latitudes below the tropics, for example, in south-eastern China and eastern Australia.

Mangrove species diversity

The decreasing number of mangrove species along gradients of increasing latitude is well documented (Ellison 2002), and areas at the extremes of mangrove distribution, such as Bermuda, southern Kyushu in Japan, southern South Africa, southern Australia and northern New Zealand, have only one to three species.

Species found at these latitudinal extremes are not cold specialists but tend to be those with wide latitudinal distribution. Among the eastern, or old-world, mangroves, they include *Aegiceras corniculatum*, *Avicennia marina*, *Bruguiera gymnorrhiza*, *Kandelia candel* and *Rhizophora mucronata*, and among the new-world species are *Avicennia germinans* and *Rhizophora mangle*.

Working definition

The primary interest in undertaking this review was to summarise information on the species-poor mangrove assemblages of temperate regions because of the potential ecological differences between them and the better-known mangroves of tropical and subtropical regions. These differences may arise from being located at the limits of mangrove distribution, with consequent potential effects on factors such as rates of growth and primary production, and from the restricted diversity of the mangrove species present, which may influence, for example, the range of habitats or shore heights that mangroves may occupy when constrained by the tolerances of only one or two species.

The focus of this review, therefore, is populations of mangroves occurring within climate zones Cs and Cf, most of which lie at latitudes higher than 29–30°, and containing limited numbers of mangrove species. Consequently, those parts of climate types Cs and Cf where mangrove communities are relatively diverse (generally more than three species occurring in the same location), such as south-eastern China (seven mangrove species at 27°N; Li & Lee 1997*), northern New South Wales and southern Queensland (north of, say, 30°S), Brazil north of 24°S, and the Florida peninsula are not considered. Also excluded are those parts of the world where mangrove species diversity is restricted by aridity, such as the northern part of eastern Africa and the Red Sea and Baja California and the Sea of Cortez.

The geographical areas included in the present review, with the types of mangroves that occur in them, are summarised in Table 2 and Figure 1.

Global distribution of temperate mangroves

According to estimates by Twilley et al. (1992, their Table 1), of about 24 × 10^6 ha of mangroves worldwide, 13.28 × 10^6 ha (55.3%) occur between the latitudes of 10°N and 10°S, 7.25 × 10^6 ha

---

[*] *Kandelia candel* was transplanted to Zhejian province (27–31°N) in the 1950s (Li & Lee, 1997), but most have been destroyed by human disturbance, and only 8 ha remained at the time of Li & Lee's review.

Table 2 Geographical areas included in the present review showing the climate type according to the Köppen-Geiger classification, the species of mangrove present in each area, and their latitudinal limits (distributional information as indicated in table footnotes)

Region	Climate type	Species	Latitudinal limit	Total mangrove species at this latitude
Louisiana, USA	Cfa	*Avicennia germinans*	30°02′N[a]	1
Bermuda	Cfa	*Avicennia germinans*	32°20′N[a]	3
	Cfa	*Conocarpus erectus*	32°20′N[a]	3
	Cfa	*Rhizophora mangle*	32°20′N[a]	3
Southern Kyushu, Tanegashima, Yakushima, Japan	Cfa	*Kandelia candel*	31°22′N[a]	1
North Island, New Zealand	Cfb	*Avicennia marina*	38°05′S[b]	1
Southern Brazil	Cfa	*Acrostichum aureum*	28°30′S[c]	3
	Cfa	*Avicennia germinans*	28°30′S[c]	3
	Cfa	*Laguncularia racemosa*	28°30′S[c]	3
	Cfa	*Rhizophora mangle*	27°53′S[c]	4
Eastern South Africa	Cfb	*Avicennia marina*	32°59′S[d,e]	1
	Cfb	*Bruguiera gymnorrhiza*	32°14′S[d]	2
	Cfa	*Rhizophora mucronata*	31°42′S[d]	4
Southern Australia	Cfb	*Avicennia marina*	38°45′S[f]	1
	Cfb	*Aegiceras corniculatum*	36°53′S[f]	2
	Cfa	*Exoecaria agallocha*	31°52′S[g]	3
	Cfa	*Rhizophora stylosa*	30°03′S[f]	4
	Cfa	*Bruguiera gymnorrhiza*	29°25′S[f]	5
	Cfa	*Lumnitzera racemosa*	27°30′S[f]	6
	Cfa	*Acrostichum aureum*	26°05′S[h]	7
Southwestern Australia	Csa	*Avicennia marina*	33°16′S[f]	1

[a] Nakasuga et al. 1974, Spalding et al. 1997.

[b] de Lange and de Lange 1994.

[c] Schaeffer-Novelli et al. 1990.

[d] Hughes and Hughes 1992.

[e] The stand of *A. marina* near the mouth of the Nahoon River (32°59′S) arose from transplanted material, but a stand further upstream may have derived from natural dispersal of propagules (Steinke 1995). The next highest latitude where this species occurs in South Africa is the Gqunube River (32°56′S).

[f] A.G. Wells 1983.

[g] West et al. 1985.

[h] Saenger 1998.

(30.2%) between latitudes 10° and 20°, 3.14 × 10^6 ha (13.1%) between 20° and 30°, and only 0.33 × 10^6 ha (1.4%) at latitudes greater than 30°. An estimate based on the data for individual temperate regions listed in Table 3, however, suggests that the total area of mangroves at latitudes >30° is in the range 0.05–0.06 × 10^6 ha. Of this last range, 48–55% are in southern Australia, 41–47% in New Zealand, 2.9–3.9% in Louisiana and 0.5–0.6% in South Africa.

Mangroves at latitudes >30° in southern Australia contain *Avicennia marina*, *Aegiceras corniculatum* and *Exoecaria agallocha*, while *Bruguiera gymnorrhiza* and *Rhizophora stylosa* also occur between 29° and 30°S (West et al. 1985). New Zealand contains only *Avicennia marina* and Louisiana only *A. germinans*. Bermuda contains three species (*A. germinans*, *Conocarpus erectus* and *Rhizophora mangle*), while in South Africa *Avicennia marina*, *Bruguiera gymnorrhiza* and *Rhizophora mucronata* occur south of latitude 30°. Only *Kandelia candel* occurs at Kiire, southern Kyushu, Japan, and on the neighbouring islands of Tanegashima and Yakushima (all north

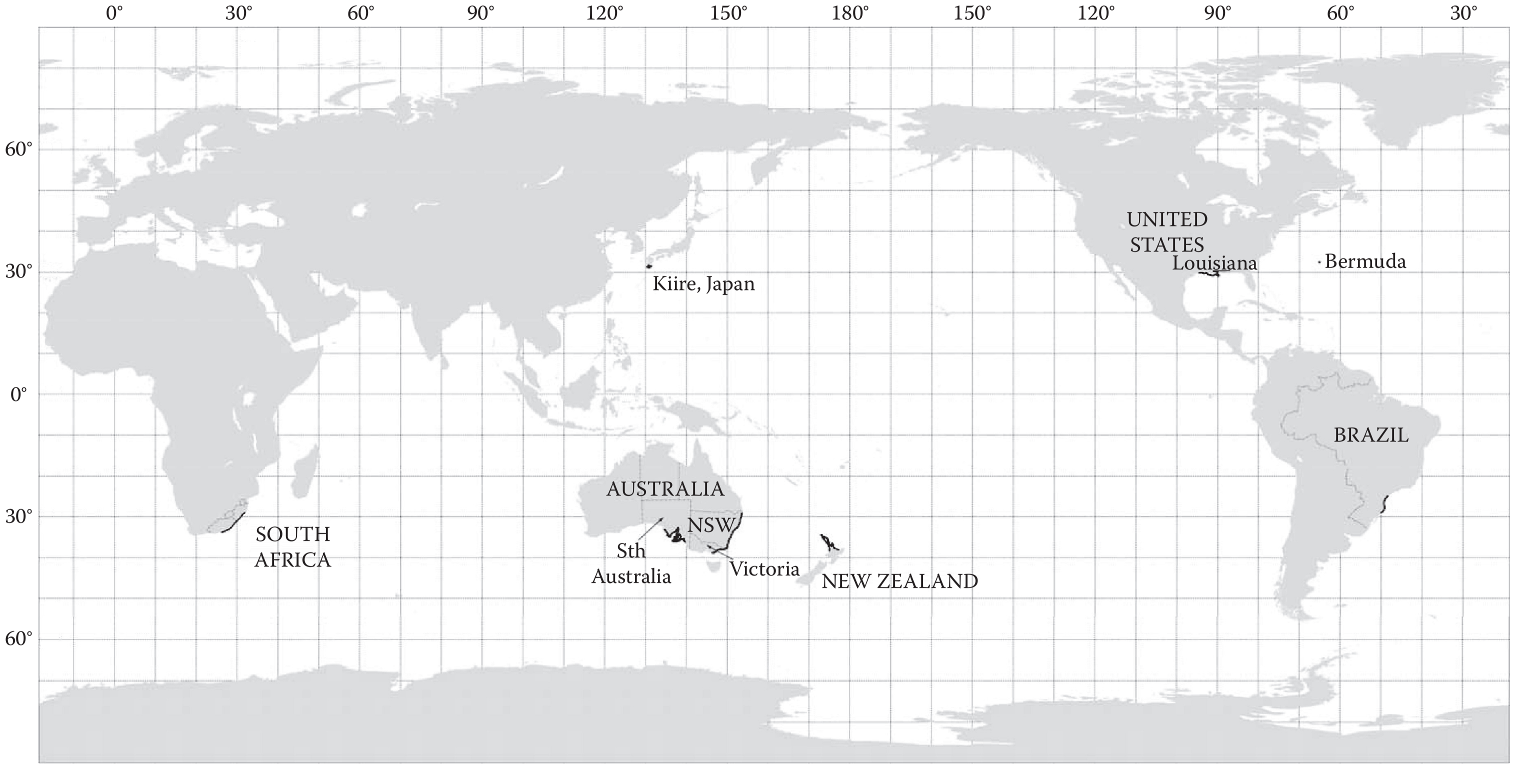

Figure 1 Global distribution of temperate mangroves as defined for the purposes of this review.

Table 3 Global distribution of temperate mangroves

Region	Area of mangroves (ha)	Notes	Reference
Louisiana	1560–2360	Value for late 1970s; since then contraction, due to freezes in the 1980s, and subsequent expansion have occurred.	Montz 1980 (cited in Lester et al. 2005)
Bermuda	10 16 17.5		Spalding et al. 1997 Wilkie & Fortuna 2003 Thomas 1993
Kyushu, Tanegashima, Yakushima and Amami Oshima, Japan	7.2 (>28°S) 7.1 (>30°S)	Total mangrove area for Japan from Nakasuga et al. (1974) is 517 ha. Wilkie & Fortuna (2003) gave a value of 400 ha for all Japan, including Kyushu (Kiire) and Okinawan Islands.	Nakasuga et al. 1974
New Zealand	28,700 22,200		Spalding et al. 1997 Wilkie & Fortuna 2003
South Africa	355 (>29°S) 295 (>30°S)	Adams et al. (2004) updated Ward & Steinke′s estimates for the Transkei region (272 ha) to 270.6 ha based on data from 1999.	Ward & Steinke 1982
Southern Australia	31,074 (>29°S) 29,500 (>30°S)	NSW south of 29°S 11,674 ha; Victoria 3800 ha; South Australia 15,600 ha.	NSW, West et al. 1985; Victoria and South Australia, Duke 2006
Southwest Australia	6.4		http://dbforms.ga.gov.au/pls/www/npm.ozest.show_mm?pBlobno=9483 (cited on Wikipedia http://en.wikipedia.org/wiki/Leschenault_Estuary#cite_ref-2)
Total >29°	54,860–62,520		
Total >30°	53,580–60,890		

of latitude 30°), although *Bruguiera gymnorrhiza* occurs at latitude 28°14′N on Amami Oshima (Nakasuga et al. 1974). The latitudinal limits of individual species are shown in Table 2.

Avicennia marina sensu lato (grey mangrove) has the greatest geographical range of all mangrove species, with its global limits occurring around latitudes 25°N in Japan and 38°S in Australia. However, *A. marina* subsp. *australasica* grows only in northern New Zealand, Lord Howe Island, New Caledonia, and the south-eastern coast of mainland Australia, where it forms the southernmost natural populations of mangrove at Corner Inlet, Wilson's Promontory, Victoria, Australia (latitude 38°45′S) (Table 2). With an ability to grow and reproduce in a variety of tidal, climatic and edaphic conditions, this species occupies a diverse range of littoral habitats and displays great variability of growth form (Duke et al. 1998, Maguire et al. 2002).

Links among populations of mangroves that occur in temperate regions have been most thoroughly studied in the species *A. marina* (Duke et al. 1998, Maguire et al. 2002, Arnaud-Haond et al. 2006) and *A. germinans* (Dodd et al. 2002). Populations of *A. marina* from temperate and often isolated locations have lower genetic diversity and higher levels of inbreeding than do core tropical populations, suggesting that populations are isolated with little gene flow among peripheral and core populations (Arnaud-Haond et al. 2006). Genetic differentiation is proposed to have occurred through bottlenecks and founder effects as well as through strong selection by temperate environments (Arnaud-Haond et al. 2006). For *A. germinans*, similar differentiation of peripheral populations has also been observed, although there is evidence for long-distance dispersal (Dodd et al. 2002).

Diversity of temperate mangroves

Mangroves are a taxonomically diverse group of halophytic (salt-tolerant) plants that, worldwide, comprise approximately 70 species within some 19 families. They are typically woody trees or shrubs taller than 0.5 m and inhabit the intertidal margins of low-energy coastal and estuarine environments over a wide range of latitude (Tomlinson 1986, Duke 1991). They normally occupy the zone between mean sea level (MSL) and high tide, growing on a variety of substrata, including volcanic rock, coral, fine sands and muddy sediments.

Although many species of mangrove are taxonomically unrelated, they all share a number of important traits that allow them to live successfully under environmental conditions that exclude many other plant species. Morphological, physiological and reproductive specialisations, such as aerial roots, support structures (buttresses or above-ground roots), and salt tolerance (Tomlinson 1986). Other traits, like vivipary (seeds that germinate while still on the adult tree) and positively buoyant propagules are also common in mangrove lineages (Rabinowitz 1978, Tomlinson 1986, Farnsworth & Farrant 1998).

Mangroves are most commonly associated with tropical and subtropical coastlines, and only a few species extend their range into the cooler warm-temperate climates typical of parts of New Zealand, Australia, Japan, South America and South Africa (Macnae 1966, Chapman 1977). A latitudinal pattern of species richness is evident, with diversity and extent both greatest at the equator and diminished towards the north and south (Ellison 2002). Mangrove communities near their northern global limits may include up to six mangrove species, whereas those at the southern limits are species poor; supporting between one and three species (Table 2). The most common species of mangroves that persist within temperate regions belong to the genus *Avicennia*.

Following Tomlinson's (1986) classification, *Avicennia* are true mangroves in that their habitat is defined solely by the intertidal zone, and they also possess specialized physiological and reproductive adaptations that allow them to grow there. Taxonomic treatments place the genus *Avicennia* either within the family Verbenaceae Jaume Saint-Hilaire (Green 1994) or as the sole genus within family *Avicenniaceae* Endlicher. However, more recent molecular evidence indicated that it may have closer affinities to the Acanthaceae sensu lato (Schwarzbach & McDade 2002).

Physiology of temperate mangroves

Key drivers of mangrove distribution: latitudinal limits

The global distribution of mangroves is approximately restricted to tropical climates where mean air temperatures of the coldest months are warmer than 20°C and where the seasonal range does not exceed 10°C (Chapman 1976, 1977). The geographic limits of mangrove growth are also coincident with ground frost occurrence and are closely linked with the 20°C winter isotherm for seawater. However, the occurrence of mangroves in New Zealand, parts of Australia, and eastern South America are notable exceptions to this pattern. Duke et al. (1998) suggested that these outlying distributions either coincide with extensions of irregular warm oceanic currents or are relict populations established during periods of warmer climate and greater poleward distributions.

Low temperatures limit the distribution of mangroves through their effects on a range of processes. One of the main hypotheses that has been proposed to account for the southern and northern latitudinal boundaries of mangroves is the lethal effects of extreme low winter temperatures (i.e., frosts) that kill trees (Chapman & Ronaldson 1958, Sakai & Wardle 1978, Sakai et al. 1981, Kangas & Lugo 1990, Saintilan et al. 2009). However, other factors may also limit the latitudinal distribution of mangroves. For example, work from New Zealand suggests that the distribution of *Avicennia* may also be constrained by its physiological limitations under low temperate (non-freezing) conditions (Walbert 2002, Beard 2006). Declining net primary production with increasing latitude (Saenger & Snedaker 1993) also suggests that photosynthetic carbon gain diminishes relative to respiratory demands. Thus, mangroves may have a more precarious carbon balance at high latitudes that may make them more vulnerable to abiotic stressors (e.g., tissue damage from freezing), competition and predation.

Limited productivity of mangroves at high latitudes may be associated with adaptations that improve resistance to freezing. Periodic freezing temperatures place a strong selective pressure for small xylem vessels that are the conduits for water transport between roots and roots. Small xylem vessels (with narrow diameters) reduce the probability of embolism of the xylem during freezing (Stuart et al. 2007), but the trade-off is that they place constraints on rate of water transport within stems (hydraulic conductivity), which in turn limits photosynthesis and carbon gain (Stuart et al. 2007). Thus, hydraulic characteristics that are required for safety during freezing temperatures come at the cost of lower carbon gain, which reduces growth rates.

Slower annual growth increments of trees at higher latitudes may also contribute to setting the latitudinal limits of mangroves by reducing the competitive ability of mangroves with co-occurring saltmarsh plants. Competitive interactions with saltmarsh plants are proposed to restrict mangrove forest development at their latitudinal limits (Saintilan et al. 2009). In addition, where herbivory of mangrove propagules is high, plant–animal interactions may also set latitudinal limits, especially when herbivore damage is combined with unfavourable abiotic conditions for growth (Patterson et al. 1997).

The timing and success of reproduction of *A. marina* vary predictably with latitude (Duke 1990). In a detailed study of its phenology over a wide range of latitudes, Duke (1990) found that the timing of reproductive events (e.g., initiation of flowering and maturation of propagules) was highly dependent on temperature. The success of flowers declined with decreasing temperature such that, at a mean annual temperature of 18°C, flowers did not develop into fruit. Thus, low temperatures at high latitudes may directly limit metabolic processes associated with reproduction, which would limit population growth and dispersal at latitudinal limits.

Finally, in addition to low temperatures, the availability of suitable habitat for mangrove growth and suitable conditions for propagule dispersal have been proposed to limit the distribution of mangroves (de Lange & de Lange 1994). Increases in suitable habitat for mangroves, for example through enhanced sedimentation (Burns 1982, Lovelock et al. 2007b, Swales & Bentley 2008) or through changes in groundwater availability (McTainsh et al. 1986, Rogers & Saintilan 2008), may increase the abundance and extend distributions of mangroves, particularly if these factors are combined with warming of air or sea temperatures or with other factors that enhance growth rates or resistance to stressors (e.g., nutrient enrichment) (Martin 2007). Thus, latitudinal limits are likely to be set by plant metabolic responses to low temperatures but are moderated by a complex suite of interacting biotic and abiotic factors.

Unique features of high-latitude mangroves

Temperate mangrove forests have many features in common with lower-latitude forests. They share common tree species and similar requirements for establishment and growth (Krauss et al. 2008).

Here, the focus is on assessing how the characteristics of temperate mangroves differ from forests in subtropical and tropical regions. This theme is continued in the following sections on biomass and productivity of temperate mangroves.

Reproductive characteristics

Reproductive traits differ among temperate and tropical mangroves. The duration required for fruit maturation increases from 200 days to 550 days from 15–30° latitude (Duke 1990). Propagule mass also correlates positively with latitude (Figure 2), suggesting that cool winter temperatures have resulted in selection for propagules that take longer to develop and that are provisioned with larger maternal reserves. The trend of increasing propagule weight with latitude is particularly evident for *A. marina* and less so for *A. germinans*, but the data for *A. germinans* are fewer and cover a more restricted latitudinal range than those for *A. marina*. In addition, the time during which newly established seedlings of *Avicennia* are dependent on maternal reserves appears to be shorter in the tropics (4 months; Smith 1987) compared with the temperate zone (12 months; Osunkoya & Creese 1997). Longer propagule development times, larger propagules and longer periods of dependency on maternal reserves within the propagule may result in differences in seedling ecology between temperate and tropical regions. Temperate seedlings may be more attractive to herbivores and predators, although declines in herbivores and predators with increasing latitude may offset increases in palatability of propagules at high latitude (Clarke & Myerscough 1993).

Prolonged periods of propagule development and dependency on cotyledonary reserves may also result in greater susceptibility of seedlings to stochastic processes such as storms and freezing. Successful establishment may become highly variable among years (e.g., Swales et al. 2007b), dependent on prolonged periods of suitable weather. It may therefore be expected that mangrove expansion at high latitudes will be pulsed and highly sensitive to climate change, with rapid establishment occurring with amelioration of key climate drivers that limit propagule development and establishment (low temperatures and storms).

Genetic differences among temperate and tropical mangroves may underlie the differences observed in some traits. Genetic differences among mangrove populations is high (Maguire et al. 2000). Introductions of new genotypes across long distances (oceanic basins) have been observed,

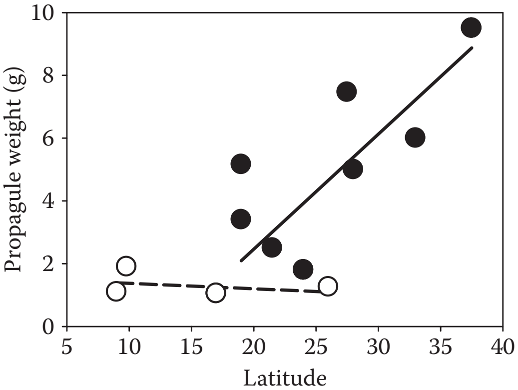

Figure 2 Variation in propagule weight of *Avicennia marina* (filled circles) and *A. germinans* (open circles) with latitude. There is a significant increase in propagule weight with latitude in *A. marina*, described by the line $y = 0.030x - 0.214$, $R^2 = 0.56$, $p = 0.013$. (Data are from Rabinowitz 1978, Downton 1982, Smith 1987, McKee 1995a,b, Clarke et al. 2001, Delgado et al 2001, Bhat et al. 2004, Ye et al. 2005, He et al. 2007, Yan et al. 2007.)

but distant populations are isolated and may have different responses to environmental change (Dodd & Afzal Rafii 2002). Few experiments have been done to test for differences in phenotypes of distant populations under common conditions. However, Duke (1990) reported that *A. marina* seedlings from a range of latitudes grown together at 19°S did not show significant differences in growth. Probing differences among temperate and tropical populations may improve predictions of the effects of climate change on temperate mangroves.

Tolerance of key environmental drivers

The constraints on the carbon balance of mangroves imposed by low temperatures and adaptations to low temperatures, as discussed, may make trees at high latitudes more sensitive to environmental drivers than those at lower latitudes. Salinity of soils is one of the most important factors that limit the growth of individual mangrove trees and of mangrove forests, with high salinity resulting in reduced growth rates, tree height and productivity (Ball 1998). Assessment of seedling growth studies conducted over a range of latitudes that examined salinity tolerance of *Avicennia marina* did not reveal any differences in tolerance of high-salinity conditions among plants from differing latitudes. When normalised for maximum growth rate (usually at ~25% seawater), growth declined similarly with increasing salinity over a range of latitudes (Figure 3).

The seaward limits of mangrove growth also appear to be higher in temperate compared with tropical latitudes (Clarke & Myerscough 1993). In Tauranga Harbour, New Zealand (37°40′S), undisturbed populations of *A. marina* occupied habitat from approximately 0.23 m above MSL (Park 2004), whereas in the southern Firth of Thames (37°13′S) the lower elevation limit (LEL) of mangroves was ≥0.5 m above MSL. In Florida, mangroves occurred higher in the intertidal zone than salt marshes. Restriction of mangroves to above the MSL have been attributed to the inhibitory effects of waves on propagule establishment (exposure) or a lag between shore accretion and mangrove colonisation (Clarke & Myerscough 1993). In addition, tolerance of inundation may differ among latitudes, although there are insufficient data to test this hypothesis.

Nutrient availability limits mangrove growth in both temperate and tropical locations (Feller 1995, Lovelock et al. 2007b, Martin 2007). In many temperate sites, nitrogen is the key limiting

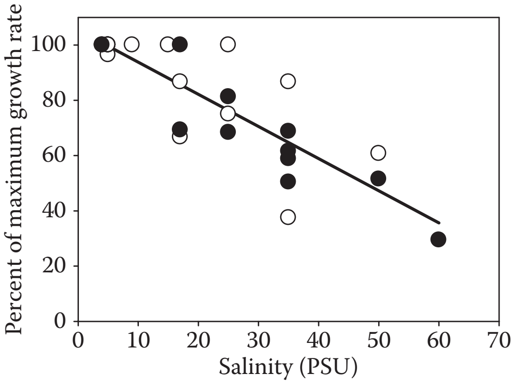

Figure 3 Decline in growth rate of *Avicennia marina* seedlings from temperate (filled circles, >28° latitude) and tropical (open symbols, <27° latitude) locations, grown over a range of salinities. There is no difference in the decrease in growth rates with increasing salinity between temperate and tropical species ($p > 0.05$). The line of best fit is described by $y = -1.16x + 105.4$, $R^2 = 0.72$, $p < 0.0001$. (Data are from Clarke & Hannon 1970, Downton 1982, Burchett et al. 1984, Clough 1984, Ball 1988, Yates et al. 2004, Ye et al. 2005, Yan et al. 2007.)

nutrient for plant growth (Lovelock et al. 2007a) and reproduction (C. Lovelock unpublished data), while both nitrogen and phosphorus may limit growth in tropical mangroves (Lovelock et al. 2007a). Differences in limiting nutrients between temperate and tropical locations are likely due to underlying differences in geochemistry over latitudes, in which tropical sites are often more highly weathered and deficient in phosphorus compared with temperate sites (Lovelock et al. 2007a).

Despite the positive effects nitrogen enrichment has on growth, nitrogen may increase susceptibility of trees to additional environmental stressors. For example, frost (Martin 2007) and drought (Lovelock et al. 2009) lead to tissue losses and increased mortality in nitrogen-fertilised trees compared with trees not enriched with nitrogen. Thus, nitrogen enrichment of estuaries may contribute to loss of resilience of mangrove ecosystems, which may be particularly important in temperate mangroves where climate conditions are variable, encompassing extreme low temperatures and extended droughts.

Productivity and biomass of temperate mangroves

Productivity of temperate mangroves

One of the strongest patterns observed over variation in latitude is that net primary production and maximum height of mangrove trees decline with increasing latitude (Twilley et al. 1992, Saenger & Snedaker 1993, Bouillon et al. 2008, Mendez-Alonso et al. 2008, Alongi 2009). Based on a review of 178 published measurements of litterfall, Bouillon et al. (2008) found significantly higher production at latitudes between 0 and 10° (average 10.4 ± 4.6 t ha^{-1} yr^{-1}, $n = 53$) than at higher latitudes (10–20°, 20–30° and >30°) and significantly lower production at latitudes >30° (4.7 ± 2.1 t ha^{-1} yr^{-1}, $n = 16$) than at lower latitudes. Average values for 10–20° and 20–30° were 9.1 (±3.4, $n = 47$) and 8.8 (±4.2, $n = 62$) t ha^{-1} yr^{-1}, respectively, and were not significantly different. There was no significant correlation between above-ground production of wood by mangroves and latitude (none of the available data were from latitudes above 30°).

Productivity is commonly measured as litter production, principally leaves, twigs and woody debris. Although this does not represent net primary production completely (because it does not include net increase in plant biomass), it represents an important component of it. It also reflects changing events in the life cycle of the mangrove (such as reproduction and senescence) and responses to environmental events (storms, variation in rainfall) and provides a measurement of inputs of organic matter and nutrients by mangroves to the estuarine system. Estimates of litter production may also include propagules, which are potentially viable material and not, strictly speaking, detritus.

Published estimates of litter production in temperate mangroves (Table 4) are generally consistent with the average value given by Bouillon et al. (2008) for latitudes >30°. Although recorded rates of litterfall for *A. marina* from New Zealand are below the maximum values reported from other parts of its distribution (e.g., those from tropical Australia), they are comparable with values from subtropical and temperate Australia (Table 4). Bunt (1995) gave an average value of 6.2 t ha^{-1} yr^{-1} from measurements taken throughout the range of *A. marina* in Australia (from Victoria to tropical Queensland, Northern Territory and Western Australia) but with a range from 1.10 to 15.98 t ha^{-1} yr^{-1}, indicative of considerable variation within and among locations.

Bouillon et al. (2008) also noted the relatively large variation about the average values for latitudinal ranges (0–10°, 10–20°, 20–30° and >30°) and pointed out that this was to be expected given the variation in primary production with numerous environmental factors that, themselves, vary at a range of spatial scales smaller than the latitudinal ranges concerned. There was variation among measured values from temperate regions, even within the same geographic area (Table 4). For example, in New Zealand the rates of litter production reported for adult trees (i.e., not saplings)

Table 4 Summary of published information on litterfall and above-ground biomass (AGB) of temperate mangroves

Country	Location	Latitude	Species	Height of trees (m)	Litter production (t ha^{-1} yr^{-1} DW)	AGB (t ha^{-1})	Notes	Reference
Australia	Northwestern Australia and Gulf of Carpentaria	10°50′–17°57′S	A.m.		2.34–4.30 (SD 2.11)		Hot, dry winter (climate zones Aw and Awi)	Bunt 1995
Australia	Darwin Harbour	12°26′S	A.m.	13	12.51 (SD 1.793)			Woodroffe et al. 1988
Australia	Darwin Harbour	12°26′S	A.m.	10.8	0.68 (SD 0.43)			Woodroffe et al. 1988
Australia	Northern Queensland	15°28′–18°21′S	A.m.		10.49 (SD 4.57)		Hot, generally short dry season (climate zone Am)	Bunt 1995
Australia	Central western coast	20°18′–24°53′S	A.m.		8.79 (SD 1.68)		Hot, arid (climate zone BWh)	Bunt 1995
Australia	Mary River, Queensland	25°26′S	A.m. A.c.			200–250 35	Upstream reaches of estuary	Saintilan 1997b
Australia	Mary River, Queensland	25°26′S	A.m. A.c.			120 50	Seaward edge of intertidal flats	Saintilan 1997b
Australia	Mary River, Queensland	25°26′S	A.m.			10	Landward edge of intertidal flats	Saintilan 1997a
Australia	Brisbane	27°25′S	A.m.			110–340		Mackey 1993
Australia	Subtropical and warm-temperate eastern Australia	27°33′–33°59′S	A.m.		3.07 (SD 1.83)		Hot summer, uniform rain (climate zone Cfa)	Bunt 1995
Australia	Kooragang Is, NSW	32°51′S	A.m.	3		7.1		Burchett & Pulkownik 1983 in Saenger & Snedaker 1993
Australia	Kooragang Is, NSW	32°51′S	A.m.	7.5		86		Burchett & Pulkownik 1983 in Saenger & Snedaker 1993
Australia	Kooragang Is, NSW	32°51′S	A.m.	10		104		Burchett & Pulkownik 1983 in Saenger & Snedaker 1993
Australia	Kooragang Is, NSW	32°51′S	A.m.	4.3	5.14	21.7		Murray 1985
Australia	Kooragang Is, NSW	32°51′S		4.4	5.62	21.8		Murray 1985

Australia	Merimbula NSW, Bunbury WA, Westernport, Victoria	33°20′–38°25′S	A.m.		4.36 (SD 1.48)		Long, mild summer, cool winter (climate zones Cfb/Csb)	Bunt 1995
Australia	Hawkesbury River, NSW	33°30′S	A.m. A.c.	<3		52.1 54.9	Hypersaline environment	Saintilan 1997a
Australia	Hawkesbury River, NSW	33°30′S	A.m. A.c.	<3		60.1 52.5	Marine environment	Saintilan 1997a
Australia	Hawkesbury River, NSW	33°30′S	A.m.	<3		A.m. 400	Riverine flats	Saintilan 1997a
Australia	Middle Harbour, Sydney	33°46′S	A.m.	8–9	5.8	220	Average 79% leaves	Goulter & Allaway 1979
Australia	Lane Cove River, Sydney	33°50′S	A.m.	<0.8		0.2–3.4		Briggs 1977
Australia	Lane Cove River, Sydney	33°50′S	A.m.	6.5–8.2		112.3–144.5	Means of 2 sites (total AGB)	Briggs 1977
Australia	Gulf of St. Vincent, South Australia	34°36′S–34°38′S	A.m.	2–3	7.67 and 11.68		Measured during summer only; 62–85% leaves	Imgraben & Dittmann 2008
Australia	Jervis Bay, NSW	35°07′S	A.m.	5–8	3.67		Fruit and flowers average 9.2% of litter	Clarke 1994
Australia	Westernport Bay, Victoria	38°46′S	A.m.		2			Attiwill & Clough 1974 in Goulter & Allaway 1979
Brazil	Babitonga Bay, Santa Caterina	26°12′S	A.s L.r. R.m.	3.2–5.7 3.1–3.8 2.6–2.8	0.20–0.55 1.02–2.35 0.59–2.36	1.9–11.4 10.2–25.0 4.6–5.9	Ranges for 3 sites across the shore profile	Cunha et al. 2006
New Zealand	Rangaunu Harbour, Northland	34°57′S	A.m.	6.23	6.24		73% leaves	May 1999
New Zealand	Rangaunu Harbour, Northland	34°57′S	A.m.	3.06	3.89			May 1999
New Zealand	Rangaunu Harbour, Northland	34°57′S	A.m.	5.12	4.83			May 1999
New Zealand	Rangaunu Harbour, Northland	34°57′S	A.m.	1.68	1.77			May 1999

(continued on next page)

Table 4 (continued) Summary of published information on litterfall and above-ground biomass (AGB) of temperate mangroves

Country	Location	Latitude	Species	Height of trees (m)	Litter production (t ha^{-1} yr^{-1} DW)	AGB (t ha^{-1})	Notes	Reference
New Zealand	Whangateau Estuary, Auckland	36°19′S	A.m.	<0.5–1.5 (sapling)	1.68			Oñate-Pacalioga 2005
New Zealand	Whangateau Estuary, Auckland	36°19′S	A.m.	2–4	1.56			Oñate-Pacalioga 2005
New Zealand	Tramcar Bay, Auckland	36°19′S	A.m.	2–4	1.3			Oñate-Pacalioga 2005
New Zealand	Tuff Crater, Auckland	36°48′S	A.m.	4	7.12–8.09	130	69% leaves, 12.3% fruits and flowers	Woodroffe 1985a
New Zealand	Tuff Crater, Auckland	36°48′S	A.m.	0.95 (stunted)	2.90–3.65	10	74% leaves, 2.6% fruits and flowers	Woodroffe 1985a
New Zealand	Puhinui Creek, Auckland	37°01′S	A.m.	0.5–1.6 (sapling)	0.11–0.38		Young stands (4–13 yr old)	Burns et al. unpublished
New Zealand	Puhinui Creek, Auckland	37°01′S	A.m.	0.8 (stunted)	0.61		Medium age (13–31 yr old)	Burns et al. unpublished
New Zealand	Puhinui Creek, Auckland	37°01′S	A.m.	2.3–2.6	2.89		Medium age (13–31 yr old)	Burns et al. unpublished
New Zealand	Puhinui Creek, Auckland	37°01′S	A.m.	3.4–4	1.55–4.05		Old stands (31+ yr old)	Burns et al. unpublished
South Africa	Mgeni River, Durban	29°48′S	A.m. B.g	9 7	6.98 8.24	19.82 74.67	Leaves 59% of litter (average over 3 yr)	Steinke & Charles 1986 Steinke et al. 1995

South Africa	Wavecrest, Nxaxo-Nqusi Estuary	32°35′S	A.m. + B.g		4.51 (range 0.3–7.3)		Average over 3 yrs; leaves 72% of litter	Steinke & Charles 1990
Various tropical	Various	23°N–23°S	Various		0.01–7.71		Minimum value for *Ceriops tagal* in Andaman Islands; maximum for *Avicennia germinans* in Guyana	Kathiresan & Bingham 2001
Various tropical	Various	23°N–23°S	Various	3.9–35	3.74–18.7	57–436	Average 193 t ha^{-1} biomass, 3.74–14.02 t ha^{-1} yr^{-1} litter; minimum value for *Avicennia* sp. in Sri Lanka; maximum for *Bruguiera* in China; maximum value recorded for *Avicennia* species was 14.0 in Australia and Malaysia	Saenger & Snedaker 1993
Various subtropical	Various	23–30°S and N	Various	1–12.5	1.3–16.31	7.9–164.0	Minimum and maximum both for *Rhizophora* in United States; maximum value for *Avicennia* species was 7.15 in South Africa	Saenger & Snedaker 1993

Note: Data for each country are ordered by increasing latitude. Data for various mangrove species in various tropical and subtropical countries are also shown for comparison. Climate zones refer to the Köppen-Geiger system. A.c. = *Aegiceras corniculatum*, A.m. = *Avicennia marina*; A.s. = *Avicennia schaueriana*; B.g = *Bruguiera gymnorrhiza*; L.r. = *Laguncularia racemosa*; R.m. = *Rhizophora mangle*; NSW = New South Wales; SD = standard deviation; WA = Western Australia.

varied from 0.61 to 8.1 t ha^{-1} yr^{-1}, with the smaller value from stunted (0.8-m tall) plants in Puhinui Creek, Auckland (B.R. Burns, Landcare Research, D.J. Morrisey, NIWA [National Institute of Water and Atmospheric Research], and J. Ellis, NIWA unpublished data) and the larger from 4-m high trees in Tuff Crater, Auckland (Woodroffe 1985a). The higher value approaches the averages for latitudes between 10 and 30°. The average value for full-size, mature trees in temperate stands of *A. marina* (Table 4) was 4.3 (standard deviation [SD] 2.09) t ha^{-1} yr^{-1}. Similar methods of sampling were used in all of these studies.

Burns, Morrisey, & Ellis (unpublished data) measured litter production in each of six stands in Puhinui Creek, near Auckland. Stands were divided into three age groups: those that first developed before 1939 (old stands), those that developed between 1969 and 1987 (medium-age stands) and those that developed between 1987 and 1996 (young stands). Each age class was replicated at two locations along the creek (young stands were generally nearer the creek and old stands highest up the shore). Litterfall in the two young stands was 0.11 and 0.38 t ha^{-1} yr^{-1}, and the stands consisted of saplings with average canopy heights of 0.5 m and 1.6 m, respectively. Of this material, 36% and 71%, respectively, consisted of leaves. One of the medium-age sites contained stunted adult trees (average canopy height 0.8 m) where litterfall was 0.61 t ha^{-1} yr^{-1} (43% wood, 33% leaves). The other stand of this age (average canopy height 2.3 m) produced 2.89 t ha^{-1} yr^{-1} (67% leaves). The two old stands also differed in rate of litter production, with the slightly taller stand (average canopy height 4.0 m) producing less than the shorter stand (average canopy height 3.4 m: litter production 1.55 and 4.05 t ha^{-1} yr^{-1}, respectively). The percentages of leaf material were 72% for the taller and 69% for the shorter stand.

May (1999) measured litterfall at two locations, separated by 250 m, on opposite sides of the mouth of the Awanui River in Rangaunu Harbour, northern New Zealand. At each location, sites were sampled low on the shore near the channel edge, where the trees were tall (3.06 m average canopy height on the northern side of the river, 6.23 m on the southern side), and the upper shore, where the trees were shorter (northern side 1.68 m, southern side 5.12 m). Upper and lower sites were less than 50 m apart. Total annual litterfall for the northern and southern low-shore sites was 3.89 t ha^{-1} yr^{-1} (75% leaf material) and 6.24 t ha^{-1} yr^{-1} (76% leaf material), respectively. Equivalent values for the high-shore sites were 1.77 t ha^{-1} yr^{-1} (86% leaf material) and 4.83 t ha^{-1} yr^{-1} (56% leaf material).

Similarly reduced litterfall at higher-shore sites was reported from Tuff Crater (Woodroffe 1985a), where the stunted (often <0.5 m), sprawling plants produced 2.90–3.65 t ha^{-1} yr^{-1} (average values for two consecutive years: 75% leaf material). Taller (up to 4 m), more erect trees growing along the banks of the major tidal creeks produced 7.12–8.1 t ha^{-1} yr^{-1} (45–69% leaf material).

These data from New Zealand mangroves reveal considerable variation in rates of litter production within and among locations. Highest levels (7–8 t ha^{-1} yr^{-1}) were recorded at the Tuff Crater site near Auckland (36°48′S) rather than at the most northerly site (Rangaunu Harbour, 34°57′′S: 2–6 t ha^{-1} yr^{-1}), even though the trees were taller at the latter site. Within locations, such as Puhinui Creek or Rangaunu Harbour, litterfall seems to be broadly proportional to tree height. At Whangateau, however, a newly establishing stand (up to 1.5 m high) produced more litter than established stands (2–4 m high) (Oñate-Pacalioga 2005). Newly establishing areas in Puhinui Creek produced much less litter than those in Whangateau (0.11–0.38 vs. 1.68 t ha^{-1} yr^{-1}).

As May (1999) noted, "The varied topography of creek-dissected mudflats characteristic of northern New Zealand estuaries results in a mosaic of mangrove biomass and litter input across the intertidal". Another factor that may increase spatial and temporal variation in litter production is the variability of populations of herbivores in space and time, and the amount of damage they inflict may influence the amount of litter shed by the trees. The small number of studies of the productivity of temperate mangroves and the large within-location variation recorded by those studies that have been made make it difficult to identify any general trends in productivity. It would be worthwhile to conduct a systematic study of productivity under standardised conditions at a large number of sites throughout the distributional range of temperate mangroves.

Standing crop and tree size

There is a trend of declining mangrove biomass with increasing latitude. Twilley et al. (1992), for example, estimated that the above-ground biomass densities for mangroves in the latitudinal ranges 0–10, 10–20, 20–30 and 30–40° are 283.6, 141.6, 120.6 and 104.2 t ha^{-1}, respectively. Alongi (2009) also compiled data on above-ground biomass and showed a declining trend with increasing latitude (his Figure 2.6). Biomass and tree height correlate reasonably closely (Saenger & Snedaker 1993, Lee 2008), but as with productivity, there is considerable variation in values of biomass at a particular latitude or within a range of latitudes, as Twilley et al. (1992) pointed out. For example, Saenger & Snedaker (1993) gave a range of 57–436 t ha^{-1} for mangrove biomass between the Tropics of Cancer and Capricorn (23°N to 23°S), and 7.9–164 t ha^{-1} between 23 and 30°.

The data representing higher latitudes in the reviews by Twilley et al. (1992) and Alongi (2009), however, omitted a number of the larger published values. Published estimates of biomass for temperate mangrove stands (Table 4) show considerable overlap with values from lower latitudes. For example, biomass was estimated at 130 t ha^{-1} in a stand in Auckland (Woodroffe 1985a) and 220 and 400 t ha^{-1} for stands around Sydney (30°30′ and 30°46′S, Goulter & Allaway 1979 and Saintilan 1997a, respectively). The largest value included by Alongi (2009) for latitudes >30°S, in contrast, was about 125 t ha^{-1}.

Osunkoya & Creese (1997) described a cline of decreasing tree height and propagule size with increasing latitude within New Zealand, and this cline would be expected to impose similar variation on rates of litterfall. There is also, however, variation among locations at the same latitude, as illustrated by the examples described, and this variation obscures or confounds latitudinal gradients.

Reasons for latitudinal trends in productivity and biomass

The physiological basis of this decline in height and productivity with increasing latitude is likely to be complex. In this section, a range of factors is considered that may contribute to the reduced tree height and productivity in temperate mangrove forests compared with more equatorial forests.

Allocation of resources to leaf production may be lower in temperate compared with tropical sites. Patterns of leaf production vary strongly with latitude (Duke 1990). Tropical sites appear to have multiple peaks in leaf fall and leaf initiation compared with the unimodal pattern observed at cooler, southern sites, where leaf flushes are typically in the summer (Duke 1990). Thus, the shorter, compressed growing season of temperate mangroves may be a strong contributing factor in reducing productivity at high latitudes.

Maximum photosynthetic carbon gain and growth (measured as stem extension) was not depressed at higher latitudes compared with tropical sites (Lovelock et al. 2007a). However, leaf nitrogen and phosphorus concentrations increased at higher latitudes compared with lower latitudes, as they do in terrestrial species (Lovelock et al. 2007a). Taken together, these data suggest that per unit leaf photosynthetic rates are maintained at high latitudes through increased investment in the metabolic components of photosynthetic pathways. Declines in forest productivity may therefore be due both to decreases in the length of time when temperatures are suitable for photosynthetic carbon gain and to increases in respiration associated with maintaining thicker, more metabolically active leaves during periods of low potential production.

Anatomical constraints on water transport associated with freezing tolerance (see ‘Key drivers’ section, p. 51), which may limit canopy development and photosynthesis, are likely to be higher in higher-latitude forests, particularly in the Southern Hemisphere, where freezing temperatures are frequent (Stuart et al. 2007). Xylem vessel diameters were smaller in southern populations of *A. marina* than at more tropical latitudes. A similar trend was not observed in the Northern Hemisphere populations of *A. germinans*, although sample size was small (Stuart et al. 2007). The differences in patterns between biogeographic regions may occur because in Florida freezing is infrequent but severe, which

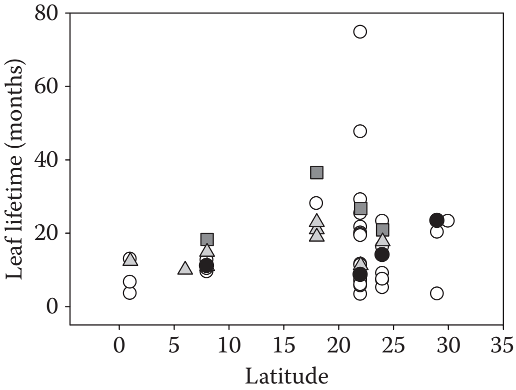

Figure 4 Leaf lifetime of a range of mangrove species over variation in latitude. There is no significant increase in lifetime with increasing latitude. *Avicennia marina* (filled circles), *Rhizophora* spp. (shaded triangles), *Ceriops* spp. (shaded squares) and other species (open circles) are included. (Data are from Saenger 2002.)

may impose different selective pressures on plants compared with those in the Southern Hemisphere (Stuart et al. 2007). In addition, mangrove competition with the saltmarsh grass *Spartina alterniflora*, which occupies similarly low regions of the intertidal zone in Florida and elsewhere, may place a significant selective pressure to maintain high levels of hydraulic conductivity and growth despite the ensuing susceptibility to embolism during freezing temperatures. In *Avicennia germinans* in the Caribbean, leaf characteristics differed over a latitudinal gradient, with leaf size decreasing and leaf mass per area and carbon content increasing with latitude (Mendez-Alonso et al. 2008). These authors suggested that the decrease in leaf area and increase in carbon content was associated with increases in leaf longevity, which helps to balance the higher leaf construction costs (Wright & Westoby 2002, Wright et al. 2002). However, the limited data on longevity of mangrove leaves does not indicate increased leaf lifespans at higher latitudes (Figure 4; Saenger 2002).

Reductions in maximum tree height with increasing latitude could be due to a number of mechanisms. Hydraulic architecture is proposed to limit tree height in tall species, with xylem tension reaching levels that are at the limits of embolism in very tall trees (Koch et al. 2004). However, gravitational forces only account for 0.0098 MPa m^{-1}; thus, in smaller-stature trees (<50 m tall) gravity will only account for about 0.5 MPa contribution to leaf water potential. Another hypothesis is that maximum height is constrained by respiratory demand of non-photosynthetic tissues. Taller trees have more woody tissue (roots and stems) than shorter trees (e.g., Clough et al. 1997). Maximum tree height occurs where photosynthetic carbon gain matches that of respiration losses. Trees may overshoot the balance in some years or seasons but then die back when conditions for photosynthetic carbon gain are less favourable. High soil salinity, which decreases hydraulic conductivity, leaf water potential and photosynthetic rates (Lovelock et al. 2006, Suarez & Medina 2006), will contribute to reducing carbon balances, further decreasing tree heights. There are few direct tests of this hypothesis. In New Zealand, however, loss of twig length was observed over the winter season (Lovelock et al. 2007b). Direct frost damage to leaves, branches and reproductive tissues of trees (Saintilan et al. 2009) and herbivory, particularly by wood-boring insects (I. Feller personal communication), also contributes to limiting height of trees.

Other primary producers in temperate mangrove forests

Although the structural elements of the mangrove forest are dominated by the trees, there is a range of other primary producers that contribute to the overall productivity of the ecosystem. Under the mangrove canopy, well-developed epiphytic algal and microbial communities adhere to roots, stems and sediments (e.g., Beanland & Woelkerling 1983). Macroalgal communities in mangroves are dominated by red algae and characterised as *Bostrychietum* (Phillips et al. 1994, King 1995). Most of the macroalgal species found in temperate mangroves are widespread globally, and species belonging to the genera *Bostrychia*, *Caloglossa* and *Catenella* are most common (Beanland & Woelkerling 1982, Davey & Woelkerling 1985, Eston et al. 1992, King 1995). The taxonomic composition of the algal community in temperate mangroves of Spencer Gulf, South Australia, was distinct from those in nearby Victoria as well as tropical mangroves, but similar to the algal species found on the open coastlines outside the gulf (Beanland & Woelkerling 1982). Several typical tropical macroalgae taxa occurred in the upper Spencer Gulf and are possible relic populations (Beanland & Woelkerling 1982). Subject to inundation, desiccation and shading by the mangrove canopy, the frequency of occurrence can decrease from the seaward to the landward edge of temperate mangroves (Davey & Woelkerling 1985). Different macroalgal species dominate underneath compared with outside the canopy, and algal cover and biomass are higher in the shaded areas (Beanland & Woelkerling 1983).

Ecophysiological adaptations of *Bostrychia* and *Caloglossa* allow them to tolerate salinity changes, desiccation and shading and can thus explain their dominance in mangrove forests. The macroalgae colonise pneumatophores mainly within 10 to 20 cm above the mud surface (Davey & Woelkerling 1985), and although colonisation experiments revealed seasonal changes in the colonisation rate, no successional stages were found (Eston et al. 1992, Gwyther & Fairweather 2002).

This community is highly productive, accounting for up to 15% of gross primary production (Dawes et al. 1999). In temperate locations, biomass can be high (e.g., Dor & Levy 1984, Phillips et al. 1994, Melville et al. 2005), particularly where there is nutrient enrichment (Melville & Pulkownik 2006). The biomass of the epiphytic algal and microbial communities can be heavily grazed (Skilleter & Warren 2000). The high nutrient quality of algal and microbial mat tissue (Lee & Joye 2006) may result in a high contribution to the food web because algae and microbial communities may be preferentially consumed and decomposed compared with the biomass of the trees, which is physically tough and chemically difficult to digest (Bouillon et al. 2008). The photosynthetic activity and nitrogen fixation by epiphytic algae and bacteria on pneumatophores has been discussed as a mutualistic relationship because algal holdfast was detected in the periderm of pneumatophores (Naidoo et al. 2008). Epiphytic algae are grazed on by snails (*Bembicium melanostomum*) (Gwyther & Fairweather 2005) and affect the colonisation of pneumatophores by meiofauna (Gwyther & Fairweather 2002).

Mangrove faunal diversity and abundance

Hutchings & Recher (1982) divided the aquatic faunas of mangroves into an encrusting epifauna (i.e., sessile taxa living on mangrove structures), a mangrove epifauna (i.e., motile species living on the mangroves), a substratum infauna, a substratum epifauna, and a wood-boring infauna. These components of the aquatic fauna are discussed in the following sections, combining substratum infauna and epifauna and encrusting and mangrove epifauna for concision. They are preceded by a review of information on the benthic meiofaunas.

Benthic meiofauna

Introduction

Meiofauna living in the interstitial spaces of sediments has long been known to be a diverse and important component of coastal marine sediments (Fenchel 1978, Giere 2009). They occur in high abundances, have fast response times to disturbances, and are important for decomposer food chains as well as constituting prey for juveniles of commercially important fishes and prawns (Coull 1990, 1999, Coull & Chandler 1992).

Meiofauna in temperate mangroves has been investigated mainly in south-eastern Australia, southern Africa and Brazil. All of these studies used different methods for sampling and extracting meiofauna and focused on different meiofaunal taxa. Although this difference complicates comparisons, some general patterns emerge from the following overview.

Meiofaunal diversity and abundance

Diversity The meiofauna in sediments of temperate mangroves is dominated by nematodes, comparable with other marine ecosystems (Alongi 1987a, Vanhove et al. 1992, Sasekumar 1994, Olafsson 1995). Nematodes and halacarid mites have been best studied, and the presence of other invertebrate taxa occurring in the interstitial spaces of temperate mangroves has been recorded, but detailed taxonomic work still has to follow, and further undescribed species will be discovered (Nicholas 1996, Marshall & Pugh 2001). The permanent meiofauna reported from temperate mangrove muds and pneumatophores includes Nematoda, Copepoda, Acari, Kinorhynchia, Platyhelmintha, Gastrotricha, Cnidaria and Foraminifera, and temporary meiofauna is represented with Oligochaeta, juvenile polychaetes and insect larvae (Diptera). The occurrence of major meiofaunal taxa in temperate mangroves around the world reflects the current state of knowledge and the level of taxonomic detail, which varies among studies. As mangroves are a transition zone between the land and the sea, meiofauna of not only marine but also terrestrial and freshwater origin can be encountered (Phleger 1970, Hodda & Nicholas 1985, Nicholas et al. 1991, Olafsson 1995, Proches 2004).

Several nematode genera (such as *Microlaimus*, *Spirina*, *Desmodora* and various representatives of the Chromadoridae), and even species, occur in mangroves across temperate latitudes of southern America, Africa and Australia and in tropical mangroves (Hodda & Nicholas 1985, Nicholas et al. 1991, Olafsson 1995, Netto & Gallucci 2003). Yet, other genera that are abundant in temperate mangroves (e.g., *Triplyoides*) are rare in tropical mangroves (Hodda 1990, Olafsson 1995, Gwyther 2003).

Abundance and biomass Nematoda account for over 70 to 100% of meiofaunal abundances (Hodda & Nicholas 1986a, Gwyther 2000), followed by copepods, ciliates or halacarid mites (Table 5). Meiofaunal abundances in temperate mangrove muds vary within and between regions (Table 5) yet are similar to abundances found in mangrove mud elsewhere or in non-mangrove estuaries or saltmarsh densities (Dye 1983a, Nicholas et al. 1991, Gwyther 2000). Meiofaunal abundances on pneumatophores were about 3 to over 40 times lower than in adjacent sediments (Gwyther 2000, Proches et al. 2001). Mean abundances on 5-cm segments of pneumatophores in South African mangroves ranged from 5 to 90 individuals for copepods and 10 to 160 individuals for acari, with copepods less abundant at the tip of the pneumatophores, where mites (Halacaridae) occurred in highest density (Proches & Marshall 2002). Gwyther (2000) found higher meiofaunal abundances on pneumatophores with algae (52 ± 11 individuals 10 cm^{-2}) than on those with barnacles (39 ± 5 individuals 10 cm^{-2}). These abundances were lower than for epifaunal meiofauna living on seagrass blades or saltmarsh grasses (Gwyther 2000).

Biomass values for nematodes in a New South Wales mangrove estuary ranged from 19 mg dry weight (DW) m^{-2} in the upper intertidal to 888 mg DW m^{-2} in the low intertidal zone, equivalent to 8 and 383 mg carbon m^{-2}, respectively (Nicholas et al. 1991). These values are comparable to estimates made by Dye (1983b) from southern Africa, where the mean biomass was 646 mg DW m^{-2} (range 91–2877 mg DW m^{-2}), but the higher biomass occurred in the upper intertidal zone at most study sites. Biomass also varied over time because Dye (1983a) reported a much higher biomass at most of the sampling sites in the Mngazana Estuary in the following year, with equivalent production of 1.48–9.32 g carbon m^{-2} yr^{-1}.

Table 5 Meiofaunal species numbers (sum of species or phyla recorded in particular studies) and individual density (mean and range of minimum and maximum values) of meiofauna from sediments in temperate mangrove studies

Region/site	Species/ taxa number	Density (ind. cm^{-2}), mean value (minimum–maximum)	Taxa recorded	Most abundant taxa	Reference
New South Wales: Hunter River, Clyde River, Candlagan Creek	21	345 (21–2968)	Nematoda	Nematoda: *Tripyloides* sp., *Desmodora cazca*, *Sabatiera* sp., *Sphaerolaimus* sp. A., *Spirina* sp., *Terschellingia longicaudata*	Hodda 1990
New South Wales: Hunter River	62	225 (63–12,057)	Nematoda, Copepoda, Platyhelminthes, Kinorhyncha, Acari, Polychaeta (Nereididae, Phyllodocidae), Oligochaeta, Insecta (larvae)	Nematoda	Hodda & Nicholas 1985
New South Wales: Hunter River	36	110 (1–9596)	Nematoda, Copepoda, Platyhelminthes, Kinorhyncha, Acari, Polychaeta, Oligochaeta, Insecta (larvae)	Nematoda: *Filipjeva* sp., *Monhystera* sp. B., *Ethmolaimus* sp., *Terschellingia longicaudata, Sabatiera* sp., *Desmodora cazca*	Hodda & Nicholas 1986b
New South Wales: Clyde River	40	183 (47–500)	Nematoda, Copepoda, Platyhelminthes, Kinorhyncha, Acari, Ostracoda, Rotifera, Polychaeta (Nereididae, Fabricinae), Oligochaeta, Insecta (larvae)	Nematoda: *Microlaimus capillaris*, *Terschellingia longicaudata, Desmodora cazca*	Nicholas et al. 1991
Victoria: Barwon Estuary		2170 (250–8622)	Nematoda, Copepoda, Halacarida, Polychaeta, Oligochaeta, Insecta (larvae), Kinorhynchia, Platyhelminthes, Cnidaria	Nematoda	Gwyther 2000
Transkei: Mngazana River			Nematoda, Ciliata, Oligochaeta, Gastrotricha, Polychaeta, Kinorhyncha, Copepoda, Insecta (larvae), Crustacea (larvae)	Nematoda	Dye 1983b
Transkei: Mngazana River	12	246 (84–530)	Nematoda, Ciliata, Oligochaeta, Platyhelminthes, Kinorhyncha, Copepoda, Polychaeta, Gastrotricha, Crustacea (larvae), Insecta (larvae)	Nematoda	Dye 1983a
South Africa: Beachwood Creek, Bayhead Lagoon	30	2	Copepoda, Insecta (larvae)	Harpacticoid copepods	Proches et al. 2001
South Brazil: Santa Catarina Island	94	(77–1589)	Nematoda, Acari, Oligochaeta, Copepoda, Polychaeta, Kinorhynchia, Platyhelminthes, Ostracoda, Insecta (larvae)	Nematoda	Netto & Gallucci 2003

Note: Studies focused on particular meiofaunal taxa (e.g., Proches et al. 2001 on arthropods) or did not differentiate on species level (e.g., Dye 1983a,b). Insect larvae encountered were mainly Ceratopogonidae and Tipulidae. The recorded taxa are listed in decreasing order of abundance if such information was available. ind. = individuals.

Feeding modes Classification of feeding modes can help elucidate whether the prevalence of particular species in certain habitats may be related to their food supply. For nematodes, classification of feeding modes can be done based on the morphology of the buccal cavity (Wieser 1953, Jensen 1987). Nematodes in mangrove sediments are deposit- or epistratum-feeders, feeding on diatoms, bacteria, plant roots or algae (Hodda & Nicholas 1986a, Nicholas et al. 1991, Netto & Gallucci 2003). Nematodes found on pneumatophores are epigrowth (Gwyther & Fairweather 2002, Gwyther 2003) or epistratum feeders (Nicholas et al. 1991), and non-selective deposit-feeders dominate on mangrove leaf litter (Gwyther 2003). Different nematode feeding modes were found to occur in different tidal zones (Nicholas et al. 1991) and substrata, with epistratum feeders more abundant at sandier sites, while deposit-feeders were dominant at sites with finer, muddier sediments (Hodda & Nicholas 1986a).

Distribution patterns of temperate mangrove meiofauna

Temporal Temperate mangroves experience more pronounced seasons than their tropical counterparts, in particular winter rainfall and dry, hot summers. Dry, hot conditions cause desiccation of the epiphyte cover on pneumatophores, with a subsequent decline in meiofaunal abundances on pneumatophores in summer (Gwyther & Fairweather 2002, 2005). For sediment meiofauna, variations in seasonal patterns of nematodes could be linked to mangrove tree density, which modifies the surface water availability, litterfall and algal blooms on the sediment (Hodda & Nicholas 1986a). Sites with few or no mangroves had highest meiofaunal densities in winter, whereas no seasonal patterns were found in tall and dense mangrove forest regions (Hodda & Nicholas 1986a). Yet, the few nematode species showing consistent seasonal patterns across sampling sites did so in different seasons (e.g., *Filipjeva* sp. highest in winter, *Chromadorina* sp. highest in spring), whereas they all belonged to similar feeding modes (epigrowth or unselective deposit-feeder) (Hodda & Nicholas 1986a). Temporal variation in meiofauna was recorded in most studies, but without clear patterns in relation to seasons or environmental changes over the year (Dye 1983a, Hodda & Nicholas 1986a,b, Gwyther 2000, Proches et al. 2001), and was even seen as stochastic variation (Hodda 1990). Seasonal changes in the species dominating in particular sites complicate the use of meiofauna to detect pollution in temperate mangroves (Hodda & Nicholas 1986b).

Spatial Apart from some taxonomic similarities across global and regional scales (Nicholas et al. 1991, Olafsson 1995, Netto & Gallucci 2003), meiofaunal species compositions in temperate mangroves can differ on a local scale, subject to habitat characteristics along estuaries (Hodda 1990, Proches et al. 2001, Netto & Gallucci 2003) or possibly pollution (Hodda & Nicholas 1985). Differences in meiofaunal assemblages were found along transects within sites, from the high towards the low intertidal zone. Nicholas et al. (1991) reported few differences in nematode diversity along their transects, yet abundances and biomass increased from the high (470×10^3 ind m^{-2}, 19 mg DW m^{-2}) towards the low intertidal zone (5000×10^3 ind m^{-2}, 888 mg DW m^{-2}). Dye (1983a,b), however, found highest meiofaunal abundances in the midintertidal zone where the mangrove forest density was highest, whereas meiofaunal biomass was higher in the upper (231–1835 mg DW m^{-2}) than the lower (91–670 mg DW m^{-2}) intertidal.

Mangroves in both temperate and tropical latitudes create complex habitats with a small-scale heterogeneity of microtopography, biogenic structures (pneumatophores, tree trunks, rootlets, leave litter, algal patches, crab burrows) and respectively varying environmental conditions, which lead to small-scale variability in meiofaunal distributions and complicating the detection of patterns (Hodda 1990, Nicholas et al. 1991, Olafsson 1995). The presence of algal patches was seen as an important determinant of meiofaunal distributions (Dye 1983a,b).

Environmental factors and pollution Sediment-dwelling meiofauna is subjected to sediment characteristics and porewater qualities. Grain size was important for nematode distributions in mangrove estuaries in New South Wales, where sites with similar grain-size compositions shared similar nematode assemblages, regardless of season or the background pollution of some areas (Hodda & Nicholas 1986b). However, the relevance of particular sediment characteristics can vary between estuaries because Hodda & Nicholas (1985) reported no correlation between grain size and nematode densities. The sediment packing, drainage and content of organic matter and detritus biomass contributed further to differences between sites and were correlated with meiofaunal abundances (Hodda 1990, Netto & Gallucci 2003).

Sediment biogeochemistry shows the greatest changes in the top 15 cm of mangrove sediments; in particular, the oxygen penetration and redox potential profile can affect the vertical distribution of meiofauna within sediments (Dye 1983a,b, Hodda & Nicholas 1985, Hodda 1990) as well as their overall abundance (Hodda & Nicholas 1986b).

Tannins leaching from mangrove leaves have been found to inhibit meiofaunal populations (Alongi 1987b), yet *Avicennia* leaves have a lower tannin content than other mangroves (Robertson 1988), and the relevance of tannins in determining meiofaunal populations and distributions in temperate mangroves may be less than in their tropical counterparts. An indication of lower tannin content can be seen in the higher meiofaunal densities found by Dye (1983b) in the denser parts of the forest.

Pollution by heavy metals in an estuary in New South Wales reduced densities of both nematodes and copepods, so that the nematode/copepod ratio could not be applied to indicate the pollution level of the sediments (Hodda & Nicholas 1985).

Temperature and pH were found to be of less importance in explaining meiofaunal distribution patterns in temperate mangroves, and environmental conditions showed no consistent patterns of seasonal variations between sites and tidal levels (Dye 1983a,b). Yet, the elevation above the low-tide mark can be important for nematode distributions (Hodda & Nicholas 1985, 1986a), and salinity differences along estuaries correlated with copepod distribution (Hodda & Nicholas 1985, 1986a). In mangroves of southern Brazil, the distribution of the most abundant nematodes along the estuary could not be explained by any environmental factors measured (Netto & Gallucci 2003). Clear relations between environmental factors and meiofauna within and between estuaries were also absent in tropical mangroves (Alongi 1987c, Armenteros et al. 2006).

Hodda (1990) argued that the stochastic variation of environmental and habitat factors in temperate mangroves favours adaptability rather than specialisation and can thus account for some of the observed coexistence of related species in mangrove nematodes.

Habitat use by temperate mangrove meiofauna

Sediments The sediments contain the vast majority of meiofauna occurring in temperate mangroves (Nicholas et al. 1991, Gwyther 2000). Due to the often anoxic conditions, a vertical stratification of meiofauna is found, with highest densities in the top 10 cm of the sediment in South African mangroves (Dye 1983b), but with suspected occurrence of some meiofauna below 60-cm sediment depth. In south-eastern Australian mangroves, nematodes were restricted (85%) to the top 1 cm, above the redox potential discontinuity (RPD) layer (Hodda & Nicholas 1985, Nicholas et al. 1991), with another 10–14% occurring to 5 cm and 2–6% in 5- to 10-cm sediment depth. Some nematode species (including *Terschellingia longicaudata*, *Sabatiera* spp., *Paracyatholaimus* sp.) occurred with >50% of all individuals at depths below the top centimetre, and one species (*Enchodelus coomansi*) was only recorded in greater sediment depths (Nicholas et al. 1991). Nematodes of the same families and genera as found in temperate mangroves have adaptations to suboxic sediments rich in H_2S, including intracellular accumulations of sulphur and symbiotic relationships with bacteria (Nicholas et al. 1987, Polz et al. 1992, Steyaert et al. 2007).

Pneumatophores Pneumatophores constitute a biogenic structure that provides habitat for sessile and mobile epifauna. Although meiofaunal diversity and abundances are lower on pneumatophores than in sediments (Nicholas et al. 1991), they reveal some interesting patterns of microhabitat use and trophic interactions. The species composition and diversity found on pneumatophores (copepods, halacarid mites, tanaids; lowest taxonomic richness) differ from the sediment meiofauna (nematodes dominant; highest taxonomic richness) (Gwyther 2000, Gwyther & Fairweather 2002, Proches & Marshall 2002) and varies between pneumatophores overgrown with barnacles (acari dominant) and algae (harpacticoid copepods, acari, nematodes) (Gwyther 2000, Gwyther & Fairweather 2002). Barnacles are known to harbour a rich halacarid fauna in their crevices, which may explain this pattern (Bartsch 1989). Pneumatophores without fouling were colonised by very few meiofauna (Gwyther 2000, Gwyther & Fairweather 2002, 2005). Insect larvae were found both on pneumatophores and in the sediment (Proches et al. 2001).

Nematode species occurring in the foliaceous brown algae on pneumatophores (*Tylendus* sp.) were different from those inhabiting filamentous green algal mats on the sediment surface (species of *Chromadorina* and *Ethmolaimus*) (Hodda & Nicholas 1985). The length of pneumatophores as such was not correlated with associated meiofaunal abundance (Proches et al. 2001), but vertical distribution on pneumatophores differed, with several species of acari and tanaids increasing in abundance towards the tip (Proches & Marshall 2002). Algal cover and sediment deposition at the base of pneumatophores was positively correlated with some acari, copepods and insect larvae (Proches & Marshall 2002). As algal and barnacle cover and sediment deposition increases towards the low-tide line, this gradient can account for some of the differences in the pneumatophore-associated meiofauna along intertidal transects (Gwyther 2000, Proches & Marshall 2002). Yet, pneumatophores on the seaward fringe of mangroves are subject to more exposure and higher desiccation in summer, and their meiofaunal assemblages had a lower species richness, but higher abundances, and formed a different assemblage compared with the meiofauna on pneumatophores from within the forest (Proches et al. 2001). Desiccation over summer, which seasonally reduces the algal epigrowth on pneumatophores, is followed by a decline in meiofauna (Gwyther & Fairweather 2002).

Colonisation of pneumatophores after experimental removal of all attached algae and sediment was not completed after 25 wk, apart from rapid colonisation by halacarids, harpacticoid copepods and ceratopogonid insect larvae (Proches & Marshall 2002). Proches & Marshall proposed that recovery was related to the recolonisation by epiphytic algae on the pneumatophores and the dispersal ability of the meiofaunal organisms.

The relevance of pneumatophore epigrowth on meiofaunal colonisation was also studied experimentally by Gwyther and Fairweather (2002, 2005), who offered transplanted and mimic pneumatophores. Natural pneumatophores always had the highest meiofaunal numbers, but mimics had a more diverse meiofaunal assemblage. The colonisation was resource dependent, as evident from the nematode feeding modes dominating during colonisation and the differences in colonisation time between experiments in winter and summer (Gwyther & Fairweather 2002, 2005). The importance of algal epiphyte cover on pneumatophores and the varying dispersal abilities of meiofauna (nematodes with sediment dislodgement or floating detritus, copepods through the water column) (Armonies 1988, Hodda 1990, Faust & Gulledge 1996, Gwyther & Fairweather 2005) caused a more ephemeral colonisation rather than a succession (Gwyther & Fairweather 2002, 2005).

Leaf litter Mangrove leaf litter on the forest floor provides another habitat for meiofauna. In a temperate mangrove forest in Victoria, Australia, Gwyther (2003) found 21 nematode species (14 on average per leaf) on leaf litter, where brown leaves and leaf litter in the shade of the canopy were preferred, possibly to avoid desiccation at more exposed sites. Copepods, oligochaetes and acari were also recorded on leaf litter, but in low numbers. Most of the nematodes were non-selective deposit-feeders, followed by epigrowth feeders, which were more common at the exposed sites at the mangrove fringe, where more light could increase microphytobenthic growth.

The diversity of nematodes on leaf litter found by Gwyther (2003) was lower than in the tropics, and whereas one or two feeding groups were dominant at her sites, all nematode feeding groups have been recorded on decaying mangrove leaves in the tropics (Gee & Somerfield 1997).

Trophic interactions of temperate mangrove meiofauna

Although nematode feeding modes in temperate mangroves have been classified using the morphological approach of Wieser (1953) and laboratory observations (Nicholas et al. 1988), detailed analyses of trophic interactions are still lacking. Leduc et al. (2009) demonstrated the usefulness of combining stable isotope, fatty acid and biomarker analyses to elucidate the diet of meiofauna, and this approach could provide valuable insight into mangrove meiofauna.

Meiofauna is a well-known food item for fishes and crustaceans (Gee 1989, Coull et al. 1995, Jenkins et al. 1996, Olafsson & Ndaro 1997), yet the dependence of fishes and prawns on deriving meiofaunal food from temperate mangroves has not yet been explored, apart from observations reported by Nicholas et al. (1991) that juvenile prawns were feeding on meiofauna. Similarly, whether mangrove crabs, which occur in lower diversity and numbers in temperate than tropical mangroves, exert predation pressure on meiofauna in temperate mangroves remains to be studied.

Benthic macrofauna

Introduction

The macrofauna, as in any soft-sediment habitat, consists of a burrowing infauna and an errant or sessile epifauna. In mangroves, in contrast to many other sediment shores, the infauna is generally dominated by crustaceans, and bivalves are usually relatively scarce (Macnae 1968). The motile epifauna is often dominated by gastropods and the sessile fauna by bivalves and barnacles (discussed in the section on encrusting fauna). Most of the species present are marine or estuarine, depending on location along the salinity gradient, but freshwater species may be present in upper estuarine locations (Hutchings & Recher 1982). Information on the composition of mangrove faunas in different temperate regions is reviewed, followed by a discussion of information on their ecology.

Review of regional information

Australia There appears to be little published information on the fauna of mangroves in the Leschenault Inlet Estuary in Western Australia (the only temperate mangroves on the western coast of the continent), although the faunas of other intertidal habitats in the estuary have been described (Semeniuk 2000, Semeniuk & Wurm 2000). The fauna of mangroves in south-eastern Australia, particularly in the Sydney region (33°S), has been the subject of relatively detailed study compared with those of other temperate regions. It is characterised by deposit-feeding oligochaetes, polychaetes (e.g., capitellids and spionids); gastropods; small crustaceans (cumaceans, tanaids, isopods and amphipods); and crabs (ocypodids, grapsids and sesarmids) (Hutchings & Recher 1974, Chapman & Underwood 1995, Chapman 1998, Lindegarth & Hoskin 2001, Chapman & Tolhurst 2004; Table 6). Taxa that were found in at least 33% of core samples from an urbanised mangrove forest in Sydney Harbour included amphipods, insect larvae, oligochaetes, crabs, capitellid, nereid, sabellid and spionid polychaetes and gastropods (Chapman & Tolhurst 2004).

A total of nine species of crabs occurs in mangrove forests in southern Australia, only three of which are common (Chapman & Underwood 1995). Six species of crabs (three ocypodids, two grapsids and a sesarmid), an alpheid prawn and five species of gastropods (including the pulmonate slug *Onchidium damelii*) were among the dominant species of mangrove habitats in the Pittwater,

Table 6 Benthic macrofaunal taxa recorded by studies of temperate mangroves

Region/site	Number of taxa	Total abundance	Taxa recorded	Mangrove species	Reference
Kyushu and Yakushima, Japan (31°22′N)			Gastropods (*Batillaria multiformis*, *Cerithideopsilla djadjariensis*, *C. cingulata*, *Cerithidea rhizophoranum*), crab (*Sesarma dehaani*)	*Kandelia candel*	Wakamatsu & Tomiyama 2000
Matapouri, New Zealand (35°34′S)	29.4 ± 2.7 (SE) per 15 × 15-cm core	43.9 ± 16.1 (SE) per 15 × 15-cm core	Oligochaetes, gastropods (*Diloma subrostrata*, *Melagraphia aethiops*, *Turbo smaragdus*, *Cominella glandiformis*, *Lepsiella scobina*, *Zeacumantus* sp.), bivalves (*Austrovenus stutchburyi*, *Paphies australis*).	*Avicennia marina*	Alfaro 2006
Whitford, New Zealand (36°55′S)	1.0–10.3 (range of means of three 13-cm diameter cores)	2.3–73.3 (range of means of three 13-cm diameter cores)	Polychaetes (*Aquilaspio aucklandica*, *Nicon* sp., *Scolecolepides* sp., *Scoloplos cylindrifer*), oligochaetes, amphipods (*Corophium* sp., Paracalliopidae), *Helice crassa* (crab)	*Avicennia marina*	Ellis et al. 2004
Various sites, New Zealand			Gastropods (*Amphibola crenata*, *Diloma subrostrata*, *Melagraphia aethiops*, *Turbo smaragdus*, *Zeacumantus lutulentus*), crabs (*Helice crassa*, *Scylla serrata*), *Nicon aestuariensis* (polychaete)	*Avicennia marina*	Morton & Miller 1968
Manukau Harbour, New Zealand (37°01′S)	Young stands: 5.5–8.0 Old stands: 2.2–5.8 (ranges of means of six 10-cm diameter cores)	Young stands: 20.7–80.0 Old stands: 17.3–72.6 (ranges of means of six 10–cm diameter cores)	Polychaetes (*Capitella capitata*, *Nicon aestuariensis*, *Scolecolepides benhami*), oligochaetes, gastropod (*Potamopyrgus antipodarum*), bivalve spat, crab (*Helice crassa*)	*Avicennia marina*	Morrisey et al. 2003
Sydney, Australia (33°50′S)			Anthozoa (1 sp.), sipunculids, echiurids, gastropods (14 spp. including *Ophicardelus* sp. and *Salinator solida*), bivalves (8 spp., including *Xenostrobus securis*), polychaetes (9 families, including capitellids, nereids, sabellids and spionids), oligochaetes, amphipods (6 spp.), isopods (7 spp.), leptostracans, cumaceans, tanaids, ostracods, maxillipods	*Avicennia marina*	Chapman, 1998, Chapman et al. 2005, Chapman & Tolhurst 2004, Tolhurst & Chapman 2007
Pittwater, Sydney, Australia (33°36′S)			Gastropods (*Littorina scabra*, *Onchidium damelii*, *Ophicardelus ornatus*, *Pyrazus ebeninus*, *Velacumantus australis*), bivalve (*Crassostrea commercialis*), *Balanus amphitrite* (barnacle), crabs (*Helograpsus* (*Helice*) *haswellianus*, *Heloecius cordiformis*, *Macrophthalmus carinimanus*, *M. setosus*, *Parasesarma erythrodactyla*)	*Aegiceras corniculatum* and *Avicennia marina*	Dakin 1966

Careel Bay, Sydney, Australia (33°37′S)	Gastropods (trochid, acmaeid, littorinid, *Velacumantus australis*, nassarid, *Ophicardelus* spp, onchidiid), penaeid prawn, mud shrimp (*Laomedia* sp.), crabs (*Scylla serrata*, 2 spp. grapsids, 3 spp. ocypodids), bivalves (arcid, mytiliid, ostreid, *Teredo* sp.)	*Avicennia marina*	Hutchings & Recher 1974
Sydney, Australia (33°50′S)	Polychaetes (*Australonereis ehlersi*, *Ceratonereis erythraensis*, *Neanthes vaallii*, *Marphysa sanguinea*, *Capitella capitata*, *Notomastus hemipodus*, *Nephtys australiensis*, *Polydora* sp., *Haploscoloplos* sp., *Owenia fusiformis*, *Phyllodoce novaehollandiae*, *Chaetopterus* sp.), isopod (*Ligia australiensis*), mud shrimps (*Laomedia healyi*), snapping shrimp (*Alpheus edwardsii*), burrowing prawns (*Callianassa australiensis*), penaeid prawn (*Penaeus plebejus*), crabs (*Helice leachi*, *Helograpsus haswellianus*, *Metopograpsus frontalis*, *Paragrapsus laevis*, *Parasesarma erythrodactyla*, *Mictyris longicarpus*, *Euplax tridentata*, *Heloecius cordiformis*, *Macrophthalmus crassipes*, *Macrophthalmus setosus*, *Scylla serrata*)	*Aegiceras corniculatum* and *Avicennia marina*	Saenger et al. 1977
South Australia: Port Wakefield (34°10′S), Port Gawler (34°36′S), Port Adelaide (34°48′S)	Gastropods (*Ophicardelus ornatus*, *Laemodonta ciliata*, *Maripythia meridionalis*, *Salinator* spp.), bivalves (*Laternula creccina*, *Modiolus inconstans*), snapping shrimps (*Alpheus* spp.), burrowing prawns (*Callianassa ceramica*, *Upogebia simsoni*), crabs (*Cyclograpsus audouini*, *Helice haswellianus*, *Paragrapsus gaimardi*)	*Avicennia marina*	Macnae 1966
Various, South Australia	Oligochaetes, nereid polychaetes, gastropods (*Austrocochlea constricta*, *Bembicium auratum*, *Cominella lineolata*, *Niotha* (*Paracanassa*) *pauperata*, *Ophicardelus ornatus*, *Phasionotrochus* sp., *Salinator solida*), bivalves (*Katelysia peronii*, *Macomona deltoidalis*, *Modiolus inconstans*), barnacles (*Balanus amphitrite*, *Elminius modestus*), crabs (*Eriocheir spinosus*, *Helograpsus haswellianus*, *Philyra laevis*)		Butler et al. 1977b
Temperate eastern Australia	Gastropods (*Assiminea tasmanica*, *Bembicium auratum*, *Ophicardelus* sp., *Pyrazus ebeninus*, *Salinator fragile*, *S. solida*, *Velacumantus australis*), crabs (*Heloecius cordiformis*, *Paragrapsus laevis*, *Parasesarma erythrodactyla*)	*Aegiceras corniculatum* and *Avicennia marina*	Chapman & Underwood 1995

(continued on next page)

Table 6 (continued) Benthic macrofaunal taxa recorded by studies of temperate mangroves

Region/site	Number of taxa	Total abundance	Taxa recorded	Mangrove species	Reference
South Africa: Mtata River (31°57′S), Mngazana River (31°42′S), Isipingo River (30°00′S), Richards Bay (28°50′S)			Polychaete (*Dendronereis arborifera*), gastropods (*Assiminea ?bifasciata*, *Cassidula labrella*, *Cerithidea decollata*, *Littorina scabra*, *Peronia peronii*, *Terebralia* (*Pyrazus*) *palustris*), bivalve (*Crassostrea cucullata*), barnacle (*Balanus amphitrite*), isopod (*Sphaeroma tenebrans*), snapping shrimp (*Alpheus crassimanus*), burrowing prawns (*Callianassa kraussi*, *Upogebia africana*), crabs (*Cardisoma carnifex*, *Clibanarius longitarsus*, *C. padavensis*, *Coenobita cavipes*, *Cyclograpsus punctatus*, *Eurycarcinus natalensis*, *Macrophthalmus convexus*, *M. grandidieri*, *Metopograpsus gracilipes*, *Panopeus africanus*, *Sesarma catenata*, *S. euillimene*, *S. guttata*, *Sesarma meinerti*, *Uca annulipes*, *U. chlorophthalmus*, *U. marionis*, *U. urvillei*), *Holothuria parva*	*Avicennia marina*, *Bruguiera gymnorrhiza*, *Rhizophora mucronata*	Macnae 1963
Mngazana River, South Africa (31°42′S)			Polychaetes (*Ceratonereis keiskama*, *Marphysa macintoshi*, *M. depressa*, *Orbinia angrapaquensis*), gastropods (*Assiminea bifasciata*, *Cerithidea* sp., *Littorina scabra*, *Nassarius kraussianus*), burrowing prawn (*Upogebia* sp.), crabs (*Sesarma catenata*, *S. meinerti*, *Uca annulipes*, *U. chlorophthalmus*, *U. urvillei*)	*Avicennia marina*, *Bruguiera gymnorrhiza*, *Rhizophora mucronata*	Branch & Grindley 1979
Santa Caterina Island, Brazil (27°29′S)	17	≤7250 m^{-2}	Oligochaetes (especially tubificids and enchytraids) and capitellid polychaetes 82% of the total macrofauna; also other polychaetes (*Laeoneries acuta*, *Polydora socialis*, *P. websteri*, *Typsyllis* sp., *Sigambra grubii*), crabs (*Uca thayeri*, *Cyrtograpsus altimanus*), tanaid (*Tanais stanfordi*), ostracods, insect larvae; no bivalves or other filter-feeders	*Avicennia schaueriana*, *Laguncularia racemosa*, *Rhizophora mangle*	Netto & Gallucci 2003
Bermuda (32°N)			Anthozoa (*Aiptasia pallida*), Scyphozoa (*Cassiopea xamachana*), polychaetes (*Arenicola cristata*, spirorbids, sabellids), gastropods (*Batillaria minima*, *Cerithium lutosum*, *Littorina angulifera*, *Melampus coffeus*, *Mitrella ocellata*), isopod (*Ligia baudiniana*), crabs (*Pachygrapsus gracilis*, *Gecarcinus lateralis*, *Goniopsis cruentata*)	*Avicennia germinans*, *Conocarpus erectus*, *Rhizophora mangle*	Thomas & Logan 1992, Thomas 1993

Note: Numbers of taxa and individuals are shown if available, and the mangrove species present are also noted. SE = standard error.

near Sydney (Table 6; Dakin 1966). The commercially harvested portunid crab *Scylla serrata* also occurs in temperate mangroves (Hutchings & Recher 1974), as far south as the Bega River, New South Wales (36°43′; New South Wales Department of Primary Industries 2009). Characteristic, and often very abundant, mangrove gastropods include the potamidids *Pyrazus ebeninus* and *Velacumantus australis* and the amphibolid pulmonates *Salinator* spp. (another amphibolid, *Amphibola crenata*, is a characteristic member of the mangrove fauna in New Zealand). Less-abundant taxa include sipunculids, echiurids, acarids and dipteran larvae.

Bermuda The mangrove fauna of Bermuda includes about 150 macrofaunal species but is characterised by large variation in species composition among locations around the island (Thomas 1993). Of the 150 species, 73 species were found at only a single location, and only 4 species were found at more than 50% of locations. There were no obvious differences in opportunity for colonisation by macrofauna among stands, and Thomas concluded that variation in macrofaunal composition was likely to be a consequence of effects of environmental factors on settlement, mortality and growth. The most widely distributed benthic species were the gastropods *Cerithium lutosum* and *Mitrella ocelata*, the isopod *Ligia baudiniana* and the grapsid crabs *Goniopsis cruentata* and *Pachygrapsus gracilis* (Table 6). The giant land crab *Cardisoma guanhumi* constructs burrows at the landward edge of some Bermudan mangrove stands, and the land hermit crab *Ceonobita clypeatus* also occurs in this zone (Thomas & Logan 1992).

Japan There appears to be little published information on the fauna of temperate mangroves in Japan. Wakamatsu & Tomiyama (2000) described seasonal variation in the distribution of the detritivorous gastropods *Batillaria multiformis*, *Cerithideopsilla djadjariensis*, *C. cingulata* and *Cerithidea rhizophoranum* in mangroves at a study site in the southern part of the island of Kyushu (31°S).

New Zealand A number of studies have been undertaken on the benthic assemblages and species of mangrove forests in New Zealand (Table 6). Taylor (1983) gave a qualitative description of the fauna of mangrove forests in Whangateau Harbour (36°18′S), a relatively pristine embayment north of Auckland. Burrowing animals were rare, apart from the grapsid crab *Helice crassa*. The pulmonate mud snail *Amphibola crenata* was common, along with the gastropods *Diloma subrostrata*, *Zeacumantus lutulentus* and *Z. subcarinatus*. The main predatory species was the whelk *Cominella glandiformis*, feeding on crabs, *Amphibola crenata* and polychaetes.

Ellis et al. (2004) recorded a benthic community at upper-shore mangrove sites in the Whitford embayment (east of Auckland: 36°55′S) dominated by corophiid and paracalliopiid amphipods, oligochaetes and the crabs *Halicarcinus whitei* and *Helice crassa*. Sites closest to intertidal sandflats were differentiated by the limpet *Notoacmea helmsi*; several bivalve species, including *Paphies australis*, *Macomona liliana*, *Austrovenus stutchburyi*, and *Nucula hartvigiana*; and the isopod *Exosphaeroma chilensis*. Subsurface deposit-feeders dominated the benthic community in the mangrove habitats, primarily polychaetes (*Scoloplos cylindrifer*, *Heteromastus filiformis* and other capitellids), oligochaetes and *Helice crassa*. The average number of species per sample was 8.13 in the mangroves and 9.1 in adjacent tidal mudflats.

Morrisey et al. (2003) investigated the effect of mangrove stand age (young 3–12 yr, and old > 60 yr) on associated benthic assemblages at two locations within the Manukau Harbour (on Auckland's western coast: 37°01′S). The overall number of species was generally higher at the younger sites, along with higher numbers of the copepod *Hemicyclops* sp., oligochaetes and *Capitella capitata*. However, the total number of individuals did not differ between the mangrove stands of different ages, largely due to the presence of large numbers of the surface-dwelling gastropod *Potamopyrgus antipodarum* at older sites. The main benthic species found under the mangrove forest were the crab *Helice crassa*, *Hemicyclops* sp., *Potamopyrgus antipodarum*, bivalve spat, oligochaetes and the polychaetes *Nicon aesturiensis*, *Scolecolepides benhami*, and *Capitella capitata*. All taxa varied in their abundance at smaller spatial scales (among sites and plots) apart from bivalve spat and *Helice crassa*, which did not vary at any of the scales examined.

Alfaro (2006) sampled six distinct habitats in Matapouri Estuary (35°34′S), eastern Northland: mangrove stands, the pneumatophore zone, patches of seagrass, channels, banks and sandflats. Each contained distinctive faunal assemblages, with seagrass patches having the highest combined abundance and species diversity per unit area and mangrove forests the lowest. The mangrove fauna contained low numbers of the cockle *Austrovenus stutchburyi*, a variety of deposit-feeding annelid worms, very few crabs, and no shrimps or amphipods. In contrast with the locations sampled by Morrisey et al. (2003) and Ellis et al. (2004), no mud snails (*Amphibola crenata*) or *Potamopyrgus antipodarum* were collected, being found only in saltmarsh areas of the estuary (outside the study area). *Helice crassa* was present in very low densities in mangroves but was common in seagrass. Large volumes of drift brown alga (Neptune's necklace, *Hormosira banksii*) were trapped in the pneumatophore zone, supporting an assemblage of the grazing gastropod snails *Turbo smaragdus*, *Diloma subrostrata* and *Melagraphia aethiops.*

South Africa The fauna of temperate mangroves in South Africa, like those of Australia and New Zealand, is characterised by polychaetes, gastropod molluscs and decapod crustaceans and is distinctly different from other estuarine habitats (Macnae 1963, Branch & Grindley 1979; Table 6). Although no species occur only in mangroves, several species, such as the crab *Sesarma guttata* and the snails *Cerithidea decollata* and *Pyrazus palustris*, are often only abundant in mangroves (Macnae 1963, Branch & Grindley 1979). These temperate mangrove faunas show stronger affinities with those of lower-latitude, subtropical estuaries than with those further south (Branch & Grindley 1979). In the case of the mangrove fauna of the Mngazana River estuary (31°50′S), 62% of the species extend northwards but not southwards.

Sesarmid crabs are a particularly conspicuous part of the mangrove fauna, and Macnae (1963) recorded four species in mangroves in Richards Bay (28°50′S), together with two species of xanthids, two species of grapsids, six species of ocypodids (including four species of fiddler crabs, genus *Uca*), the portunid *Scylla serrata*, the land crab *Cardisoma carnifex* and three species of hermit crabs. Further south, in the Mngazana Estuary, Branch and Grindley (1979) found two species of sesarmids and three of ocypodids (species of *Uca*, apparently more abundant on the fringe of the mangroves, creek banks and the lower edge of salt marshes; Branch & Grindley 1979). In the Mngazana Estuary, *Sesarma catenata* and *Uca* spp. occur in very large numbers on the mud surface at low tide but retreat to their burrows at high tide.

Other components of the benthic fauna of South African mangroves include alpheid and callianassid prawns; rissoid, potamid and cerithid gastropods; nereid, orbiniid and eunicid polychaetes; and the holothurian *Holothuria parva* (Macnae 1963, Branch & Grindley 1979). Branch & Grindley recorded several species of polychaetes and gastropods from transects through mangrove stands in the Mngazana Estuary, but in an earlier study of the same estuary Macnae reported no polychaetes or molluscs in sediments among the mangroves. This suggests that faunal distributions can be spatially or temporally very variable. The rissoid *Assiminea bifasciata* may occur in very large abundances and is preyed on by fish and mud crabs (*Scylla serrata*) (Branch & Grindley 1979).

United States No specific information on the fauna of Louisiana mangroves could be found.

Summary The benthic invertebrate fauna of temperate mangrove forests often appear to be modest in both abundances and species diversity compared with other nearby estuarine habitats. Differences between assemblages from mangroves and adjacent unvegetated sediments are generally identifiable as differences in relative abundance of a largely common suite of species rather than differences in species composition (Morrisey et al. 2003, Alfaro 2006). In Australia, observed lower densities and biodiversity of macrofauna within mangroves relative to other habitats has been attributed (in a tropical context) to the high proportion of tannins from mangrove detritus and mud associated with mangrove habitats (Alongi & Christoffersen 1992, Lee 1999, Alongi et al. 2000). Another contributing factor in older mangrove stands may be the effect of the compacted nature of the sediment on infaunal diversity and abundance.

In general, the fauna is characterised by surface-living detritivorous and predatory gastropods, burrowing crabs, alpheid and callianassid prawns and small crustaceans (such as cumaceans, tanaids, isopods and amphipods). The infauna includes oligochaetes and polychaete worms, but infaunal bivalves are generally absent in mature areas of mangrove stands, presumably because of the compacted nature of the sediment. There is no evidence for a distinct mangrove fauna in any of the other regions considered in this review (Macnae 1963, Butler et al. 1977a, Alfaro 2006). Butler et al. (1977a) noted that even the species occurring most commonly in South Australian mangroves (such as the burrowing crab *Helograpsus haswellianus* and the gastropod *Bembicium auratum*) were rare or absent at some sites, and none was found exclusively in mangroves.

There was spatial variability in taxonomic composition among different locations even within a relatively limited area such as northern New Zealand. For example, Alfaro (2006), working in a small, less-impacted estuarine system (Matapouri Estuary, northern New Zealand), did not record mudsnails (*Amphibola crenata*) or gastropods (*Potamopyrgus antipodarum*) from her mangrove sites and only very low abundances of the crab *Helice crassa*, in contrast to most other New Zealand mangrove forests studied to date. She also recorded an assemblage of the grazing gastropod snails *Turbo smaragdus*, *Diloma subrostrata* and *Melagraphia aethiops*, as did Taylor (1983), working in Whangateau Harbour (another less-impacted system). These species were rare or absent from other mangrove systems that have been sampled in New Zealand (e.g., Morrisey et al. 2003, Ellis et al. 2004). Chapman & Tolhurst (2004) found that variation in faunal diversity and abundances among habitats (open mudflats, shaded and unshaded areas within mangrove stands) was generally small and less than that among sites 10–30 m apart and bays about 2 km apart within each habitat. Again, these observations emphasise the often relatively large variation in diversity among mangrove stands at small or regional scales compared with differences between mangroves and other estuarine habitats.

The ecology of benthic macrofauna in temperate mangroves

Zonation Mangroves occupy the area of the shore roughly between MSL and mean high water. The fauna of mangrove stands often shows broad patterns of zonation within this tidal range, as they do on other types of shore.

Kaly (1988) examined spatial patterns of distribution of gastropods within mangroves near Sydney. Species found in the upper parts of mangrove forests, such as *Assiminea tasmanica*, *Ophicardelus* sp. and *Salinator solida*, were also found in adjacent salt marshes (Morrisey 1995). Other species (*Bembicium auratum*, *Pyrazus ebeninus* and *Velacumantus australis*) generally occurred in seaward parts of mangrove stands, but *Salinator fragile*, in contrast, occurred throughout the stands. There was overlap in the ranges of tidal height of many of these species and variation in patterns of distribution among different locations. Transplant experiments showed that several species were capable of surviving in other areas of the mangrove stand than those in which they normally occurred (Kaly 1988). Manipulative experiments also indicated that pneumatophores or the algae growing on them were important habitat-components for *Assiminea tasmanica*, *A. solida* and *Ophicardelus*.

In the same region as Kaly's study, the ocypodid *Heloecius cordiformis* did not show clear patterns of distribution with shore height within the mangroves, but was always associated with mounds of well-drained sediment (Warren 1987). Individuals higher on the shore tended to be larger than those in more seaward parts of the forest. *Heloecius cordiformis* hibernated in its burrows during winter (June–September). *Paragrapsus laevis* was generally more abundant in lower parts of the forest and tended to live in burrows in moist or submerged flat areas rather than mounds. A third species, *Parasesarma* (*Sesarma*) *erythrodactyla*, was evenly distributed across tidal heights and between mounds and flat areas. This species has also been observed climbing mangrove trees in South Australia (S. Dittmann personal observation).

In the *Kandelia candel* forests in the Atago River estuary, Kyushu, Japan, the cerithid gastropod *Cerithideopsilla rhizophorarum* showed greater tolerance of desiccation than three other, co-occurring members of the same family. Adults of *C. rhizophorarum* occurred at higher tidal levels than those of the other species. Juveniles of all four species, however, were limited to lower tidal levels in the forest. The ability of *C. rhizophorarum* to tolerate desiccation allows it to climb up and hibernate on the trunks of mangrove trees during winter.

Macnae (1963) described zonation of fauna in the Mngazana Estuary in South Africa, from the lower boundary of the mangrove at the level of neap high tides (occupied by a fringe of *Avicennia marina*), through the *Bruguiera gymnorrhiza* thickets further up the shore, a higher band of *Avicennia marina* to the salt marsh in the upper shore. *Sesarma catenata* is the dominant crab from the lower salt marsh downshore to the lowermost *Avicennia marina* pneumatophore zone. *Sesarma meinerti* was also present throughout the mangrove forest but was most abundant at higher levels and in the mangrove fringes. The fiddler crabs *Uca chlorophthalmus* and *U. urvillei* occurred in the salt marsh but only rarely extended in the mangrove thickets.

Animal–habitat relationships Faunal distribution patterns reflect environmental factors other than, or in combination with, tidal height. Chapman & Tolhurst (2004), working on an urbanised mangrove forest in Sydney Harbour, attempted to relate the invertebrate assemblages that were present to the properties of the sediments. Across three habitats, the benthos showed less variation among mangrove patches with and without leaf litter or mudflats adjacent to mangrove patches than within and among sites in each habitat type. In contrast, biodependent properties of the sediment (water content, water-soluble fraction of carbohydrates, total carbohydrate, chlorophylls *a* and *b*) showed less variation at small scales than among habitats. For the faunal assemblage as a whole, and for all individual taxa examined, most (50–100%) of the variation was at the scale of metres within each habitat. This variation could not be fully explained by tidal inundation, amounts of leaf litter or macroalgal cover. There was no clear correlation between variation in the benthos and variation in the sediment properties at any of the spatial scales. The strongest correlate, albeit still weak (Spearman rank correlation coefficient = −0.10) was chlorophyll *a* concentration.

Chapman & Tolhurst (2007) expanded the approach taken in their earlier work (Chapman & Tolhurst 2004) across three bays in the same system. They found that those sediment properties that contributed most to the differences among habitats, and those that best correlated with the benthos, differed among bays. The single taxon that best correlated with the sediment was spionid polychaetes, but such correlations were generally weak. It was concluded that all spatial scales contributed to variability; that there was little predictability from the patterns shown in one habitat to those in other habitats, or from one component of the sediment to other components; and that such variability suggested structural redundancy in the fauna (i.e., different components of the benthos contributed similar functions in different places). Sediment-related variables showed weaker patterns relating to habitats than the fauna, indicating that the suite of measured, sediment-related variables had failed to capture important environmental differences among sites (Tolhurst & Chapman 2007).

Other environmental variables, however, did appear to influence faunal distribution, and manipulative experiments showed that abundances of the gastropods *Ophicardelus* spp. and *Salinator solida* decreased rapidly in plots where the amount of leaf litter had been reduced (Chapman et al. 2005). Experimental reduction of the heights of pneumatophores did not affect abundances of snails. Responses to manipulations of the amount of macroalgae were inconsistent between two sets of experiments at different times and locations, with no response in one case and reduced densities of both species of snails in the other.

Biogenic structures (including the mangroves themselves; see p. 79) can be important components of the benthic habitat within mangrove forests. In mangroves in south-eastern Australia, abundances of the dominant gastropod *Bembicium auratum* vary with height above low water and are more abundant on oysters (*Crassostrea commercialis*) than other substrata (Underwood & Barrett 1990). Abundances are highest at lower levels of the shore, where oysters are naturally present, and the proportion of small individuals in the population is also highest here. Caging experiments (Branch & Branch 1980) demonstrated that increased population density of *Bembicium auratum* resulted in increased mortality (particularly of juveniles) and reduced growth and food availability (measured as chlorophyll concentrations in the sediment). Growth and mortality (particularly of juveniles) were also reduced in snails caged without access to hard substrata. Branch & Branch (1980) suggested that the observed decline in abundance but increase in body size of *B. auratum* with height on the shore was a result of higher settlement or survival of juveniles on the lower shore, where oysters provide hard substrata. As they grow, individuals become less dependent on hard substrata and may disperse up the shore. The density-dependent relationship between growth or mortality and the availability of food was interpreted as evidence that population density is restricted by intraspecific competition for food, and that predation is unlikely to be important.

This interpretation was disputed by Underwood & Barrett (1990), who found no correlation between the distribution of chlorophyll and that of *B. auratum* and argued that the density-dependent relationship between growth and chlorophyll standing stock could not be interpreted as evidence that population size is limited by availability of food without information on microalgal productivity. Using manipulative experiments, they demonstrated that removal of oysters from areas where they occurred naturally resulted in a rapid decrease in density and mean size of *B. auratum*. More snails, particularly juveniles, emigrated or disappeared from plots without oysters. Conversely, when oysters and snails were transplanted to areas higher up the shore, more snails remained in plots with oysters than in those without; again, the effect was more obvious among juvenile snails. Underwood & Barrett (1990) concluded that the role played by oysters in the distribution, abundance and size of *B. auratum* is a consequence of provision of refuges from predation by crabs or fishes during high tide, although they emphasised that further experimentation is required to support this conclusion.

Oysters also provide a habitat for the limpet *Patelloida mimula* in mangrove forests in south-eastern Australia, and limpets are generally only found on oysters (Minchinton & Ross 1999). Most (98%) oysters with limpets living on them have only one limpet, and >70% of limpets returned to the same scar on their host oyster when tracked for 13 days. Although the distribution of oysters in the mangrove forest sets the limits of distribution of limpets, the abundance of limpets is not directly related to the abundance of oyster habitat present. Oyster abundance decreases with tidal height, both across the shore and with position on the trunks of trees, but this is not reflected in the abundances of limpets.

Warren (1987) experimentally investigated the roles of habitat selection and interspecific interactions in partitioning of mangrove habitat between the crabs *Heloecius cordiformis* (found on well-drained mounds of sediment), *Paragrapsus laevis* (usually found in wetter flats between mounds) and *Parasesarma erythrodactyla* (found equally in flats and mounds). The presence of other species in experimental enclosures had little effect on the habitat a species colonised. Topography and the type of sediment, on the other hand, did influence habitat selection. *Heloecius cordiformis* would colonise artificial mounds if these were composed of sediment obtained from mounds but not from flats. *Paragrapsus laevis* and *P. erythrodactyla* would colonise mounds or flats if artificial burrows were provided but *Heloecius cordiformis* preferred mounds to flats provided with artificial burrows. There was also evidence that *H. cordiformis* was itself at least partly responsible for the presence of hummocky topography, and that by burrowing through the finer surficial sediments into the underlying coarser material, it also made the texture of mound sediments coarser (Warren & Underwood 1986).

Most activities performed by these crabs took place at or near burrow entrances, although collection of mud balls (which were then brought to the burrow to be sifted for food) and courtship took place away from the entrance (at the entrance to a female's burrow in the case of courtship). All three species were active on the surface during daytime low tides, but *Paragrapsus laevis* and *P. erythrodactyla* were also active at night. Burrows played a significant role in reducing mortality from predation by fishes during high tide (Warren 1990).

In South Australian mangroves, field experiments with the crab *Helograpsus haswellianus* showed that crabs ceased digging new burrows in response to experimentally increased population density when the density of burrows reached a critical level (McKillup & Butler 1979). Collapse of the sediment surface occurred when burrow density exceeded this critical value, as determined by experimental manipulations. When the density of crabs exceeded that of holes, crabs entered holes that were already occupied rather than digging new ones, and after a few minutes either the original or new occupant was evicted and entered another hole. McKillup and Butler suggested that, as population density increases, more crabs are exposed to predation as they move from burrow to burrow, and density is reduced back towards the carrying capacity of the sediment. Along tidal channels in South Australian mangroves, burrowing by polychaetes gives rise to mound-covered terraces (Butler et al. 1977b).

Morrisey et al. (2003) investigated the effect of mangrove stand age (young 3–12 yr, and old > 60 yr) on associated benthic assemblages at two locations within the Manukau Harbour (on Auckland's western coast; 37°01′S). The overall number of species was generally higher at the younger sites, along with higher numbers of the copepod *Hemicyclops* sp., oligochaetes and *Capitella capitata*. However, the total number of individuals did not vary between the two ages, largely due to the presence of large numbers of the surface-dwelling gastropod *Potamopyrgus antipodarum* at older sites. All other taxa present varied in their abundance at smaller spatial scales (among sites and plots) apart from bivalve spat and *Helice crassa*, which did not vary at any of the scales examined. It was suggested that, as mangrove stands grow older, the abundance and diversity of the associated fauna shift towards animals living on the mangrove plants themselves (e.g., insects and spiders). This change would correlate with an increase in the size and structural complexity of the plants and perhaps a decrease in the quality of the benthic habitat as the sediment becomes more compacted and the interstitial water more saline and less oxygenated. However, the fauna on the mangrove plants themselves was not sampled.

Ellis et al. (2004) examined the effects of high sedimentation rates on mangrove plant communities and associated benthic community composition, including a comparison with adjacent tidal flats (the Whitford embayment, east of Auckland, New Zealand). Macrofaunal diversity and abundance within the mangrove habitats were lower than expected, and there were clear functional differences along a sedimentation gradient, with lower numbers of suspension-feeders, low macrobenthic diversity and a predominance of deposit-feeding polychaetes and oligochaetes in areas with higher sedimentation rates. All mangroves sites had lower abundance and diversity than nearby sandflats, but heavily sedimented mudflats without mangroves were similar in their benthic composition to mangrove sites. They suggested that this pattern was a response to the increased silt/clay fraction from sedimentation rather than to the presence or absence of the mangroves themselves.

Ellis et al. (2004) concluded that high sediment mud content and rates of deposition were possibly more important than the presence or absence of mangroves in terms of reducing faunal diversity and abundance. Alfaro (2006) also suggested that lower temperatures and lower tidal inundations in New Zealand coastal areas might result in slower organic matter decomposition rates compared with tropical and subtropical mangrove ecosystems, causing reduced productivities. The absence of large crabs from New Zealand mangrove forests, considered to be important sediment bioturbators and consumers of mangrove leaves and detritus in tropical mangroves (Robertson & Daniel 1989, McIvor & Smith 1995, Slim et al. 1997), might also play a role. The dominant crab species in New Zealand mangroves, *H. crassa*, grows to a maximum of around 4 cm carapace length, which is relatively small when compared with tropical species (Alfaro 2006).

Encrusting and motile epifauna of mangrove trees

Introduction

The fauna of mangrove trees includes immobile, encrusting species and motile species that move around on the trees, either as permanent residents or transient visitors. There is also a fauna that bores into the tissues of mangrove trees and woody debris within the forest. Members of each component may derive from adjacent marine or terrestrial environments.

Encrusting marine invertebrates

In general, the encrusting fauna of mangroves is of relatively low diversity compared with that of many other intertidal hard substrata. This low diversity is partly a consequence of the nature of the available substratum, such as the likely inability of limpets to create home scars on mangrove bark (Minchinton & Ross 1999) but also of the general unsuitability of muddy, depositional coastal habitats for sessile organisms because of high suspended sediment loads. In more open coastal situations, the encrusting fauna can be relatively diverse, as in some mangrove stands in Bermuda (see p. 80).

The most common encrusting organisms in temperate mangroves are oysters, mussels, tube-dwelling polychaetes and barnacles, of which barnacles are the most studied. In New Zealand mangroves, rock oysters (*Crassostrea glomerata*) and the introduced Pacific oyster (*Saccostrea glomerata*) are found attached to trunks and pneumatophores; barnacles (*Elminius modestus*) are also characteristic of pneumatophores, trunks and leaves (Taylor 1983). Oysters (*Crassostrea commercialis*) are also common on the trunks and pneumatophores of mangroves in southern Australia (Branch & Branch 1980).

Ross & Underwood (1997) described the distribution and abundance of three barnacle species (*Elminius covertus*, *Hexaminius popeiana* and *H. foliorum*) in *Avicennia marina* forests near Sydney. *Elminius covertus* was more abundant on bark than on leaves or twigs. *Hexaminius popeiana* was only found on bark, whereas *H. foliorum* was most abundant on twigs and did not occur on bark. Densities of all species were higher in seaward parts of the forest than in landward parts, and *H. popeiana* was virtually absent in landward parts. In seaward parts of the forest, barnacles were most abundant at midtidal levels on trunks and more abundant on the lower than upper surfaces of leaves. These patterns of distribution arise primarily from patterns of larval settlement, with subsequent mortality of juveniles and adults modifying density but not distribution (Ross 2001). Cyprid larvae of *Elminius covertus* are most abundant in winter, coinciding with relatively large night-time tides, giving them greater access to landward parts of the forest than the larvae of *Hexaminius popeiana*, which are most abundant in spring and summer. Cyprid abundances are stratified in the water column (Ross 2001), so that variation in density of settling larvae with tidal height is a function of larval abundance at that height and the time available for settlement (which also varies with height).

Two other species of barnacle, *Balanus amphitrite* and *Elminius adelaidae*, occur in *Avicennia marina* forests in South Australia and are present in aggregations on pneumatophores, occurring on some pneumatophores but not others and present in aggregations on those pneumatophores where they do occur (Bayliss 1993). Manipulative experiments with modified pneumatophores demonstrated that cyprids of both species preferred to settle on pneumatophores bearing adults of their own species. Adults of the other species, and juveniles of *E. adelaidae*, did not attract settlers. Aggregations of barnacles may also attract their predators. In Bayliss's study area, large numbers of predatory gastropods, *Bedeva paivae*, occasionally migrate from adjacent mudflats into the seaward part of the mangrove forest and feed on clusters of barnacles on pneumatophores, sometimes eliminating the whole cluster. These aggregations of *B. paivae* are, however, infrequent. The whelk *Lepsiella vinosa* is a more consistent predator on the barnacles but does not form feeding aggregations and rarely consumes all of the barnacles on a pneumatophore (Bayliss 1982).

Poor survival and growth of mangrove seedlings are common in natural and replanted populations of mangroves (e.g., Clarke & Myerscough 1993, Osunkoya & Creese 1997), and this effect has been attributed to the presence of large numbers of fouling organisms, particularly barnacles (e.g., Macnae 1968). Satumanatpan & Keough (1999) found, however, that survival of seedlings of *Avicennia marina* in Westernport, Victoria, Australia, was not influenced by the presence of barnacles on the stems or the upper or lower surfaces of leaves over a 2-yr period following experimental manipulations of barnacle abundances. There was no significant effect on growth. They suggested that other factors were more important, including algal or seagrass cover, smothering by sediments, damage by herbivores and climatic conditions.

In addition to fringing, coastal mangrove stands, Bermuda contains hundreds of landlocked marine ponds, most of which are connected to the sea via underground tunnels and caves (Thomas & Logan 1992). The mangroves in these 'anchialine' ponds have a rich biota compared with other stands on the island. The prop roots of *Rhizophora mangle* and the pneumatophores of *Avicennia germinans* contain some of the richest faunas in the ponds (Thomas & Logan 1992). The fauna also display variation with tidal height, often with a shallow (10 cm below mean low-tide level in the pond) zone of relatively low diversity and a deeper, more diverse assemblage.

Roots in the intertidal zone generally contain spirorbid polychaetes, cyanobacteria and green and red algae (the last of these are largely *Bostrychia montagnei*, which is only found on mangrove roots). Roots in the shallow subtidal are characterised by bryozoans (usually *Bugula neritina*) and spirorbid and sabellid polychaetes. Diversity increases markedly in the deeper zone, but there is also considerable variation in the composition of this fauna among ponds. In some, the roots are dominated by oysters *Isognomon alatus*, which provide a substratum for encrusting sponges and the green alga *Cladophora* sp. Spaces among the oysters may be occupied by sponges (e.g., *Chondrila nucula* and *Terpios aurantiaca*), anemones (*Bartholomea annulata*), bryozoans (including *Schizoporella serialis*, *Bugula neritina* and *B. annulata*) and the solitary ascidian *Styela plicata*.

The ponds with the most diverse assemblages contain species that are rare or absent elsewhere on the island, including several sponges. Large, branching bryozoans (*Amathia vidovici* and *Zoobotryon verticillatum*) form extensive growths, and colonial and solitary ascidians are also abundant, together with the green alga *Caulerpa verticillata* and various anemones.

The high diversity of the fauna living on roots of mangroves in these ponds and the predominant role played by filter-feeders contrast strongly with the epifauna of mangroves in most sheltered coastal environments. It probably reflects the relatively stable temperature and salinity regimes of the ponds and perhaps the availability of suspended organic matter (Thomas & Logan 1992).

Motile marine invertebrates

The pneumatophores and trunks of mangroves in the Whangateau Harbour, New Zealand, are colonised by cyanobacteria and red algae, and the former included active nitrogen fixers (Taylor 1983). Living amongst these are isopods and amphipods. The main grazer at Taylor's study site was a gastropod, the cat's-eye *Turbo smaragdus*, and in the mangrove forest, populations of this species consisted of only large individuals. These animals were up to 45 mm long, with 90% of individuals over 30 mm. Taylor estimated these animals were around 25 yr old, with the nearest younger animals some 500 m away on a rocky shore. The mangrove population of *T. smaragdus* was described as either a relict population or a chance drift event from rafting on a tree trunk, although

T. smaragdus larvae are planktonic for about 12 h, so it would be possible for periodic recruitment to occur (K. Grange, NIWA, personal communication).

In south-eastern Australian mangrove forests, the gastropod *Littoraria luteola* is common on the trunks and branches of the trees. It is able to survive for long periods and occurs on parts of the trees well above the level of high water (Chapman & Underwood 1995). The coffee bean snail *Melampus coffeus* occupies the same habitat in Bermudan mangrove stands (Thomas & Logan 1992).

Several species of crabs in the families Grapsidae and Sesarmidae have evolved a tree-climbing habit in mangrove forests in various parts of the world, and this has apparently occurred on a number of independent occasions (Fratini et al. 2005). The extent of the arboreal habitat varies from species that live predominantly on the ground but also climb roots, through those that live mainly or exclusively on trunks, to those that live in the canopy, sometimes feeding on fresh leaves. The more specialist arboreal species, including the three known to feed on leaves (*Aratus pisonii* on the Atlantic and Pacific coasts of America, *Armases elegans* in West Africa, and *Parasesarma leptosoma* in the western Indo-Pacific), are largely tropical. *Parasesarma leptosoma* has, however, been discovered in the Mngazana Estuary (31°42′S) in South Africa (Emmerson & Ndenze 2007), where they were most abundant on *Rhizophora mucronata* (present on 92% of trees on which traps were deployed), less abundant on *Bruguiera gymnorrhiza* (38%) and absent on *Avicennia marina*. Abundance of crabs was also positively correlated with tree circumference.

Terrestrial invertebrates

The terrestrial invertebrate fauna of tropical mangroves can be abundant and diverse (Kathiresan & Bingham 2001). Common taxa include mites, termites, cockroaches, dragonflies, butterflies and moths, beetles, ants, bees, mosquitoes and spiders. Honey bees living in mangroves produce significant harvests of honey for humans in India, Bangladesh, the Caribbean and Florida. Wood-boring larvae of moths and beetles are common components of the fauna; their tunnels, in turn, provide accommodation for other species. More than 70 species of ants, spiders, mites, moths, cockroaches, termites and scorpions were found in tunnels bored in the wood of mangroves in Belize (see review by Kathiresan & Bingham 2001).

The terrestrial invertebrate fauna of temperate mangroves is poorly known but likely to be less diverse than those of tropical mangroves given the smaller numbers of species of trees and other habitat-related factors. Hutchings and Recher (1974) published a list of 57 taxa of insects and 18 of spiders from a survey of Careel Bay, near Sydney. The insects represented the orders Diptera, Lepidoptera and Hymenoptera, and many belonged to undescribed species. They also cited a study of another site near Sydney in which 35 species of spiders were recorded.

The diversity of spider assemblages in mangroves apparently increases sharply from temperate to tropical regions but, according to Hutchings & Recher (1982), derives from adjacent terrestrial habitats, and none is known to be endemic to mangroves. Orb-weaving species are certainly conspicuous in temperate mangroves (D. Morrisey personal observation), but Hutchings & Recher (1982) suggested that foliage-living species were relatively uncommon. The last observation may simply be a consequence of the lack of appropriate studies. Other species of spiders occur in the lowest vegetation of mangroves in south-eastern Australia or on the substratum among the trees, including wolf spiders (*Geolycosa* spp.) and members of the Pisauridae, such as *Dolomedes* spp. (Hutchings & Recher 1982). Butler et al. (1977b) recorded at least six species of spiders in South Australian mangroves.

In contrast to the marine fauna of mangroves, there appears to be some degree of dependence on mangroves among the terrestrial fauna. Burrows (2003) sampled insects from tropical mangroves at two sites near Townsville, northern Australia, and recorded 61 species, “more than doubling the number of insects recorded from Australian mangroves” and thereby illustrating the scant attention that this component of the mangrove fauna has received to date, even in a relatively thoroughly studied part of the distributional range of mangroves. Among the folivorous species, there was a high level of host specificity, particularly for *Avicennia marina* (largely because of the diversity of gall-forming species on this mangrove). By means of a literature review and by sampling insects on mangroves and adjacent terrestrial trees, Burrows (2003) contested the suggestion that mangroves (at least in this tropical region) do not have depauperate folivore faunas except, perhaps, in comparison to rainforests. Whether the same is true for other regions, including temperate ones, has not been investigated but is not unlikely given the prevalence of *Avicennia* species in temperate mangrove systems.

There are also examples of host specificity among temperate mangroves. Three species of moths, the tortricids *Ctenopseustis obliquana* and *Planotortrix avicenniae* (Cox 1977, Dugdale 1990), the pyralid *Ptyomaxia* sp. (J. Dugdale, Landcare Research, New Zealand [retired], personal communication) and an eriophyid mite, *Aceria avicenniae* (Lamb 1952), have been described from mangroves in New Zealand. *Aceria avicenniae* and the larvae of *Planotortrix avicenniae* are restricted to *Avicennia marina*, whereas *Ctenopseustis obliquana* is distributed throughout New Zealand, and its larvae are polyphagous (Dugdale 1990). All three moths have been collected in Waitemata Harbour, near Auckland, and *Planotortrix avicenniae* and *Ptyomaxia* sp. have been collected from Matakana Island, Tauranga Harbour (J. Dugdale personal communication) on the eastern coast of the central North Island, near the southern limit of mangroves in New Zealand.

The larvae of *Ptyomaxia* sp. cause distinctive distortion of the growing tips of the shoots, and *Aceria avicenniae* cause leaf galls. The larvae of *Ctenopseustis obliquana* cause damage to the leaves, fruit and buds of host plants, including horticultural crops, and presumably do the same to *Avicennia marina*. Young larvae live on the shoot tips or areas of new growth, binding the leaves together with silk and feeding on the inner surface of the leaf, whereas older larvae eat through the leaf (Horticulture and Food Research Institute of New Zealand Ltd. 1998a).

Meades et al. (2002) recorded 252 morphospecies from 13 orders of arthropods in mangrove stands surveyed twice at three locations (separated by kilometres or tens of kilometres) along the coast of southern New South Wales, Australia. Diptera was the most abundant (38% of the total numbers of individuals collected across all three sites) and most diverse (27% of species) order recorded. Contrary to expectations derived from a model of high spatial variability among mangrove patches as a result of natural or anthropogenic disturbance, there was no significant variation among locations in abundance or species composition of the terrestrial arthropod fauna. The results suggested that mangroves in the study area have a common suite of species, with most species occurring in all three locations. Species composition was, however, sometimes variable within a location. The findings were consistent with the hypothesis that the low diversity of mangrove tree species in a geographical region (particularly in temperate areas) contributes to the observed spatial homogeneity of their terrestrial fauna (Farnsworth 1998). The observations did not necessarily support the related hypothesis that low diversity of tree species results in low diversity of terrestrial invertebrates.

In south-eastern Australia, *Avicennia marina* acts as host plant for the larvae of the mangrove fruit fly *Euphranta marina*, which is consequently restricted to mangrove habitats (Hutchings & Recher 1974). The female fly lays its egg within the fruit while it is still on the tree, and the larva bores into and feeds on the developing cotyledons (Minchinton 2006 and references therein). When ready to pupate, the larva burrows to the surface of the fruit, makes an exit hole, but then pupates within the fruit, emerging later through the exit hole as an adult. Individual fruit contained up to six exit holes. In the same geographic region, mangrove fruit are also consumed by the mangrove plume moth *Cenoloba obliteralis*, whose larvae are restricted to the fruit and young shoots of *Avicennia marina* (Hutchings & Recher 1974). The eggs of this species are laid on the outside of the flower cluster or the surface of the fruit, into either of which the larvae burrow on hatching, to feed on the flower buds or cotyledons. The mature larvae leave their galleries within the host tissue to pupate within silk cocoons inside or outside the fruit. At Minchinton's (2006) study site near Sydney, flies and moths emerged from mangrove propagules after being transported tens of kilometres by water currents, potentially representing an important method of dispersal for the insects. Both species are also potential pollinators of mangroves (Minchinton 2006). In addition to fruit flies and plume moths, fruit of mangroves near Sydney contained larvae of other dipterans, lepidopterans and hymenopterans (Minchinton & Dalby-Ball 2001). Larvae of several taxa may occur in the same fruit.

Mosquitoes and biting midges have been studied in relative detail in mangroves generally because of their potential impacts on human health (Hutchings & Recher 1982). *Aedes vigilax* is the major vector of Ross River and Barmah Forest virus in coastal New South Wales. It lays its eggs around drying pools in salt marshes and mangroves, but the adults can disperse tens of kilometres (Department of Medical Entomology, University of Sydney, n.d.). *Aedes alternans* also occurs in estuarine habitats in south-eastern Australia. It is a nuisance to humans but is not known as a vector of disease, although the Ross River virus has been isolated from individuals collected from the southern coast of New South Wales. It breeds in stagnant pools and the larvae feed on larvae of other mosquitoes (Hutchings & Recher 1982).

Small numbers of chironomids and their larvae were collected from sediments among mangroves in Rangaunu and Mahurangi Harbours during a study of fish and their prey in mangrove habitats in several harbours in northern New Zealand (M. Lowe, NIWA, personal communication). Larvae of some tipulid flies feed on intertidal green algae and may exploit this food source that grows on the trunks and pneumatophores of mangroves (J. Dugdale personal communication). These animals, in turn, provide food for fishes and birds.

Ants play a potentially important role in tropical mangrove forests, including deterring herbivorous crabs and sap-feeding scale insects (reviewed by Cannicci et al. 2008), although evidence of long-term effects on the host trees is scarce. Although ants may also have adverse effects on mangroves trees, for example, by reducing longevity of leaves used to form their nests, their positive effects have been estimated to be 3–20 times larger (Cannicci et al. 2008). Ant colonies may establish within the tunnels in mangrove stems created by boring insects in New Zealand (J. Dugdale personal communication), and the ants may perhaps ‘farm’ the introduced scale insect *Ceroplastes sinensis*, which is also common on mangroves in New Zealand (Brejaart & Brownell 2004). Given their ecological importance in virtually every other terrestrial environment and their abundance and diversity in tropical mangroves (Hutchings & Recher 1982), it seems likely that ants play an ecologically important role in temperate mangroves. There has, however, been little work on them to date.

Animals that bore into mangrove tissues

Worldwide, a number of invertebrate taxa have been reported as burrowing into the living or dead woody tissues of mangroves (Hutchings & Recher 1982). Marine examples include teredinid molluscs (ship worms) and limnorid, sphaeromatid and chelurid isopods, while those from the terrestrial fauna include the larvae of various beetles, such as those of the cerambycid *Oemona hirta* (the lemon-tree borer) in New Zealand (J. Dugdale personal communication).

Fishes

Tropical mangrove systems are well documented as supporting diverse and abundant fish (and prawn) assemblages, including the juveniles of many commercially important species (e.g., Laegdsgaard & Johnson 1995, Vance et al. 1996, Nagelkerken et al. 2000, 2001). Their role as important or critical juvenile nurseries has also been well established, although debate continues regarding exactly how much of total production they contribute relative to alternative nursery habitats (Beck et al. 2001, Dalgren et al. 2006). These tropical mangrove assemblages are usually composed of multiple mangrove species, with very different growth forms and morphologies, including buttress roots. Some mangrove systems are also permanently inundated by water, allowing for continuous access by aquatic organisms (e.g., Curacao, Dutch Antilles, Nagelkerken et al. 2001; Florida, Ley et al.

1994). Until recently, these findings from subtropical and tropical mangroves (high fish abundance and diversity, important nursery role) were uncritically applied to temperate mangroves without any supporting quantitative investigations or data.

However, temperate mangrove systems differ from tropical systems in many ways, including lower mangrove species diversity, less structural complexity and smaller species pools of potentially associated organisms. Only since the year 2000 have scientific studies been directly conducted on fishes in temperate mangrove systems (with the notable exception of Bell et al. 1984). In a review of research on fishes in mangroves over the last 50 years (Faunce & Serafy 2006), only 1 (Bell et al. 1984) of the 111 papers assessed dealt with temperate mangroves. To the best of our knowledge, only one other study of fishes in temperate mangroves existed at that time, that of Clynick & Chapman (2002). Since then, a further 11 studies have been published (10 in temperate Australia, 1 in New Zealand).

As with subtropical and tropical mangrove systems, research on fishes in temperate mangroves has focused strongly on the role of mangroves as fish nurseries, with the types of sampling gear deliberately biased towards the quantification of juvenile or small fishes. More broadly speaking in terms of habitats, only recently have formal definitions been developed of what constitutes a nursery habitat. Beck et al. (2001) suggested that one or more of the following conditions need to be fulfilled for any given habitat to be considered a nursery habitat when contrasted with alternative habitats: (1) greater average densities of juvenile fishes, (2) lower predation rates, (3) higher growth rates or (4) greater than average contributions to adult populations. Of these aspects, most of the temperate mangrove studies have largely focused on condition 1, one study included tethering experiments to address condition 2 (for a fish species widespread across temperate Australasian mangroves), while no work has been done on condition 3. Aspect 4 has been indirectly addressed by Saintilan (2004), who examined commercial catch records (for a range of species) across 55 temperate estuaries along the coast of New South Wales, Australia, with varying proportions of different habitats (e.g., mangroves, seagrass, tidal flats, and deep mud basins). He found that the correlation of catch levels with the proportion of an estuary covered by mangroves was modest at best, and that indeed "as estuaries infill and the area of seagrass and mud basin declines [and mangroves increase], so too does the catch of species dependent upon these habitats".

Additional studies have assessed the relative importance of the proximity of mangroves to other habitats, whether there are artefacts from different fish-sampling methodologies in mangroves and, to a limited extent, connectivity with other adjacent habitats. Table 7 lists the various studies and the aspects that they addressed. Because there were relatively few studies of fish in temperate mangroves, each is briefly discussed individually in the following section.

Individual studies

Bell et al. (1984) sampled the fish assemblage in a temperate, tidal mangrove creek in Botany Bay, near Sydney, New South Wales, using the fish poison rotenone and associated blocking nets. They collected 46 species from 24 families. Six species dominated the assemblage (Table 7), contributing 84% of all individuals. Seasonal variations in abundance were driven largely by restricted recruitment periods of these species, representing young of the year. They suggested that four species (*Gerres ovatus*, the sparid *Acanthopagrus australis*, *Liza argentea* and *Girella tricuspidata*) were almost exclusively restricted to mangrove habitats, and as such these mangrove areas (or more correctly, the tidal creek) were important juvenile nursery areas. Reference was made to earlier studies in other habitats, although none was actually sampled as part of this study.

Clynick & Chapman (2002) sampled small mangrove stands around Sydney Harbour (New South Wales) and found little evidence of mangroves playing an important role as fish nurseries, with the possible exception of one goby species (transparent goby *Gobiopterus semivestitus*), which was more abundant (although highly variable) within the mangrove stands. Overall catches were

Table 7 Summary of information from studies of fish in temperate mangroves

Location	Mangrove species	Method	Design details	Dominant fish species	Reference
Botany Bay, New South Wales, Australia 34°1′S 151°11′E	*Avicennia marina*	Rotenone, block net, and hand-picking recovery	Lower reaches of tidal mangrove creek, sampled every second month between December 1977 and October 1980.	46 species (41 represented by the presence of juveniles), 26 families. Six dominant species: the glassfish *Velambassis jacksoniensis* (31.8%), parore/luderick (*Girella tricuspidata*) (18.6%), blue eye (*Pseudomugil signifer*) (11.5%), the fantail mullet (*Liza argentea*) (9.0%), the common toadfish (*Torquigener hamiltoni*) (6.8%), and the biddy (*Gerres ovatus*) (6.3%); another four relatively common: largemouth goby *Redigobius macrostomas* (2.9%), glass goby *Gobiopterus semivestitus* (2.8%), yellowfin bream *Acanthopagrus australis* (2.4%), exquisite goby *Favonigobius exquisitus* (2.2%)	Bell et al. (1984)
Sydney Harbour, Australia	*Avicennia marina*	Fyke nets 3-m wings, 1 m tall, 1-mm mesh	Initial day/night test, then day sampling only, 4 h each side of high tide.	17 species, 10 families (mangrove and mudflat samples combined)	
33°49′S to 33°51′S 151°7′E to 151°119′E			Four sites, at each 2 mangrove and 2 mudflat sites (within 50 m of forest), gang of 5 nets at each. Each bay sampled twice. May–June 1999.	Dominated by Gobiidae (*Gobiopterus semivestitus,* >90% abundance); juveniles of five commercially important species (*Gerres subfasciatus*, *Mugil cephalus*, *Liza argentea*, *Myxus elongatus*, and one of two species of Sparidae (bream and tarwhine) extremely small, so not identified; numbers of individuals by species not presented by authors	Clynick & Chapman 2002

(continued on next page)

Table 7 (continued) Summary of information from studies of fish in temperate mangroves

Location	Mangrove species	Method	Design details	Dominant fish species	Reference
Westernport, and Corner Inlet, Victoria, Australia 38°30′ S to 38°50′S 145°30′E to 146°30′E	*Avicennia marina*	Gill nets 1.5 m deep × 30 m long, five panels of different mesh sizes Fyke nets Square bag 70 × 70 cm, wings 10 m long by 70 cm deep; 6-mm mesh; beach seine 10 m × 2 m × 1 mm	Three sites within each of two embayments quarterly Four replicates of gill and fyke in each habitat, 1–2 h before high tide; 3 replicate beach-seine tows adjacent to mangroves at high tide. January 2002–November 2002	41 species (30 in mangroves), 18 of commercial/recreational importance All methods combined by authors for species numbers: silver fish *Leptatherina presbyteroides* (48.6%), sandy sprat *Hyperlophus vittatus* (14.7%), yellow-eyed mullet *Aldrichetta forsteri* (14.5%), smooth toadfish *Tetractenos glaber* (10.8%), blue spot goby *Pseudogobius olorum* (3.7%), glass goby *Gobiopterus semivestitus* (2.4%)	Hindell & Jenkins 2004
Barwon River, Victoria, Australia 38°16′S 144°30′E	*Avicennia marina*	Gill nets 1.5 m deep × 30 m long, five panels of different mesh sizes Fyke nets Square bag 70 × 70 cm, wings 10 m long × 70 cm deep; 6-mm mesh; beach seine 10 m × 2 m × 1 mm Pop nets 25-m^2 area, 1.2 m high, 1-mm mesh	Both day and night sampling on 5 occasions in 3 mangrove zones (forest, pneumatophore, channel) with 2 fyke and 2 gill nets in each zone. Day sampling on 5 occasions to compare fyke and pop nets, 1 of each type of net in each of forest and pneumatophore zones. September 2003–April 2004	20 species, 15 families Across all zones: Australian salmon *Arripis truttacea* and yellow-eyed mullet *Aldrichetta forsteri* represented 63% of catch Channel, day: *Arripis truttacea* 39.8%, *Favonigobius tamarensis* 15.5%, *Aldrichetta fosteri* 25.6%, total no. fish 246 Channel, night: *Arripis truttacea* 39.4%, *Aldrichetta fosteri* 25.1%, total no. fish 203 Pneumatophore, day: *Galaxias maculatus* 30.0%, *Aldrichetta fosteri* 36.0%, *Tetractenos glaber* 20.0%, total no. fish 50 Pneumatophore, night: *Arripis truttacea* 33.5%, *Aldrichetta fosteri* 33.5%, total no. fish 170 Forest, day: *Tetractenos glaber* 50.0%, total no. fish 4 Forest, night: *Aldrichetta fosteri* 65.0%, total no. fish 20	Smith & Hindell 2005

Port Phillip Bay, Victoria, Australia 38°07′S 144°38′E	*Avicennia marina*	Pop nets 25-m^2 area, 1.2 m high, 1-mm mesh	Three mangrove zones (forest, edge, mudflat). Sampled on 7 occasions, between October 2003 and January 2004.	15 species (8 in mangroves, 14 on edge), 7 families Forest and edge combined: blue spot goby *Pseudogobius olorum* (59.9%), *Atherinosoma microstoma* (10.9%), half-bridled goby *Areniogobius frenatus* (10.4%), smooth toadfish *Tetractenos glaber* (5.6%), mangrove goby *Mugilogobius paludis* (4.8%), *Favonigobius lateralis* (3.4%)	Hindell & Jenkins 2005
Torrens Island and Barker Inlet, Port River Estuary, Adelaide, South Australia 34°49′S 138°30′E	*Avicennia marina*	Pop nets 9-m^2 area, 1-mm mesh (Also seine nets [non-vegetated and seagrass habitats only])	Mangroves, seagrass and non-vegetated areas sampled by pop nets, 2 replicate samples from each habitat taken on each of 3 consecutive days. Monthly sampling from May to August and December to February.	19 species sampled by pop-net (10 in mangroves) *Atherinosoma microstoma* (44.5%), unidentified athernid larvae (37.9%), yellow-eyed mullet *Aldrichetta forsteri* (13.3%), *Sillaginodes punctata* (2.3%), *Favonigobius lateralis* (1.2%)	Bloomfield & Gillanders 2005
Towra Point, Botany Bay, New South Wales 34°1′S 151°10′E	*Avicennia marina*	Pop nets 5.5-m^2 area, 1.5 m high in mangroves and salt marsh	Four replicate nets in each. Sampled monthly from March 2001 to February 2002.	26 species (25 in mangroves), 12 of 25 species of commercial importance Glassfish *Ambassis jacksoniensis* (27.3%), mangrove goby *Mugilogobius paludis* (19.5%), silver biddy *Gerres subfasciatus* (10.1%), and snakehead goby *Taenioides mordax* (6.5%)	Mazumder et al. 2005
Bicentennial Park, Sydney Towra Point, Allens Creek, Botany Bay, New South Wales 34° 1′ S to 34°50′S 151°10′E	*Avicennia marina*	Fyke nets 4 m long funnel-shaped fyke net, one central and two lateral wings, 40 cm wide and 25 cm high entrance; 2-mm mesh size	Four replicate fyke nets in the salt marsh, 2 replicate fyke nets from mangroves. Set before tides flooded habitats; retrieved after tide had fully receded. Fish collected during December 2001, January and August 2002 during spring high tides.	21 species (19 in mangroves), 10 families (8 in mangroves) Mangroves: glassfish *Ambassis jacksonensis* (34.7%), blue spot goby *Pseudogobius olorum* (18.1%), silver biddy *Gerres subfasciatus* (11.3%), glass goby *Gobiopterus semivestitus* (7.3%), blue eye *Pseudomugil signafer* (5.6%), mosquito fish *Gambusia holbrooki* (4.7%), mangrove goby *Mugilogobius paludis* (3.8%), yellowfin bream *Acanthopagrus australis* (2.5%), checkered mangrove goby (*Mugilogobius stigmaticus*) (2.5%)	Mazumder et al. 2006

(continued on next page)

Table 7 (continued) Summary of information from studies of fish in temperate mangroves

Location	Mangrove species	Method	Design details	Dominant fish species	Reference
Towra Point, Botany Bay, New South Wales 34°1′S 151°10′E	*Avicennia marina*, patches of *Aegiceras corniculatum* to landward	Pop nets 5.5-m^2 area, 1.5 m high in mangroves and salt marsh, 2 m high in seagrass, 0.6-mm mesh	Three nets per habitat. Monthly sampling of mangroves and salt marsh during spring tides, fortnightly of seagrass during both spring and neap tides.	28 species (24 in mangroves) Dominated by glassfish *Ambassis jacksoniensis* (28%), mangrove goby *Mugilogobius paludis* (20%), silver biddy *Gerres subfasciatus* (10.4%), snakehead goby *Taenioides mordax* (6.7%), yellowfin bream *Rhabdosargus sarba* (5.7%), checkered mangrove goby *Mugilogobius stigmaticus* (5.6%), blue spot goby *Pseudogobius olorum* (4.5%), flat tail mullet *Liza argentea* (2.5%)	Saintilan et al. 2007
Northern New Zealand	*Avicennia marina*	Fyke nets 1.8 m high, 14.5 m extent across wings 9-mm heavy braid mesh	Eight estuaries (2 western coast, 6 eastern coast), 6 sites in each. February–April 2006.	19 species (mangrove sampling only) Yellow-eyed mullet *Aldrichetta forsteri* (65.6%), grey mullet *Mugil cephalus* (17.9%), estuarine triplefin *Grahamina nigripenne* (5.2%), pilchard *Sardinops neopilchardus* (3.8%), smelt *Retropina retropina* (2%), short-finned eel *Anguilla australis* (1.6%)	Morrisey et al. 2007
Port Pirie, Port Broughton, Port Wakefield, South Australia 33°S to 35°51′S 137°50′E to 138°E	*Avicennia marina*	Fyke nets 0.7 × 0.7 m frames, 6-mm mesh, mesh wing of 0.7 × 6 m long each side of frame	Set within 1 h of low tide, samples collected 24 h later, sampling 2 tidal cycles. Six distance classes from mangroves: 10 m within forest, in pneumatophore zone; directly adjacent to pneumatophore zone; 25 m, 200 m, 500 m seaward of mangrove fringe.	26 species (18 in mangroves), 17 families (14 in mangroves) First two distance classes (mangroves) dominated by *Atherinosoma microstoma* (73.7%), yellow-eyed mullet *Aldrichetta forsteri* (19.5%), *Sillaginodes punctata* (1.6%), and *Pelates octolineatus* (1.4%)	Payne & Gillanders 2009

dominated by this one species (>90% of all individuals sampled), and overall species diversity was low (17 species).

Hindell & Jenkins (2004) sampled fish assemblages on the seaward side of mangrove forests and on the adjacent mudflats in Westernport and Corner Inlet, Victoria, Australia. They collected 41 fish species, of which five were found exclusively in the mangrove forest: congolli (*Pseudaphritis urvillii*), atherinid postlarvae, mosaic leatherjacket (*Eubalichthys mosaicus*), parore/luderick (*Girella tricuspidata*) and kahawai/Australian salmon (*Arripis trutta*). An additional six species were found exclusively in the mudflat habitats: hairy pipefish (*Urocampus carinirostris*), garfish (*Hyporhamphus regularis*), the mangrove goby (*Mugilogobius paludis*), sand mullet (*Myxus elongatus*), yank flathead/stargazer (*Platycephalus laevigatus*), and ornate cowfish (*Aracana ornata*). However, many of these 'unique' habitat species were represented by only one to three individuals each. The general fish assemblage was numerically dominated (74% of all individuals) by silver fish (*Leptatherina presbyteroides*), smooth toadfish (*Tetractenos glaber*) and yellow-eyed mullet (*Aldrichetta forsteri*). Overall, fish abundances were always greater in mangroves than mudflats for juveniles, but there were no apparent differences for larger subadult and adult fish. Most of the variability was determined by atherinids, mugulids (mullets), gobiids (gobies), tetraodontids (pufferfishes), pleuronectids (flatfishes) and clupeids. However, there were also strong interactions depending on where and when the three mangrove sites were sampled because the importance of mangroves was both spatially and temporally variable.

Smith & Hindell (2005) sampled the seaward side of mangroves, in the pneumatophore zone and in adjacent subtidal channels during the day and at night in the Barwon River, Victoria, Australia. Overall fish abundance, biomass and species richness were generally lower in the forest than the other two habitats, but varied with date, time of day, and water depth. The general fish assemblage was dominated by yellow-eyed mullet (*Aldrichetta forsteri*). Channel habitats held the highest fish abundances, biomass and species richness (total species pool was 20). Short-finned eels (*Anguilla australis*) and bream (*Acanthopagrus butcheri*) were found across all three habitats, mainly during the night. The authors concluded that the system was relatively low in species richness.

Hindell & Jenkins (2005) collected 15 fish species in and adjacent to mangroves in Port Phillip Bay, Victoria (Table 7). Catches in mangrove forest were dominated by small (<30 mm) gobies (*Pseudogobius olorum*, *Mugilogobius paludis*) and juveniles of the atherinid *Atherinasoma microstoma*. On the forest edges and adjacent mudflats, catches were dominated by King George whiting (*Sillaginodes punctata*), smooth toadfish (*Tetractenos glaber*) and two gobies (the half-bridled goby, *Arenigobius frenatus* and the long-fin goby *Favonigobius lateralis*). Fish densities were highest in the forest (1.98 ± 0.36 m^{-2}, mean ± SE), followed by the forest edge (1.42 ± 0.43 m^{-2}) and the mudflats (0.25 ± 0.19 m^{-2}). Species richness was highest at the mangrove forest edge (0.25 ± 0.19 m^{-2}), followed by the forest (0.17 ± 0.06 m^{-2}) and the mudflats (0.12 ± 0.02 m^{-2}). Fish biomass was highest at the forest edge (4.64 g ± 2.09 m^{-2}), followed by the mudflats (4.06 ± 1.79 m^{-2}) and the forest (1.2 ± 0.38 m^{-2}).

Bloomfield & Gillanders (2005) sampled fishes in seagrass, mangrove (*Avicennia marina*), saltmarsh and non-vegetated habitats in the Barker Inlet–Port River estuary, South Australia. Mangrove forests and non-vegetated habitats had more fish (257 vs. 377) and species (7 vs. 14) than salt marsh (only one fish collected), but less than seagrass (15 species, 590 individuals). Mangrove catches were dominated by unidentified atherinid larvae, the atherinid *Atherinosoma microstoma* and yellow-eyed mullet *Aldrichetta forsteri*, with five other species also caught in low numbers: King George whiting *Sillaginodes punctata*, the long-fin goby *Favonigobius lateralis*, the blue spot goby *Pseudogobius olorum*, a clingfish *Heteroclinus* sp., and an unidentified tetraodontid larva. In contrast, the seagrass samples were dominated by the two goby species and King George whiting (71% of individuals).

Mazumder et al. (2005) sampled small fishes in saltmarsh and mangrove habitats in Botany Bay, New South Wales. Forty-eight samples were collected from each of the two habitats, with 16 species collected from salt marsh at an average total fish density of 0.56 m^{-2} and 25 species at an overall density of 0.76 m^{-2} from mangroves. Twelve species of commercial importance were more common in mangroves, dominated by silver biddy (*Gerres subfasciatus*) and yellow-fin bream (*Acanthopagrus australis*) and including parore/luderick (*Girella tricuspidata*). Overall, in mangrove and salt marsh combined, the dominant species were glass gobies (*Gobiopterus semivestitus*), mangrove gobies (*Mugilogobius paludis*) and glassfish (*Ambassis jacksoniensis*). In a subsequent study in Botany Bay, Mazumder et al. (2006) sampled fishes leaving mangroves with the falling tide and caught 19 species. Species diversity was relatively low and dominated by nine species (Table 7).

Morrison and coworkers (data presented in Morrisey et al. 2007) sampled mangrove forests across eight estuaries in northern New Zealand in the austral summer/autumn, with stations sampled once in each estuary and extending from the upper to the lower reaches of the forest. Seventeen species were caught, but the assemblages were dominated numerically by yellow-eyed mullet (*Aldrichetta forsteri*), grey mullet (*Mugil cephalus*), pilchards and anchovies (the last two species represented by one to two single large catches, each in a different estuarine system). Grey mullet juveniles were generally found only in western coast mangrove forests, while the parore (*Girella tricuspidata*) was common only in eastern coast estuaries. This matched the coast-specific abundance of adult populations. Short-finned eels (*Anguilla australis*) were a common component of the fish–mangrove assemblages on both coasts, and this was the only species to show a positive correlation with the structural complexity of the forests (as measured by the number of mangrove samplings and young trees). No comparisons were made with adjacent habitats.

Finally, Payne & Gillanders (2009) sampled three estuaries (Port Wakefield, Port Broughton, and Port Pirie) in South Australia for small fishes. Neither total abundance nor species richness was found to vary between the mangrove and mudflat locations. Twenty-six species were sampled overall, with 18 of these occurring within mangrove habitats (inside forest or pneumatophore zones). However, only three of these were classified as mangrove residents (defined as total abundance more than five individuals sampled, >70% of these in mangroves): yellow-eyed mullet (*Aldrichetta forsteri*), *Sillago schomburgkii* and *Arripis georgiana*, although the abundances of the last two species were modest. In mangrove habitats, total fish abundance, mangrove residents and *Aldrichetta forsteri* were positively associated with pneumatophore density, indicating that structural complexity probably influences the distribution of some fish species.

Connectivity of temperate fish assemblages with surrounding habitat mosaics

Work by Nagelkerken et al. (2001) on tropical systems has shown that the presence of mangroves significantly increases species richness and abundance of fish assemblages in adjacent seagrass beds relative to seagrass beds without adjacent mangroves. Jelbart et al. (2007), working in the Pittwater Estuary just north of Sydney, sampled three seagrass (*Zostera capricorni*) beds close to mangroves (*Avicennia marina*) (<200 m) and three seagrass beds further away (>500 m). They found seagrass beds closer to mangroves had greater fish densities and diversities than more distant beds, especially for juveniles. Six species followed this pattern: the half-bridled goby *Arenigobius frenatus*, bridled leatherjacket *Acanthaluteres spilomelanurus*, parore/luderick *Girella tricuspidata*, *Pelates sexlineatus*, tarwhine (a sparid) *Rhabdosargus sarba* and hairy pipefish *Urocampus carinirostris*. Conversely, the density of those fish species in the seagrass at low tide that were also found in mangroves at high tide was negatively correlated with the distance of the seagrass bed from the mangroves. This finding showed the important daily connectivity that exists through tidal movements between mangrove and seagrass habitats.

Saintilan et al. (2007) sampled mangroves (*Avicennia marina*, although *Aegiceras corniculatum* was also present in the wider area) at Towra Point, Botany Bay, New South Wales. They sampled three habitats: seagrass, mangroves and salt marsh. Samples were taken monthly during spring tides in the mangrove and saltmarsh habitats and fortnightly in the seagrass, covering both spring and neap tides (salt marsh dries out during neap tides, and only the seaward sections of the mangrove forest are inundated). Twenty-eight species were sampled overall (24 from mangroves), with each habitat containing consistently different fish assemblages. The mangrove assemblage was dominated by gobies, including the mangrove goby *Mugilogobius paludis*, the checkered mangrove goby *Mugilogobius stigmaticus*, the snakehead goby *Taenioides mordax* and the blue spot goby *Psuedogobius olorum*, along with the glassfish *Ambassis jacksoniensis*, the silver biddy *Gerres subfasciatus* and the yellow-fin bream *Acanthopagrus australis*. Contrasts of the spring and neap tide assemblages (across habitats) found that seagrass assemblages had greater fish abundances during neap tides, especially of those species that visited the adjacent habitats (saltmarsh, mangroves) when they were available during spring tides. This was interpreted as evidence that fish were moving from seagrass into these adjacent habitats during spring tides, to exploit high abundances of zooplankton, and retreating to seagrass habitats as a refuge during low tides.

Why are juvenile fish in mangroves?

A number of hypotheses have been advanced regarding why mangrove habitat might be disproportionately important as nurseries for juvenile fish in areas where this has been shown to be the case. The main hypotheses are that they provide protection from predation (e.g., larger fish and birds) and elevated foraging opportunities through high prey abundances. Using experimental manipulations, Laegdsgaard & Johnson (2001) looked at the interactions between fish predation and root densities of the mangrove species *Avicennia marina*. They concluded that (1) habitat complexity regulates predation, (2) not all prey species use structurally complex habitats in the absence of predators and (3) the use of structurally complex habitats decreases with fish size. Further support for these findings comes from surveys documenting higher densities and biomass of demersal fishes in shallow, inland mangroves with dense pneumatophores relative to prop-root habitats, where almost all predatory fish collected were found to inhabit the more open, seaward sites (Vance et al. 1996, Rönnbäck et al. 1999). However, these studies were undertaken in tropical mangroves. Smith & Hindell (2005) undertook tethering experiments with small yellow-eyed mullet (*Aldrichetta forsteri*) across a range of temperate mangrove microhabitats (mangrove forest, pneumatophore zone and adjacent channels) in the Barwon River, Victoria, Australia. They found low rates of daytime predation across all of these habitats. They suggested that predation refuges provided by mangroves might be less important in temperate systems, and that the lower number of fish in temperate mangrove forests was likely to be due to a lack of food, in agreement with models of lower productivity in temperate mangrove forests (Alongi et al. 2002). They argued that more attention should be given to assessing changes in the distribution of invertebrate prey across such microhabitats. Such studies are rare in general for mangrove systems (Faunce & Serafy 2006).

Summary of studies of fish in temperate mangroves

Collectively, the studies discussed, all undertaken in temperate Australasia, encompass many shared species given their bias towards the southern and south-eastern Australian seaboard, and northern New Zealand. They all focused on one common mangrove species (the grey mangrove *Avicennia marina*) and a range of temperate estuarine fish species. Diversity of fish species was consistently low relative to subtropical and tropical mangroves, and a few key species consistently dominated the fish assemblages, notably members of the families Gobiidae, Atherinidae and Mullidae (especially the yellow-eyed mullet *Aldrichetta forsteri*). Although a range of commercial species was found in mangroves across these studies, the species were often present in low numbers and were species known to occur in schools (e.g., species from the families Arripidae, Sparidae and Sillaginidae), making them more prone to large random variations in abundance during sampling. This was also true for a broader range of non-commercial species. The general conclusion from these temperate mangrove studies is that, although mangrove habitats do provide habitat for fishes, many of the species involved are small bodied, of little or no commercial value, and often equally abundant in alternative habitats. No temperate species appeared to be dependent solely on mangrove habitat.

Reptiles and amphibians

According to Hutchings & Recher (1982), reptiles are uncommon in temperate mangroves but common in tropical ones, although for most species mangroves are marginal habitats. In some situations, where other types of forest are scarce, they may serve as corridors for movement of individuals. Nagelkerken et al. (2008) suggested that mangroves may be important to marine turtles, including providing habitat for algae on which turtles feed, although there is a lack of information. Given that most of the examples of use of mangroves by turtles and other reptiles in their review were from tropical regions, this lack seems to be particularly severe for temperate areas.

Thomas & Logan (1992) listed the lizard *Anolis grahami*, the green turtle (*Chelonia mydas*) and the diamondback terrapin *Malaclemys terrapin* as present in mangrove forests in Bermuda. In North America, *M. terrapin* occurs in coastal and estuarine marshes, flats and lagoons (Tortoise & Freshwater Turtle Specialist Group 1996). Green and loggerhead (*Caretta caretta*) turtles also enter mangrove waterways in Australia (Milward 1982).

Two amphibians were also recorded in Bermudan mangroves, the frog *Eleutherodactylus johnstoni* and the cane toad *Bufo marinus*. *Eleutherodactylus johnstoni* is an invasive species found in disturbed habitats. It is native to several Caribbean islands but introduced to parts of north-eastern South America (Hedges et al. 2008) and possibly also to Bermuda. *Bufo marinus* is a notoriously invasive species native to Central and South America but introduced to islands in the Caribbean (among many other places) and, presumably, Bermuda (Solís et al. 2008).

Crisp et al. (1990) noted that various geckos have been found among mangroves in northern harbours of New Zealand (particularly Rangaunu and Hokianga), most commonly Pacific and forest geckos (*Hoplodactylus pacificus* and *H. granulatus*), but did not reference their sources of information. They also noted that sea snakes (*Laticauda colubrina*, *L. laticordata* and *Pelamis platurus*) sometimes occur in New Zealand mangroves as far south as Tauranga Harbour (37°40′S), but these are likely to be rare and chance events.

Birds

Worldwide, mangroves harbour a moderate number of species of birds (Nagelkerken et al. 2008). Among these, however, are a surprisingly small number of mangrove specialists. No species have been recorded exclusively in mangroves in Africa and only one in north-eastern South America (Surinam) and the Caribbean (Trinidad). Even the relatively diverse mangrove avifauna of Australia (Schodde et al. 1982) includes only 13 mangrove endemics among more than 200 species that occur in this habitat (Saenger et al. 1977).

Schodde et al. (1982) provided one of the most detailed discussions to date of the composition, structure and origin of assemblages of birds in mangroves, focusing on Australia. They concluded that, across Australia, the avifauna of mangroves has developed relatively recently and mainly from rainforest sources in Australo-Papua. The number and diversity of mangrove endemics or mangrove-dependent species decreases with the number of tree species but has been limited, at least partly, by historical factors.

Saenger et al. (1977) listed 242 species of birds recorded from mangroves in Australia, of which 13 species (5%) were found exclusively in mangroves and 60 species (25%) used mangroves as an integral part of their habitat. The total number of species in this list that have been recorded in south-eastern Australia is 131, including 4 that occur only in mangroves and 20 for which mangroves are an integral part of their habitat. The remainder visit mangroves opportunistically, for example, to take advantage of food resources provided by flowering mangroves and the insects that they attract (Schodde et al. 1982).

The south-eastern Australian species found exclusively in mangroves, as reported by Saenger et al. (1977), were the mangrove heron (*Butorides striatus*), the mangrove warbler (*Gerygone laevigaster*) and the mangrove honeyeater (*Meliphaga fasciogularis*). Species closely associated with mangroves include a heron, two species of ibis, a sea eagle, a kite, an osprey, a rail, an oyster catcher, a plover, a godwit, a whimbrel, a stone-curlew, a dove, a cuckoo, a triller (family Grallinidae), a flycatcher (family Muscicapidae), the red-browed finch (family Meliphagidae), an oriole (family Oriolidae) and a wood swallow (family Artamidae).

In Careel Bay, near Sydney, relatively few birds were recorded as feeding in mangroves or salt marshes compared with adjacent intertidal seagrass beds (Hutchings & Recher 1974). Species that did feed in the mangroves included black cormorants (*Phalacrocorax carbo*), white-faced herons (*Ardea novaehollandiae*), white egrets (*Egretta alba*), mangrove herons white and straw-necked ibis (*Threskiornis molucca* and *T. spinocollis*), black-billed spoonbills (*Platalea regia*), yellow-billed spoonbills (*P. flavipes*), eastern curlews (*Numenius madagascariensis*) and bar-tailed godwits (*Limosa lapponica*). The mangroves and salt marshes also provided an important high-tide refuge, and a number of species, including herons, nested in the mangroves.

Saenger et al. (1977) listed Australian pelicans (*Pelicanus conspicillatus*) as visitors to mangroves, although they do not nest in this habitat (G. Johnston, Flinders University of South Australia, personal communication). In the United States in Louisiana, however, brown pelicans (*Pelicanus occidentalis*) nest in mangroves (Lester et al. 2005).

Raines et al. (2000) included one site where mangroves were present in a series of waterbird surveys of the Leschenault Inlet Estuary in south-western Australia. They recorded a "small variety of species in small numbers for feeding", but noted that, because mangroves were underrepresented among the habitats in their surveys, the actual importance of mangroves to waterbirds in the inlet may be greater than the surveys suggested. The site was used as a dry-season refuge by many species, and the authors suggested that, in general, mangroves may be of moderate conservation value to waterbirds.

There is relatively little published information on the use of mangroves by birds in New Zealand, and some of what is available consists of chance observations (e.g., Miller & Miller 1991). In the most detailed such study to date, Cox (1977) investigated use by birds of a mangrove stand in the Kaipara Harbour (north-west of Auckland) over 2 years and made one-off surveys of other locations. The Kaipara site consisted of tall (5- to 6-m) trees along the seaward fringe, backed by a broad, flat area of stunted (1.5-m) trees, bounded by a dyke at the top of the shore. Cox (1977) recorded 22 species at the Kaipara site, of which 12 occurred regularly within the mangroves, and 6–7 bred. The 11 species regularly recorded were white-faced heron (*Ardea novaehollandiae*), harrier (*Circus approximans*), chaffinch (*Fringilla coelebs*), grey warbler (*Gerygone igata*), Australian magpie (*Gymnorhina tibicen*), kingfisher (*Halcyon sancta*), welcome swallow (*Hirundo tahitica neoxena*), house sparrow (*Passer domesticus*), pukeko (*Porphyrio porphyrio*), blackbird (*Turdus merula*) and silvereye (*Zosterops lateralis*). The species breeding in the mangroves were grey warbler, silvereye, fantail (*Rhipidura fuliginosa*), house sparrow and shining cuckoo (*Chrysococcyx lucidus*) (in the nest of a grey warbler). A further five species, including roosting colonies of little black shags (*Phalacrocorax sulcirostris*) and pied shags (*P. varius*), were recorded in mangroves at other locations (Parengarenga, Hatea, Kaipara, Manukau, Waitemata and Ohiwa Harbours). Cox (1977) concluded that mangroves are generally a marginal habitat for birds and in no case were they a major habitat, even though surveys of the invertebrate fauna of the Kaipara site indicated that prey was abundant in the mangroves.

Although all the species recorded at Cox's Kaipara site were either common natives or introduced species (such as house sparrows), other studies have documented use of mangroves by less abundant species. Miller & Miller (1991) reported bitterns (*Botaurus poiciloptilus*) using mangroves near

Whangarei in the north-east of the North Island. Royal spoonbills (*Platalea regia*) used mangroves on a small island as their principle roost site in the sediment settlement ponds at Port Whangarei (Beauchamp & Parrish 1999). White-faced herons and various species of shags also roosted in these mangroves, and there were resident populations of grey warbler, blackbirds, song thrushes (*Turdus philomelos*) and dunnock (*Prunella modularis*) and transient silvereyes, shining cuckoos and fantails. Thousands of starlings (*Sturnus vulgaris*) and hundreds of house sparrows and chaffinches roosted in mangroves in other parts of the settlement ponds. Cox (1977) cited information from other studies indicating that banded rail (*Gallirallus philippensis assimilis*) were the "only New Zealand bird typically described as associated with mangrove swamp", but that this was probably only the case where the mangroves were adjacent to suitable high-tide habitat. Beauchamp (n.d.) noted that mangroves are "the only northern habitat of the banded rail … and are a substantial breeding habitat for New Zealand kingfisher". Of the species that occurred in both Australia and New Zealand (including royal or black-billed spoonbills, banded rails and bitterns), all those found in mangroves in New Zealand were also found in this habitat in Australia.

Crisp et al. (1990) provided a list of 48 species of native or introduced birds using mangroves in New Zealand (no references were given, but parts of their commentary appeared to derive from Cox's thesis). Like Cox (1977), they concluded that mangroves are a marginal habitat for birds. Available evidence therefore suggests that there are no New Zealand birds that are exclusively found in mangroves, but that many species make extensive use of them for roosting, feeding or breeding. Given the difference in total numbers of birds found in mangroves in Australia and New Zealand and the small percentage of Australian species found exclusively in this habitat, it is perhaps not surprising that New Zealand does not appear to have any mangrove-dependent species.

Other than as pollinators, the ecological importance of birds in mangroves has received little attention. One exception, however, is a comparison of growth rates of stands of *Rhizophora mangle* in Florida with and without breeding colonies of pelicans and egrets (Onuf et al. 1977). Growth began earlier in the year and was faster at a site with colonies of birds than at a nearby site without birds. The former site also exhibited greater production of leaves, propagules, branches and rates of growth of existing branches, and growth showed two maxima per year, in contrast to one at the site without birds. The authors attributed these differences to higher inputs of nutrients, in the form of guano, to the site with birds. Unfortunately, there was no replication of sites with or without bird colonies, so that the influence of birds may be confounded with other differences between the two sites.

Mammals

The use of mangroves by mammals appears to be at least as opportunistic, and possibly even less studied, than that by birds. Other than their role as pollinators, there appears to be little or no information on the ecological roles of mammals in mangroves.

No Australian mammals are restricted to mangroves (Hutchings & Recher 1982), but various species of native and introduced mammals have been recorded in them, including bandicoots, wallabies, possums, various rodents and feral pigs (Lovelock 1993). Given the ubiquity of the introduced brush-tailed possum (*Trichosurus vulpecula*) in New Zealand, it seems likely that they also make use of mangroves in that country. Weasels (*Mustela nivalis*) have occasionally been sighted in mangrove forests in New Zealand (Blom 1992).

The presence of rats (*Rattus* spp.) in mangroves is sometimes cited as a reason for clearing mangroves, and there is plenty of anecdotal evidence of their occurrence. We are not aware, however, of any quantitative evidence for their use of mangroves. It is very likely that rats would use mangroves as habitats even at high tide because they can swim and climb well. Mature stands of large trees are more likely to provide refuges for rats in the form of holes in their trunks and a firmer ground among the trees. Mangroves are likely to provide a good source of food for rats, as they do for birds, in the form of invertebrates and plant material, such as propagules. Cox (1977) noted rat footprints and droppings at his study site in the Kaipara Harbour (New Zealand) and concluded that they were feeding on vegetable matter. As far as is known, there is no information concerning feeding on mangrove propagules by rats or on the palatability of mangrove material.

There does not seem to be any reason to presume that rats would occur in mangroves in larger population densities than other similarly vegetated habitats. It is possible that if mangroves colonise more open habitats, such as mud- or sandflats, they will locally increase the area of suitable habit for rats by raising the height of the ground and reducing frequency of tidal flooding and provide a source of food and shelter. Abundances of rats in mangrove areas are likely to vary with the nature of adjoining habitats (open pasture, freshwater wetland, urban or industrial areas) and probably reflect the relative abundance of rats in these habitats.

In temperate parts of South Africa, vervet monkeys [*Chlorocebus* (*Cercopithecus*) *aethiops*] are common in the canopy and on the ground in mangrove forests, and blue duiker (*Cephalophus monticola*), reedbuck (*Redunca arundinum*) and bushbuck (*Tragecephalus scriptus*) visit mangrove forests from adjacent habitats (Hughes & Hughes 1992).

Bats also use mangroves as feeding and roosting habitats. In south-eastern Australia, the grey-headed flying fox *Pteropus poliocephalus* feeds on the pollen and nectar of mangrove flowers and also roosts in mangrove forests (Hutchings & Recher 1982). This species shows strong fidelity to roosting sites and may occupy the same site for years. In southern Brazil, the fishing bat *Noctilio leporinus* forages in and around mangroves. Analysis of faeces indicated that its main food items were fish (90% of samples examined), moths and beetles (Bordignon 2006).

Primary consumption

Mangrove material may be consumed fresh by direct herbivory or indirectly by consumption of dead leaves and other tissues by detritivores. The latter trophic pathway has been studied in considerable detail in tropical mangrove systems (reviewed by Alongi 2009) but much less so in temperate systems. Direct consumption has, in general, been less studied, but again the emphasis has been on tropical systems.

Direct consumption of mangrove material by animals

The role of herbivores in mangrove forests has, until relatively recently, been considered minimal compared with their role in terrestrial forests (e.g., Macnae 1968, Tomlinson 1986). However, the importance of crabs in mangrove trophic pathways has become evident (reviewed by Cannicci et al. 2008, Alongi 2009), particularly as processors of leaf litter but also, in the case of arboreal species in the New World and the Indo-Pacific, as herbivores. Hartnoll et al. (2002) suggested that biomass of crabs in mangroves is highest in warm temperate regions, although abundances may decrease with latitude. They also argued that a shift from ocypodids (which are deposit-feeders) to grapsids (which are herbivores) with increasing latitude may result in latitudinal changes in patterns of transfer of primary production through trophic pathways.

Herbivory: consumption of mangrove foliage

Several species of arboreal crabs live on the trunks and in the canopies of mangroves and feed on living plant tissues, including leaves and propagules. The large majority are tropical, but the exclusively arboreal *Parasesarma leptosoma* also occurs in mangroves in warm temperate parts of South Africa (Emmerson & Ndenze 2007). Intensity of browsing varied with height on the shore and with species of mangrove; from 100% of *Rhizophora mucronata* and 52% of *Bruguiera gymnorrhiza* near the low-tide creek showing evidence of browsing, 25.7% of *Rhizophora mucronata* but 0% of *Bruguiera gymnorrhiza* browsed away from the creek and no browsing occurred on

Avicennia marina (near or away from the creek). These differences reflected relative palatability as both *Rhizophora mucronata* and *Bruguiera gymnorrhiza* are salt excluders, and *Avicennia marina* secretes salt from its leaves. Leaves of *Rhizophora mucronata* also had a higher nutrient content, particularly nearer the creek. The average area of leaf damaged was 1.7–2.6% for R. mucronata and 0–1.76% for *Bruguiera gymnorrhiza*. There was a significant correlation between the number of crabs caught in traps on the trees and the amount of leaf damage for both species of trees.

Insect herbivores have been even more overlooked than crabs, with their perceived lack of abundance and diversity in mangroves relative to terrestrial forests leading, in turn, to an assumption that their ecological role is similarly minimal (Burrows 2003, Cannicci et al. 2008). Again, however, more detailed study has revealed their previously underestimated importance. In the most thorough study to date, Burrows (2003) showed that the diversity of folivorous insects on *Rhizophora stylosa* and *Avicennia marina* in northern Queensland, Australia, was similar to that of other tropical species of trees.

Insects and other herbivores may cause a number of types of damage to mangrove trees, including loss of leaf area, premature abscission of leaves, leaf mining, leaf deformation or stunting and gall formation (Burrows 2003). Indirect damage may result from destruction of growing tips and branches, causing a loss of leaf biomass, or from and sap feeding, leading to necrosis. In northern Queensland, *Rhizophora stylosa* and *Avicennia marina* contained specialised but different assemblages of herbivores, with gall-forming species comprising nearly a third of the fauna on *A. marina* but none occurring on *Rhizophora stylosa* (Burrows 2003). Temperate examples are scarce (probably because of a lack of research) but include the distinctive distortion of the growing tips of the shoots of *Avicennia marina* caused by larvae of the moth *Ptyomaxia* sp. and leaf galls caused by the mite *Aceria avicenniae* in New Zealand (Lamb 1952, J. Dugdale personal communication).

The large majority of studies of herbivory in mangroves have been based on measures of damage to leaves sampled at a single point in time (Burrows 2003). When Burrows (2003) compared such ‘discrete’ data with those from long-term methods, he found that the former failed to account for loss of leaves that were entirely consumed by herbivores or that were prematurely abscised as a result of damage. Loss of leaf biomass as a result of premature abscission caused by insect damage was equal to or greater than direct damage or consumption. Consequently, discrete methods underestimated consumption by herbivores by three to six times, and in Burrows’s study in northern Queensland, discrete measurements gave estimates of loss of leaf area for *Avicennia marina* of 6–7%, compared with 28–36% from long-term studies. Susceptibility to herbivore damage varied between the two mangrove species studied, with 5–8% of the leaves of *Rhizophora stylosa* either completely consumed or prematurely abscised, compared with 19–29% of those of *Avicennia marina*.

Although most of the studies of insect herbivory reviewed by Burrows were of tropical mangrove systems, these conclusions may well apply to temperate systems, where the insect fauna has been equally neglected. The only study of herbivore damage to leaves of temperate mangroves of which we are aware is that by Johnstone (1981), who recorded 0–2.6% of leaf area loss in *Avicennia marina* in Auckland, New Zealand, using discrete measurements.

In their study of stands of *Rhizophora mangle* with and without breeding colonies of birds in Florida, Onuf et al. (1977) found that, in addition to higher rates of growth, the stand with birds experienced a much higher level of insect herbivory. Five lepidopteran species and a scolytid beetle were either more abundant or only occurred at the site with birds. The authors hypothesised that the higher rate of herbivory was due to higher nutritive value of leaves at this site. The difference in relative levels of herbivory disappeared when the birds migrated away from the site after breeding (although, of course, this could simply reflect a response of both groups of organisms to seasonality of some other environmental factor).

Animals that bore into plant tissues may lead to death of mangrove limbs and loss of leaves. In some areas of mangroves in New Zealand, such as Puhinui Creek, Manukau Harbour west of Auckland (D. Morrisey personal observation) and Puhoi Estuary north of Auckland (Kronen 2001), damage to woody mangrove tissue by boring insects is common. The insect responsible is a cerambycid beetle, the lemon-tree borer *Oemona hirta* (J. Dugdale personal communication), which occurs on a wide range of species of trees throughout New Zealand. The larvae excavate long tunnels throughout the woody tissue, with side tunnels leading to holes to the outside, through which waste materials are ejected (Horticulture and Food Research Institute of New Zealand Ltd. 1998b).

Frugivory: predation of mangrove propagules

In a worldwide survey of herbivore damage to mangrove propagules (germinated seeds) prior to dispersal from the parent tree, Farnsworth & Ellison (1997) concluded that predispersal herbivory is a ubiquitous feature of mangrove forests worldwide and must be accounted for in estimates of reproductive output. Clarke & Allaway (1993) commented that herbivory of postdispersal mangrove propagules by crabs was less important in temperate than tropical parts of Australia. Consistent with this suggestion, individuals of the temperate Australian mangrove crab *Helograpsus haswellianus* did not consume propagules of *Avicennia marina* when offered them in laboratory experiments (Imgraben & Dittmann 2008).

In contrast to herbivory of leaves, there have been several studies of herbivory of propagules in temperate mangroves. Farnsworth & Ellison (1997) also noted that crabs consumed the largest number of propagules and at the widest range of locations around the world. Other important consumers of propagules were scolytid beetles and, to a lesser extent, lepidopteran larvae. The last of these groups was relatively more important in the Southern Hemisphere.

Farnsworth & Ellison's study (1997) surveyed propagules for predispersal herbivory across 10 species of mangrove and 42 sites around the world, including 2 near Durban, South Africa (29°48′ and 29°53′S). Across these two sites, their samples showed no damage to propagules of *Bruguiera gymnorrhiza* ($n = 85$ propagules) or *Rhizophora mucronata* ($n = 7$), but damage to *Avicennia marina* propagules ranged from 10 to 90% ($n = 80$) and was caused by lepidopteran larvae.

In the Sydney region and at Westernport, Victoria, larvae of phycitine moths attack up to 60% of fruit, and several cohorts may feed on an individual fruit as it develops (Clarke 1992). The larvae also feed on flower buds, as do cantherid beetles, but exclusion experiments showed that they not reduce the proportion of buds that survive to become fruits. Exclusions did, however, result in a doubling of fruit survival, but Clarke concluded that the impact of predation was minor in comparison with that of maternal regulation of fruit survival, which was responsible for 75% of mortality. Of the fruit that showed evidence of damage by herbivores, only 1–16% were consequently found not to be viable.

Fruit of *Avicennia marina* are attacked by insect herbivores throughout their development, and at a site near Sydney, Minchinton & Dalby-Ball (2001) recorded larval exit holes of the mangrove fruit fly *Euphranta marina* and the mangrove plume moth *Cenoloba obliteralis* in the cotyledons of 53% of predispersal fruit, 69% of abscised propagules and 80% of established seedlings, with the number of holes increasing with time since abscission. Because the larvae attacked only the cotyledons and not the embryonic axis, they did not affect establishment of seedlings, but by reducing the food supply of the developing seedlings, they did reduce their rates of growth. Mortality of early seedlings was, nevertheless, minimal and not related to the level of frugivory. Whether decreased size may lead to reduced competitive ability as seedlings wait for release from the 'seedling bank' (Burns & Ogden 1985) is not yet known.

In the United States, Louisiana mangroves (*Avicennia germinans*) are constrained in their distribution to higher levels of the shore than the saltmarsh grass *Spartina alterniflora*. The controlling factors include dispersal of propagules by tidal movement and relative rates of desiccation, decay and herbivory (Patterson et al. 1997). Herbivory was more intense in the *Spartina* zone, where 40% (±4%) of experimentally placed propagules were attacked compared with 5% (±4%) in the mangrove zone. Few propagules were consumed completely, but damage to the cotyledons resulted in increased rates of decay.

Summary

The available evidence suggests that the recently recognised importance of herbivores in tropical mangroves may also apply to their temperate equivalents, at least in the case of feeding on propagules. In contrast to the detritivorous trophic pathway described next, much of this direct herbivory may be exported to adjacent terrestrial systems through migration of adult insects or their predation by birds.

Detritivory

Whether or not insects and other herbivores play a significant role as consumers of mangrove primary production, it is likely that the largest component of production enters the food web as detritus (Bouillon et al. 2008, Alongi 2009).

Decomposition of mangrove and other plant material

The nutritional value of detrital material to consumers increases over time as it is colonised and broken down by microbial organisms, with concurrent increase in nitrogen content (mainly in the form of mucopolysaccharides produced by bacteria but also in the bodies of bacteria and fungi; Steinke et al. 1990) and decreases in carbon content and net weight (Robertson 1988). Concentrations of tannins also decrease rapidly during the early stages of decomposition (Robertson 1988). Leaves of *Avicennia* and *Kandelia* are inherently rapidly decomposed relative to other mangrove species because of their relatively high nitrogen content, low carbon-to-nitrogen ratio, low content of structural lignocellulose and low tannin content (Robertson 1988, Alongi 2009). This relative rapidity may suggest that decomposition processes are faster in temperate compared with tropical forests given the predominant role of these genera in temperate forests, although lower temperatures in temperate regions may offset enhanced rates of tissue decomposition. Concentrations of nitrogen in the leaves of young (0.6–1.6 m tall, 2.72% DW) and mature (1.88% DW) *Avicennia marina* in Auckland (Morrisey et al. 2003) are slightly higher than the concentration reported by Robertson (1988) in Queensland (~0.9% DW from his Figure 2). The percentage of nitrogen in senescent leaves of *A. marina* was 0.7% DW in both Westernport Bay, Victoria, Australia (van der Valk & Attiwill 1984), and the Mgeni Estuary, South Africa (Steinke et al. 1983).

Rates of decay vary with climate and latitude (Figure 5 and see Mackey & Smail 1996). However, effects of latitude can apparently be obscured by local differences in position within the

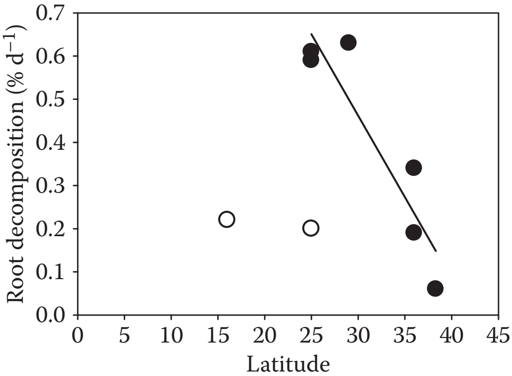

Figure 5 Variation in root decomposition of *Avicennia* sp. with latitude in mineral soils (filled circles) and in peat soils (open circles). The line of best fit for mineral soils is described by $y = -0.038x + 1.595$, $R^2 = 0.85$, $p = 0.0084$. (Data are from Albright 1976, van der Valk & Attiwill 1984, Middleton & McKee 2001, Perry & Mendelssohn 2009, D. Salomone & C.E. Lovelock, unpublished data.)

intertidal area and associated period of immersion and by seasonal effects. Middleton & McKee (2001) reviewed published rates of decomposition (mainly from tropical and subtropical locations), and among species of *Avicennia*, the average daily per cent loss of DW on the low/middle shore was 0.42 (±0.05 SE). The two temperate examples included in Middleton & McKee's (2001) review (Woodroffe 1982, van der Valk & Attiwill 1984) were below this average value but were not the lowest values for *Avicennia*.

This variation in rates of decomposition with latitude is illustrated more clearly by comparison of studies of decomposition of leaves of *A. marina* at different latitudes in eastern Australia (Table 8). Robertson (1988) recorded a time of 11 days for 50% reduction in ash-free dry weight (AFDW) of leaves of *A. marina* submerged in small mangrove creeks in northern Queensland (latitude 19°17′S) and 90 days for leaves in the midintertidal area (leaves of *A. marina* decomposed considerably faster than those of other mangrove species at the same locations). Further south, near Brisbane (27°24′S), Mackey & Smail (1996) recorded times for 50% loss of AFDW of 44 days low on the shore (inundated by 100% of high tides) and 59 days higher on the shore (inundated by 20% of high tides) in summer. Both of these rates are faster than the intertidal value reported by Robertson (1988). Equivalent times for winter were 78 days (low shore) and 98 days (high shore). In Sydney Harbour (33°46′S), newly senesced leaves of *A. marina* lost 50% of their oven-dried weight in about 56 days in winter (May–July) (Goulter & Allaway 1979), although changes in AFDW and DW are not strictly comparable. The rate of decomposition at a location near Adelaide, South Australia (34°36′), in summer (February–April) was even faster than near Brisbane, with 50% loss of air-dried weight in the first 14 days (Imgraben & Dittmann 2008). Rates of decomposition varied among heights on the shore, being highest at the seaward fringe, and the rates at this location were significantly higher than at another 7 km away (50% loss of DW in about 6 wk). In Westernport Bay, Victoria (latitude 38°20′S), times for 50% loss of oven-dried weight in summer (beginning in October and November) were about 70 days for leaves placed on the sediment surface in mesh bags and about 40 days for unbagged leaves (van der Valk & Attiwill 1984). Unbagged leaves lost weight faster because of loss of small fragments that were retained by the bags.

In New Zealand, 50% loss of leaf weight occurred after about 53 days in early summer (October–December) for leaves placed on the mud surface in Whangateau Harbour (latitude 36°19′S; Albright 1976). The rate of decomposition was much slower for leaves buried 20 cm below the sediment surface, where decomposition processes would have been anaerobic. Woodroffe (1982) measured rates of decomposition of mangrove leaves in the Tuff Crater (Auckland) of 6–8 wk for 50% reduction in oven-dried weight, with little variation between summer and winter or between a site in tall mangroves along a creek bank and a site in low mangroves on the intertidal flats (there was no measure of variation in rates of decay in summer because only one sample was measured each time). A subsequent study at the same location resulted in 50% reduction in AFDW over 10 wk (time of year not stated; Woodroffe 1985a). The lack of difference between summer and winter in the first of these studies is surprising given that decomposition rates are generally considered to be temperature dependent (Mackey & Smail 1996). The lack of seasonal difference in Woodroffe's study contrasts with that of Oñate-Pacalioga (2005) near Auckland. She found that 50% loss of AFDW occurred after 8 wk in mature stands in autumn but took more than 12 wk in winter and spring. Equivalent times for newly establishing stands were 12 wk in autumn and more than 12 wk in winter and spring.

In the Mgeni Estuary, South Africa (29°48′S), senescent leaves of *A. marina* lost 50% of their oven-dried weight over 3 wk (starting in spring to late October), whereas those of *Bruguiera gymnorrhiza* took about 6 wk to lose the same amount (Steinke et al. 1983). Stems of these two species were more recalcitrant, with only 20% loss after 6 mo. Similar rates of decomposition (~2 wk and 9 wk for 50% loss of oven-dried weight by *Avicennia marina* and *Bruguiera gymnorrhiza*, respectively) were recorded in a later study at the same site but starting in February (Steinke et al. 1990).

Table 8 Rates of decomposition (as number of days for 50% loss of weight) of mangrove leaf litter at temperate locations

Location	Latitude	Species	Season	Time for 50% loss (d)	Notes	Reference
North Queensland, Australia	19°17′S	A.m.		11 90	Creek Midintertidal AFDW, senescent	Robertson 1988
Brisbane, Australia	27°24′S	A.m.	Summer	44 59	Low shore Midshore AFDW, senescent	Mackey & Smail 1996
Brisbane, Australia	27°24′S	A.m.	Winter	78 98	Low shore Midshore AFDW, senescent	Mackey & Smail 1996
Newcastle, Australia	32°52′S	A.m.	Summer	<30 >180	Downstream of floodgate Upstream of floodgate DW, fresh	Dick & Osunkoya 2000
Sydney, Australia	33°46′S	A.m.	Winter	56	Submerged by all high tides; same times for 1- and 7-mm bags DW, senescent	Goulter & Allaway 1979
Middle Beach, South Australia	34°36′S	A.m.	Summer	11 14	Low and high shore Midshore DW, senescent	Imgraben & Dittmann 2008
Port Gawler, South Australia	34°38′S	A.m.	Summer	42 —	Low shore Mid- and high shore sites did not reach 50% reduction within 8-wk duration of study DW, senescent	Imgraben & Dittmann 2008
Westernport Bay, Australia	38°20′S	A.m.	Summer	70 40	Mesh bags Unbagged Midshore, DW, senescent	Van der Valk & Attiwill 1984
Whangateau Harbour, New Zealand	36°19′S	A.m.	Summer	53	DW, fresh?	Albright 1976
Auckland, New Zealand	36°48′S	A.m.	Summer	42 56	Creek bank Tidal flat AFDW, fresh	Woodroffe 1982
Auckland, New Zealand	36°48′S	A.m.	Winter	35–70 39–42	Creek bank Tidal flat AFDW, fresh	Woodroffe 1982
Auckland, New Zealand	36°48′S	A.m.	Not stated	70	Creek bank and tidal flat AFDW, fresh?	Woodroffe 1985a
Auckland, New Zealand	36°19′S	A.m.	Autumn Spring	56 >84	AFDW	Oñate-Pacalioga 2005
Mgeni Estuary, South Africa	29°48′S	A.m. B.g.	Spring	21 42	DW, senescent	Steinke et al. 1983
Mgeni Estuary, South Africa	29°48′S	A.m. B.g.	Summer	14 63	DW, senescent	Steinke et al. 1990

Note: Examples of rates from lower latitudes in Australia are also shown for comparison. Whether fresh or senescent leaves were used also noted if known. A.m. = *Avicennia marina*; B.g. = *Bruguiera gymnorrhiza*; AFDW = ash-free dry weight; DW = air- or oven-dried weight.

These comparisons of the decomposition rates reported by Robertson (1988) and Mackey & Smail (1996) with those for temperate Australia, New Zealand and South Africa (Table 8) suggest that rates are not necessarily slower at higher latitudes.

Variation among locations at a given latitude, and among times at a given location, seems to be as large as variation among latitudes. There also seems to be variation with salinity (Steinke & Charles 1986) and among species of mangrove, as indicated by the comparison of leaves of *Avicennia marina* and *Bruguiera gymnorrhiza* in South Africa (Steinke et al. 1990). As noted, leaves of *Avicennia* and *Kandelia* decompose relatively rapidly because of their high nitrogen content, low carbon-to-nitrogen ratio and low tannin content compared with other species (Robertson 1988, Alongi 2009). Because temperate mangrove stands tend to contain only one or two species, differences in the dominant species present in different temperate regions (e.g., *Avicennia marina* in southern Australia and New Zealand, *Kandelia candel* in Japan, *Bruguiera gymnorrhiza* in South Africa) may give rise to large variations in the rates at which mangrove litter enters trophic pathways.

Experimental differences among the studies cited may also contribute to apparent variation in rates of decomposition. Most studies use litter bags to contain the decomposing material, but the size of the mesh varies among studies and may influence decay rates. The evidence for the effects of mesh size is equivocal because Goulter & Allaway (1979) found no difference in rates of decay measured in litter bags of 1-mm and 7-mm mesh. The majority of studies also used senescent (yellow) leaves picked from the tree before abscission, but since up to 61% of the nutrients in leaves of *Avicennia marina* may be absorbed prior to abscission (Ochieng & Erftemeijer 2002), there may be a difference in nutritive value between leaves still on the tree and those that have abscised naturally, as Imgraben & Dittmann (2008) pointed out.

Decomposition rates of fine roots of *Avicennia* sp. published in the literature appear to decline with increasing latitude in mineral soils (Figure 5), although few studies have been published from tropical latitudes. Decomposition of fine roots of *Avicennia* spp. in peat soils is slower than in mineral soils, but data are limited.

Decomposition is carried out by assemblages of bacteria and fungi (Steinke et al. 1990, Singh et al. 1991, Kristensen et al. 2008) and often proceeds relatively rapidly at first, followed by a slower rate of decrease or an increase in DW (Woodroffe 1982, 1985a, Steinke et al. 1990, Imgraben & Dittmann 2008). Although concentrations of nutrients such as nitrogen, phosphorus, potassium, magnesium and calcium decline steadily during decomposition (Steinke et al. 1983, van der Valk & Attiwill 1984, Steinke & Charles 1986), concentrations of nitrogen subsequently increase, reflecting colonisation of the detritus by bacteria, fungi, cyanobacteria and diatoms (Steinke et al. 1983).

Microbial colonisation of litter during decomposition increases its nutritive value for larger organisms, and in turn, the rate of decomposition of litter is increased by the activities of animals that break it down into smaller fragments, providing a larger surface area for microbial activity. In some parts of the world, crabs are particularly important in this role (northern Australia, Robertson & Daniel 1989; South Africa, Emmerson & McGwynne 1992). Kristensen et al. (2008) estimated consumption of mangrove litter as a percentage of litterfall from data collected in various locations, including the Mngazana Estuary in South Africa (Emmerson & McGwynne 1992). Although the biomass of sesarmids at this location was low relative to other locations, even this value (and other conservative assumptions) suggested that the crabs were capable of removing up to 30% of litter from the surface of the sediment in mangrove stands.

Lee (2008) suggested that gastropods may provide a similar service in parts of the world where crabs are a less-dominant part of the macrofauna. This may be the case in New Zealand, where the mangrove crab fauna is of relatively low diversity, but as yet, there is little information available. In Florida, the gastropod *Melampus coffeus* is capable of assimilating mangrove leaf material, but its grazing also increases rates of leaf decomposition (Proffitt & Devlin 2005). In the presence of snails, DW of decomposing leaves decreased by 90% in 4 wk in the case of *Avicennia germinans* and 7 wk in the case of *Rhizophora mucronata*, compared with 12–26 wk and more than 26 wk, respectively, when snails were excluded.

In New Zealand, Oñate-Pacalioga (2005) showed that decomposition rates of mangrove leaves in the laboratory were 8–12% slower when macrofauna were removed from the sediment on which the leaves were placed (leaves and sediment were collected from Whangateau Harbour, near Auckland). It is not known whether *Helice crassa* or other crabs found in New Zealand mangrove habitats have the same effect on rates of decomposition as crabs in tropical mangroves. A study in subtropical Japanese mangroves (Mchenga et al. 2007) suggested that a related species, *H. formosensis*, is an important bioturbator, increasing oxygenation of sediments at the landward edge of the mangroves and significantly influencing the distribution and rate of decomposition of organic matter. Amphipods and deposit-feeding snails may also be important, but their abundance appears to vary among locations. The amphipod *Orchestia* sp. was abundant in litter decomposition bags deployed in the Tuff Crater (Woodroffe 1985a), but amphipods were generally absent in mangrove and pneumatophore habitats in Matapouri Estuary (Alfaro 2006). Because most studies of rates of decomposition of mangrove litter use mesh bags to prevent the litter being washed away by the tide, the bags may exclude larger macrofauna and, by preventing them from breaking up the litter, underestimate rates of decomposition, as most studies have acknowledged.

Uptake of mangrove-derived material within the mangrove forest and export to adjacent habitats

Nutrients derived from mangrove material, either through direct grazing or via detritus, may be recycled within the mangrove system or exported. Material may be exported in the form of leaves, twigs, fragmented detritus, dissolved organic matter or inorganic matter or as living organisms. The proportion of detrital material that is retained in the sediment within the mangroves relative to the proportion exported by water movement is not known. Although net primary production is lower in temperate compared with tropical mangroves, knowledge of how temperate mangroves differ from tropical mangroves in other components of the carbon budget and how carbon and nutrients derived from mangroves is incorporated into marine food webs through inwelling and outwelling is less well documented. Generalised carbon budgets for mangroves, based mainly on tropical forests, have been developed most recently by Alongi (2009). Carbon fixation by the trees is the largest input of carbon to the system, and respiration by trees is the largest efflux of carbon. This is unlikely to differ between temperate and tropical forests, but other components of carbon budgets may well do so.

The proportional contribution of benthic primary producers may be higher in temperate than in tropical mangroves. Many temperate forests are short, scrub forests where light penetration to the sediment is relatively high, leading to substantial rates of primary production of algae and microbial communities (Joye & Lee 2004). Increased production by these components may increase the availability of labile carbon for consumption and outwelling in temperate compared with tropical mangroves.

Carbon allocation between shoots and roots may differ between temperate and tropical mangroves. Shorter scrub forests typical of temperate sites tend to allocate a greater proportion of carbon below ground than taller forests (Lovelock 2008). Allocation to roots may contribute to enhancing microbial carbon mineralization and thus carbon availability for export from temperate compared with tropical mangrove estuaries. Few data are available to allow this hypothesis to be assessed.

Woodroffe (1985a) noted that the organic content of sediments in mangrove areas in the Tuff Crater (Auckland) was high, and although not all of it necessarily derived from mangroves, at least a portion of detrital production was clearly retained and recycled *in situ*. Morrisey et al. (2003) also measured high percentage cover of the sediment surface by detrital material (4.5–72.5%) and high proportions of organic matter (7.9–17.2% DW) in the sediment in mature stands of mangroves in Puhinui Creek, Auckland, but not in newly establishing stands (0–1.3% and 4.4–5.8%, respectively).

However, concentrations of particulate organic matter (POM) were also high in the water in the tidal creeks of Tuff Crater, indicating that some of this material is exported (Woodroffe 1985a).

The interplay of factors influencing the relative rates of litter decomposition and export from temperate mangroves is illustrated by a study of the effects of feeding by *Sesarma meinerti* in the Mgeni Estuary, South Africa (Steinke et al. 1993). In the field, leaf litter represented 75% of the diet of the crabs, and they showed differential preferences for different mangrove species and in different states of decomposition, in the order yellow *Bruguiera gymnorrhiza* > yellow *Avicennia marina* > green *Bruguiera gymnorrhiza* > green *Avicennia marina*. Laboratory studies showed a correlation between the relative amount consumed and the degree of decomposition. The role of the crabs varied with tidal height and therefore between the two mangroves species, being relatively more important in *Bruguiera gymnorrhiza* stands. In *Avicennia marina* stands, there was more detritus present on the sediment surface, and microbial decomposition may play a larger role. At the same location, *Rhizophora mucronata* lines the banks of creeks, and this may result in relatively large export of detritus from these stands. In stands of *Bruguiera gymnorrhiza*, the feeding behaviour of *Sesarma meinerti* results in removal of mangrove leaves from the sediment surface and their retention within the forest. It also leads to increased rates of degradation of detrital particle size, so that the material is more rapidly decomposed by detritivores and microbes.

Although it has been assumed for a long time that mangroves export detritus and faunal biomass to adjacent habitats and offshore (see discussion in Lee 1995), this hypothesis has only been tested relatively recently. Mass balance studies tend to support the hypothesis, but estimates of net imports and exports from such studies are strongly dependent on the method of calculation (Murray & Spencer 1997). Studies using stable isotopes to track the fate of organic matter originating within mangrove habitats have suggested that this ‘outwelling’ may be less extensive and ecologically significant than previously assumed (Lee 1995, Loneragan et al. 1997, Kathiresan & Bingham 2001, Bouillon et al. 2008).

Guest & Connolly (2004, 2006) found that the ^{13}C signatures of crabs (*Parasesarma erythrodactyla* and *Australoplax tridentata*) and slugs (the pulmonate *Onchidina australis*) in salt marshes in south-east Australia reflected that of the dominant saltmarsh plant (*Sporobolus virginica*). The signatures of the same animals living in mangroves reflected those of *Avicennia marina*. The sharply defined zone of transitional ^{13}C values between the two habitats suggested that movement and assimilation of carbon from one habitat to the other is limited to 5–7 m. Animals living in large (>0.4-ha) patches of salt marsh had signatures matching those of *Sporobolus virginica*, while the signatures of those in smaller patches indicated that they had assimilated carbon from both *S. virginica* and mangroves.

In Westernport, Victoria, the stable isotope signatures of a deposit-feeding callianassid shrimps (*Biffarius arenosus* and *Callianassa* (*Trypea*) *australiensis*) indicated that mangroves (*Avicennia marina*) and salt marshes (dominated by *Sarcocornia quiqeflora*) were not major sources of food, even though these habitats occurred close to the intertidal flats on which the shrimps lived (Boon et al. 1997).

Alfaro et al. (2006) used lipid biomarkers and stable isotopes to identify the trophic pathways of an estuarine food web in Matapouri Estuary, Northland. Mangroves are the dominant habitat in the estuary, but seagrass beds, sandflats and salt marshes are also present. Mangroves and brown algae were identified as important contributors of suspended organic matter in the creeks draining the harbour, but seagrass detritus is also likely to be important. Suspension of bacteria associated with detritus in surficial sediments probably represents another route by which mangroves and seagrasses contribute to suspended organic material. Biomarkers characteristic of bacteria were dominant in sediments. Biomarkers for fresh mangrove material were present in sediments collected adjacent to mangrove stands but not in those from a sandflat further down the estuary, suggesting that distribution of fresh mangrove organic matter may be quite localised.

Mangrove detritus, however, is probably more widely distributed because detrital biomarkers found at the sandflat site were likely to have derived from both seagrass and mangroves. This detrital material then becomes available to the infauna of the sandflats, particularly filter-feeders. This was confirmed by the presence of mangrove biomarkers in three filter-feeding bivalve species (cockles *Austrovenus stutchburyi*, pipis *Paphies australis*, and particularly oysters *Crassostrea gigas*, which were collected from trunks and roots of mangroves). Two grazing gastropods (*Turbo smaragdus* and *Nerita atramentosa*) both contained relatively large amounts of diatom, seagrass and fresh mangrove biomarkers. *Turbo smaragdus* occurs in association with mangrove pneumatophores, in addition to brown algae and seagrass, while *Nerita atramentosa* occurs on mangrove trunks; hence, the presence of fresh mangrove material in their diets is not surprising. Stable isotope signatures suggested that *N. atramentosa* consumes equal amounts of mangrove and seagrass material, whereas *Turbo smaragdus* consumes relatively more brown algae and seagrass.

The predatory whelk *Lepsiella scobina* contained relatively large amounts of mangrove biomarkers, possibly because it preys on oysters, which in turn consume mangrove material in suspension. Biomarkers found in glass shrimps (*Palaemon affinis*) indicated that they consume a wide range of organic matter, but with diatoms and mangrove material predominant. The mud crab *Helice crassa* is abundant in mangroves in some parts of New Zealand (e.g., Morrisey et al. 2003), although not in Matapouri, where it has been found only in small numbers (Alfaro 2006). Its diet includes diatoms, macroalgae, sediment-related bacteria and meiofauna (Morton 2004), and this dietary diversity was reflected by the diversity of biomarkers found in these crabs in Matapouri. However, it appears to consume little fresh mangrove or seagrass material, in contrast to the grapsid crabs of tropical mangroves.

Alfaro et al. (2006) concluded that the food web in the Matapouri Estuary thus incorporates several sources of organic matter and a range of trophic pathways. The various consumers (primary, secondary and higher order) appear to exploit different sources to different degrees, with none of the food sources being obligatory for the dominant organisms studied. Little fresh mangrove material appears to be incorporated directly into adjacent habitats, but mangrove detritus, in contrast, appears to be important to a range of organisms via the detrital food web. May (1999) also deduced that mangrove detritus was potentially important to deposit-feeding organisms in northern New Zealand estuaries, as did Knox (1983) in a study of the Waitemata Harbour, Auckland, although neither of these studies could provide the resolution achieved by use of stable isotopes or other biomarkers. The brown alga *Hormosira banksii* was found to contribute a relatively large amount of organic material to the estuarine system (Alfaro et al. 2006). *Hormosira banksii* is present all year and is very abundant among mangrove pneumatophores, presumably because they trap the alga and provide a substratum for it. Mangroves may therefore provide a further, indirect contribution to trophic pathways in the estuary. Like mangroves, the contribution of seagrass as a direct food source was smaller than expected but did provide material to the detrital food chain. May (1999) noted that in Rangaunu Harbour (35°00′S), a large estuarine system with high water clarity, extensive seagrass beds and mangrove forests, prevalent south-easterly winds often imported drift seagrass into mangrove forests on the windward side of the harbour, implying that primary production by seagrasses can subsidise mangrove forests in some situations. Observations in late April 2007 of the mangrove forest in the most southern arm of this harbour found dried seagrass drift festooned across the mangrove trees, up to the high-tide mark (M. Morrison personal observation). The seagrass meadows present extended from the low-tide channel up and into the pneumatophore zone.

Work on the trophic role mangroves play in supporting fish production has also shown them to be less critical than traditionally thought. Melville & Connolly (2003) examined the carbon and nitrogen stable isotope signatures of three commercially important fish species (yellow-fin bream *Acanthopagrus australis*, sand whiting *Sillago ciliata* and winter whiting *Sillago maculata*) over bare mudflats in a subtropical estuary (Morton Bay, southern Queensland). They undertook this both at the whole estuary scale and through finer-scale ‘spatial tracking’ by sampling nine separate locations and looking for spatial trends in the isotope signatures. The primary producer signatures identified were mangroves, seagrass, seagrass epiphytes, saltmarsh grass and saltmarsh succulent plants, POM and microphytobenthos. For yellow-fin bream, seagrass, salt marsh and POM were important trophic sources at the whole estuary scale, but the use of spatial tracking also identified mangroves as an additional important source dependent on spatial location (up to 33% of the carbon used—upper 95% confidence limit of the mean contribution derived from an isotope mixing model). Similarly, for sand whiting, only POM appeared to be important at the whole-estuary scale. At more localised scales, mangroves and microphytobenthos were also important, with up to 25% (upper 95% confidence interval) of carbon contributed by mangroves. Relative contributions for different producers could not be assigned for winter whiting, possibly because of either site-specific diet selection or movement of individuals among sites.

Subsequent to their 2003 study, Melville & Connolly (2005) examined ^{13}C isotope markers in 22 species of estuarine fishes collected from bare mudflats in the same estuary. They pooled the similar isotopic signatures of three mangrove species (*Avicennia marina*, *Aegiceras corniculatum* and *Rhizophora stylosa*) and those of three seagrass species (*Zostera capricorni*, *Halophila ovalis*, and *H. spinulosa*). Other primary producers identifiable by their isotopic signatures included epiphytes on seagrass, saltmarsh plants and microphytobenthos. The majority of the carbon in the fishes caught over mudflats was clearly derived from adjacent habitats, with seagrass contributions dominating strongly. The authors found it difficult to separate the contributions of mangroves from that of saltmarsh succulents and microphytobenthos, but for most fishes the maximum mangroves could have contributed was 30%. For five species, however, the contribution from mangroves may be up to 50% and possibly even higher for yellow perchlet (*Ambassis jacksonienis*).

In summary, evidence worldwide for the suggested importance of mangrove productivity to estuarine and coastal food webs is equivocal (Lee 1995). Kristensen et al. (2008) concluded that globally mangroves are an important net source of detritus to adjacent coastal waters, with an average export rate equivalent to 50% of total litter production. Utilisation of this material is, however, inconsistent and dependent on local conditions, including net primary production, the abundance of litter-collecting fauna and the local tidal range.

Information on nutrient and energy flows between mangroves and other habitats in temperate estuaries is relatively limited, but recent studies, such as that in Matapouri Estuary, northern New Zealand (Alfaro et al. 2006), suggested that estuarine consumers exploit a range of sources of primary production (seagrasses, mangroves, benthic microalgae and macroalgae) rather than being dependent on one particular source. Fresh mangrove and seagrass material appears to play a relatively minor, local role in the overall estuarine food web, but detritus derived from these plants and exported via tidal movement may play a more significant role via the detrital pathway. Macroalgae, such as *Hormosira banksii* in southern Australia and New Zealand, can be an important source of organic material to estuarine food webs and is abundant year round among mangrove pneumatophores and seagrass beds, indicating an additional, indirect role for these habitats.

Mangroves and sediments

Geomorphic distribution of temperate mangroves

Globally, the largest mangrove forests occur on deltas and muddy coasts of the tropical Indo–West Pacific (IWP) (Thom et al. 1975, Robertson et al. 1991, Walsh & Nittrouer 2004) and Atlantic–East Pacific (AEP) (Wells & Coleman 1981, Woodroffe & Davies 2009). Examples include the Ganges–Brahmaputra–Meghna, Irrawaddy, Mekong, Red and Pearl Rivers (IWP) and the mangrove coast of the Amazon River mouth (AEP) (Araújo da Silva et al. 2009, Woodroffe & Davies 2009). These rivers supply billions of tonnes of terrigenous sediment to tropical continental margins each year (Syvitski et al. 2005), some of which is deposited in shallow nearshore environments, including mangrove forests (Allison et al. 1995, Walsh & Nittrouer 2004). Extensive tropical mangrove forests develop on meso- and macrotidal coasts, where deposition of fine sediments builds extensive deltas and low-gradient intertidal mudflats (Schaeffer-Novelli et al. 2002, Ellison 2009, Woodroffe & Davies 2009). Large mudflat systems also develop in mesotidal (tidal range 2–4 m) settings with large terrigenous sediment supply (Healy 2002) and on coasts subjected to high wave energy (Wells & Coleman 1981, Mathew & Baba 1995).

In contrast to tropical systems, the temperate mangrove forests of south-eastern Australia, northern New Zealand and South Africa's eastern coast predominantly occur in estuaries, rather than on river deltas or muddy coasts. These Southern Hemisphere forests account for about 95% of temperate mangrove habitat worldwide. The estuary classification of Roy et al. (2001) for south-eastern Australian estuaries, which is generally applicable to New Zealand, provides a framework to describe the geomorphic distribution of temperate mangroves in these systems. In this scheme, estuaries are classified into types based on their geological setting, rate of sediment infilling and the relative dominance of tides and waves in controlling water circulation and sediment transport. This scheme has similarities with Thom's (1982) geomorphic classification of mangroves, which describes coastal environments dominated by terrigenous sediment supply (i.e., deltas, barrier islands, spits, lagoons and estuaries), although the vast majority of temperate mangrove forests are found in estuaries.

Temperate mangroves occur in bays with small freshwater inflow, drowned river valleys, tidal basins, barrier estuaries and lagoons. Bays, river valleys and basins have tidal ranges similar to the ocean, and circulation is dominated by tidal exchange except during floods, which episodically discharge freshwater. Tidal ranges in barrier estuaries and lagoons are reduced by sand deposits at their inlets, so that tidal currents are weak and wind waves and wind-driven circulation control sediment transport (Roy et al. 2001). In northern New Zealand, many drowned river valley estuaries have reached an advanced stage of infilling, and sediment transport on intertidal flats is controlled by wind waves rather than tidal currents (Green et al. 1997, Hume 2003, Swales et al. 2004, Green & Coco 2007). Along South Africa's eastern coast, temperate mangroves occupy tidal flats in narrow, bedrock-confined drowned river valleys and river-dominated barrier estuaries and lagoons (Cooper et al. 1999, Steinke 1999). Many of these estuaries have infilled with terrigenous sediments and have limited tidal prisms so that sediment transport is largely driven by river discharge rather than tides. River-dominated estuaries display cyclic sedimentation and erosion due to episodic large floods, and sediment deposits maybe completely eroded down to bedrock. River-dominated lagoons are also subject to episodic inlet closure during periods of low freshwater discharge. Inlets are re-established by high river flows during the early summer wet season (Cooper et al. 1999, Schumann et al. 1999). Thus, intertidal flat habitats suitable for mangroves are limited by the inherent morphology and dynamics of South Africa's river-dominated estuaries.

During the last 6000–7000 years since sea level has been stable, estuaries have filled with sediment at different rates and have reach different stages of evolution (Cooper et al. 1999, Roy et al. 2001, Hume 2003). Stages of development range from youthful systems that retain much of their original tidal volume to mature estuaries dominated by river discharge. In semimature estuaries, sediment infilling is usually associated with the seaward expansion of accreting intertidal flats that progressively displace subtidal basins. The rate of estuary infilling primarily reflects the original volume of the tidal basin and rate of sediment supply.

In south-eastern Australia, the largest mangrove forests occur in the mature drowned river valley and barrier estuaries of New South Wales, which reflects the larger intertidal flat areas found in these systems (Roy et al. 2001). Drowned river valley estuaries in particular display a trend, independent of estuary size, of expanding mangrove and saltmarsh habitat with increasing estuary maturity. Port Stephens is an exception to this pattern, and it remains at a relatively youthful stage of development due to its relatively small catchment; it contains the largest area of mangrove forest (2330 ha) in New South Wales (Roy et al. 2001, their Appendix 1). Mangrove forests also occur in ocean embayments with small river catchments, such as Westernport Bay (Victoria), where *Avicennia marina* forests fringe 40% of the shoreline (Bird 1986). Drowned river valley estuaries are also numerous along the coast of northern New Zealand, within the climatic range of *A. marina* (Hume 2003). However, the largest temperate mangrove forests occur in estuarine embayments with large terrigenous sediment supply. Examples include the Firth of Thames (1100 ha) and Rangaunu Harbour (2415.5 ha) as well as large barrier-enclosed estuaries such as the Kaipara (6167 ha) and Tauranga (623 ha) Harbours (Hume et al. 2007 and see Table 9). The area of temperate mangrove forest in these four estuaries accounts for 47% of the New Zealand total (data in Table 9 and from S. Park, Environment Bay of Plenty, personal communication). In South Africa, the largest temperate mangrove forests occur in the drowned river valley estuaries of northern Kwazulu-Natal that have formed in unconsolidated Tertiary–Pleistocene sediments (Cooper et al. 1999). Shoreline erosion has produced relatively large, shallow, sandy estuaries with extensive intertidal flats. The Umhlatuze (Richards Bay), St. Lucia, Kosi and Mfolozi estuaries of Kwazulu-Natal account for about 75% (~734 ha) of South Africa's temperate mangrove forests (Steinke 1999, Bedin 2001).

Sediment sources

Sediment supply to mangrove forests can be classified as either external (allochthonous) associated with transport and deposition of inorganic fine sediments or *in situ* (autochthonous) production of organic peat. Mangrove peat sediments occur in systems isolated from terrigenous sediment sources and are most commonly associated with isolated oceanic low islands in the tropical Pacific and Caribbean (Woodroffe & Davies 2009). With the exception of the peat-forming *Avicennia germinans* and *Rhizophora mangle* stands of Bermuda (Ellison 1993), most temperate mangroves occur on sediment-rich continental margins and high islands. Thus, sedimentation in temperate mangrove systems is characterised by accumulation of terrigenous mineral sediments that are ultimately derived from the erosion of catchment soils and coastal margins (Bird 1986, Ellison 2009).

Terrigenous sediment yields have increased by an order of magnitude or more as a consequence of land use changes associated with human activities in catchments (Walling 1999). The impact of humans on the terrigenous suspended sediment flux to the coastal ocean has been evaluated by Syvitski et al. (2005) based on long-term hydrological records and modelling of the world's major river systems. In the warm temperate zone (10–25°C), the annual flux to the coastal ocean of about $8 \times 10^6 \pm 1.25$ (observational uncertainty) $\times 10^6$ t yr^{-1} is about 10% lower than the prehuman flux. A similar trend is observed for the global sediment flux and was attributed to sediment storage in floodplains and reservoirs constructed in large river basins during the twentieth century. However, the sediment loads delivered by small river systems that drain islands on tectonically active plate margins, such as occur in New Zealand, may be similar to loads delivered by large rivers on passive margins (Milliman & Syvitski 1992). The average size of catchments draining to estuaries with temperate mangroves in northern New Zealand is 239 km^2 (range 6–4194 km^2; Hume et al. 2007). These small, steep basins are subject to episodic intense rainstorms and have relatively small capacity to store eroded sediments, and sediment delivery to estuaries and coasts will generally be higher than for large basins (Griffiths & Glasby 1985, Milliman & Syvitski 1992, Elliot et al. 2009), such as those in south-eastern Australia (Wasson & Galloway 1986, Wasson 1994). For example, catchments draining to New South Wales estuaries with temperate mangrove habitat are an order of magnitude larger (average 2545 km^2, range 9–22,400 km^2; Roy et al. 2001) than occur in northern New Zealand.

The natural process of estuary infilling in New Zealand and south-eastern Australia has accelerated over the last approximately 200 years following catchment deforestation by European settlers. Environmental changes (i.e., catchment deforestation, drainage of wetlands, clearing of riparian vegetation and land conversion for pastoral agriculture and cropping) occurred rapidly and on a large scale. Widespread urbanisation of coastal margins has also occurred since the 1950s. At the peak of

Table 9 Summary of historical changes in temperate mangrove habitat in southern Australia, New Zealand and South Africa compiled from published sources

Location	Species	Time period	Habitat area (ha)	Habitat area change %	Habitat area change % yr^{-1}	Reference
Southern Australia						
Light River and Swan Alley, South Australia	A.m.	1949–1979	624–1221	96	3.2	Burton 1982
Jackson-Paramata River, NSW	A.m., A.c.	1930–1951	182–217.5	20	0.95	Thorogood 1985
Minnamurra River, NSW	A.m., A.c.	1938–1997	56.5–95.4	69	1.2	Chafer 1998
North Arm Creek, South Australia	A.m.	1979–1993	7.4–8.8	19	1.4	Coleman 1998
Tweed River, NSW	A.m.	1930–1994	144.1–281.9	96	1.5	Saintilan 1998
Kurnell Peninsula, Botany Bay, NSW	A.m., A.c.	1956–1996	80.8–120.3	49	1.3	Evans & Williams 2001
Currambene Creek, Jervis Bay, NSW	A.m.	1949–1993	34.1–44.9	32	0.7	Saintilan & Wilton 2001
Pittwater, NSW	A.m., A.c.	1940–1996	2–12.2	510	9.1	Wilton 2001
Kooweerup, Westernport Bay, Victoria	A.m.	1939–1999	11.3–18.1	60	1	Rogers et al. 2005b
Rhyll, Westernport Bay, Victoria	A.m.	1939–1999	40–62.3	56	0.9	Rogers et al. 2005b
New Zealand						
Houhora, Northland	A.m.	1944–1979	52.3–56.4	8	0.2	NCC 1984
Rangaunu, Northland	A.m.	1944–1981	1821.5–2415.5	33	0.9	NCC 1984
Ngunguru, Northland	A.m.	1942–1979	139.9–175.5	25	0.7	NCC 1984
Whangapae, Northland	A.m.	1939–1993	280–338.8	21	0.4	Creese et al. 1998
Tauranga, Bay of Plenty (8 subestuaries)	A.m.	1940–1999	13–168.2	1193	20.2	Park 2004
Whangapoua, Great Barrier Island, Auckland	A.m.	1960–1999	88–162.8	85	2.2	Morrisey et al. 1999
Puhinui, Auckland	A.m.	1939–1996	14.4–37.7	162	2.8	Morrisey et al. 2003
Puhoi, Auckland	A.m.	1960–2007	46.6–59.7	28	0.6	Swales et al. 2009
Waiwera, Auckland	A.m.	1960–2007	7.5–37.8	404	8.6	Swales et al. 2009
Orewa, Auckland	A.m.	1960–2007	17.9–41.9	134	2.9	Swales et al. 2009

Okura, Auckland	A.m.	1959–2007	12.1–25	106	2.2	Swales et al. 2009
Lucas Creek, Auckland	A.m.	1950–1996	47.5–50.5	6	0.14	Morrisey et al. 1999
Central Waitemata, Auckland	A.m.	1959–2007	722.5–665	−8	−0.17	Swales et al. 2009
Shoal Bay, Auckland	A.m.	1959–2007	149–139	−7	−0.15	Swales et al. 2009
Orakei, Auckland	A.m.	1959–2007	18.7–26	39	0.8	Swales et al. 2009
Whitford, Auckland	A.m.	1955–2007	72.4–112.1	55	1.1	Swales et al. 2009
Wairoa, Auckland	A.m.	1955–2007	124.7–161.7	30	0.6	Swales et al. 2009
Te Matuku, Auckland	A.m.	1940–2007	33–47.4	44	0.7	Swales et al. 2009
Wharekawa, Coromandel	A.m.	1983–2008	20.1–40	99	4	NCC 1984, EW 2009
Tairua, Coromandel	A.m.	1983–2008	12.1–35.6	194	7.8	NCC 1984, EW 2009
Manaia, Coromandel	A.m.	1971–2008	58.6–168.7	187.7	5.1	NCC 1984, EW 2009
Whangamata, Coromandel	A.m.	1978–2007	73.8–95.8	30	1	NCC 1984, EW 2009
Otahu, Coromandel	A.m.	1978–2007	1.9–10.2	448	15.4	NCC 1984, EW 2009
Coromandel Harbour	A.m.	1971–1999	27.5–61.6	124	4.4	NCC 1984, EW 2009
Te Kouma, Coromandel	A.m.	1971–1999	9.1–15.1	67	2.4	NCC 1984, EW 2009
Whitianga, Coromandel	A.m.	1970–1999	444.9–488.6	10	0.3	NCC 1984, EW 2009
Raglan, Waikato	A.m.	1979–2005	6.3–27.4	336	12.9	NCC 1984, EW 2009
Firth of Thames (south shore)	A.m.	1952–2006	75–741	888	16.4	Swales et al. 2007b
Firth of Thames (total)	A.m.	1983–2004	662–1100	66	3.1	NCC 1984, Brownell, 2004
South Africa						
Umhlatuze (Richards Bay), Kwazulu-Natal	A.m., B.g., R.m.	1974–1999	197–489	148	5.9	Bedin 2001, Ward & Steinke 1982
Mtamvuna, Eastern Cape	B.g.	1982–1999	1–0.25	−133	−7.8	Adams et al. 2004
Mzamba, Eastern Cape	B.g.	1982–1999	1–0.15	−118	−6.9	Adams et al. 2004
Mnyameni, Eastern Cape	A.m., B.g.	1982–1999	3–0	−100	−5.9	Adams et al. 2004
Mtentu, Eastern Cape	A.m., B.g.	1982–1999	1–2	100	5.9	Adams et al. 2004

(continued on next page)

Table 9 (continued) Summary of historical changes in temperate mangrove habitat in southern Australia, New Zealand and South Africa compiled from published sources

Location	Species	Time period	Habitat area (ha)	Habitat area change %	Habitat area change % yr^{-1}	Reference
Mzintlava, Eastern Cape	B.g.	1982–1999	1.5–1.75	17	1	Adams et al. 2004
Mntafufu, Eastern Cape	Am., B.g., R.m.	1982–1999	10–12.4	24	1.4	Adams et al. 2004
Mzimvubu, Eastern Cape	A.m., B.g.	1982–1999	1–0	−100	−5.9	Adams et al. 2004
Mngazana, Eastern Cape	Am., B.g., R.m.	1982–1999	150–145	−3	−0.2	Adams et al. 2004
Mtakatye, Eastern Cape	Am., B.g., R.m.	1982–1999	7.5–9	20	1.2	Adams et al. 2004
Mdumbi, Eastern Cape	A.m.	1982–1999	1–0.5	−50	−2.9	Adams et al. 2004
Mtata, Eastern Cape	Am., B.g., R.m.	1982–1999	34–42	24	1.4	Adams et al. 2004
Bulungula, Eastern Cape	Am., B.g., R.m.	1982–1999	3.5–0	−100	−5.9	Adams et al. 2004
Xora, Eastern Cape	Am., B.g.	1982–1999	16–16.5	3	0.2	Adams et al. 2004
Mbashe, Eastern Cape	Am., B.g.	1982–1999	12.5–14	12	0.7	Adams et al. 2004
Nqabara, Eastern Cape	A.m.	1982–1999	9–8.5	6	0.35	Adams et al. 2004
Nxaxo/Ngqusi, Eastern Cape	Am., B.g., R.m.	1982–1999	14–15	7	0.4	Adams et al. 2004
Kobonqaba, Eastern Cape	A.m.	1982–1999	6–3.5	−42	−2.5	Adams et al. 2004
Total, Eastern Cape (17 estuaries)		1982–1999	272–270.6	−0.4	−0.02	Adams et al. 2004

Note: A.c. = *Aegiceras corniculatum*; A.m. = *Avicennia marina*; B.g. = *Bruguiera gymnorrhiza*; R.m. = *Rhizophora mucronata*; NCC = Nature Conservation Council; EW = Environment Waikato.

these catchment land use changes in the mid- to late 1800s, catchment sediment yields were as much as several orders of magnitude higher than pre-European values of several tonnes km^{-2} yr^{-1} (Wasson & Galloway 1986, Prosser et al. 2001, Olley & Wasson 2003). Sediment yields have declined over the last century due to reforestation, destocking or reduced sediment supply but remain several times higher than pre-European values (Wasson 1994, Wilmshurst 1997, Erskine et al. 2002, Healy 2002, Swales et al. 2002, Olley & Wasson 2003). In South Africa, human activities in catchments had similar environmental effects: increased soil erosion due to overgrazing and poor farming methods and destruction of wetlands and riparian vegetation (Kakembo & Rowntree 2003, Adams et al. 2004, Foster et al. 2009) that have accelerated estuary infilling (Morant & Quinn 1999). Modern rates of terrigenous sediment supply to South Africa's eastern coast, associated with human activities in catchments, remain 10–20 times higher than geological rates of 15–25 t km^{-2} yr^{-1} (Martin 1987).

In temperate estuaries, these increased terrigenous sediment loads have resulted in increased water turbidity and accelerated sedimentation, with a shift to increasingly muddy intertidal systems and changing plant and animal communities (Chenhall et al. 1995, Morant & Quinn 1999, Nichol et al. 2000, Roy et al. 2001, Swales et al. 2002, Thrush et al. 2004). Although such studies have quantified the effects of human activities in catchments on temperate estuaries, there is a general paucity of data on rates of sediment delivery to receiving estuaries.

Sediment delivery to temperate mangrove forests

Mechanisms controlling delivery of terrigenous sediments to temperate mangrove forests in estuaries are spatially and temporally variable and reflect the relative importance of sediment transport by rivers, tides and waves. Fine suspended sediments are delivered directly or indirectly to mangrove forests by buoyant silt plumes discharged from rivers (Geyer et al. 1991), remobilisation and transport of muds stored in intertidal and subtidal deposits in estuaries by waves or currents (Green et al. 1997, Christie et al. 1999, Perry 2007), erosion of mangrove-fringed muddy coasts (Semeniuk 1980, J.T. Wells 1983, Mathew & Baba 1995, Walsh & Nittrouer 2004) and erosion and retreat of low-lying shorelines (Bird 1986).

Terrigenous sediments are largely delivered to estuaries during storms, and infrequent large-magnitude storms can account for years or decades of the average annual sediment load (Nichols 1977, Schubel & Pritchard 1986, Stern et al. 1986). Most of the terrigenous sediment load delivered to New Zealand and south-eastern Australian estuaries is composed of silt and clay particles transported in suspension (Griffiths & Glasby 1985, Roy et al. 2001, Healy 2002). By contrast, rivers deliver sand-rich sediments to many South African estuaries (Cooper et al. 1999). The cohesive behaviour of clay and fine silt particles differs markedly from sand (Dyer 1986). Mangrove forests preferentially accumulate these fine sediments in temperate (Woodroffe 1992, Kathiresan & Bingham 2001, Swales et al. 2002, Ellis et al. 2004, Swales et al. 2007b) and tropical environments (Bird 1972, Walsh & Nittrouer 2004).

Along tidal rivers and creeks in the upper reaches of estuaries, fine-sediment delivery to mangrove forests is primarily controlled by riverine and tidal forcing. Key mechanisms include tidal pumping, density-driven circulation and flocculation (Dyer 1986, Friedrichs & Aubrey 1988, Chant & Stoner 2001, Wolanski et al. 2001, Mehta 2002, Uncles 2002). In meso- and macrotidal estuaries, turbulent flows, density-driven circulation and tidal pumping maintains high suspended sediment concentrations (SSCs) in their upper reaches. Within this turbidity maximum, SSCs are higher than in the river system and receiving estuary (Dyer 1997), which supplies fine suspended sediments to riverine mangrove forests. Stormwater discharge alters the hydrodynamics of estuaries, such as the vertical stratification of the water column that develops due to differences in the density of freshwater run-off and saline estuarine waters (Fugate & Chant 2005, Traynum & Styles 2007). Under conditions of high freshwater discharge, baroclinic (salt-wedge) circulation can develop (Dyer 1997). Silt-laden stormwater in the seaward-flowing surface layer is delivered to riverine mangroves fringing the creeks during stratified-flow conditions when the water spills over the creek banks. Deposition of cohesive fine suspended sediments in mangrove forests is enhanced by flocculation (Furukawa et al. 1997), which produces aggregates composed of clay and fine silt-size particles. Settling velocities of these constituent particles, typically less than 0.005 cm s^{-1}, are orders of magnitude lower than for flocs (Wolanski et al. 2002). The process of floc formation and decay is modulated by tidal cycle variations in flow turbulence (Dyer 1986, Wolanski 1995, Augustinus 2002).

Seawards of the tidal creeks, temperate mangroves occupy intertidal flats fringing the central subtidal basin of semimature estuaries. The extent of these forests increases with tidal range and system maturity. In large estuaries, mangrove forests fringe extensive intertidal flats where sediment transport is controlled by waves (Green et al. 1997, Roy et al. 2001, Swales et al. 2007b). Tidal currents are relatively less important in mature infilled estuaries largely due to the small tidal volume exchanged (i.e., tidal prism) (Friedrichs & Aubrey 1988, Roy et al. 2001, Hume 2003). The short-period waves that typify fetch-limited estuaries are rapidly attenuated within the upper few metres of the water column. Consequently, sediment resuspension by waves is strongly modulated by tidal variations in water depth (Dyer 1986, Uncles 2002). Seasonal variations in biofilm production by benthic diatoms and fauna also influence tidal flat accretion and erosion (Grant et al. 1986, Meadows et al. 1990, Andersen 2001). In large muddy estuaries, wave attenuation may also occur in hyperconcentrated suspensions (i.e., SSC ~ 10 g l^{-1}) due to viscous-energy dissipation in fluid-mud wave-boundary layers (Mehta 2002, Gratiot et al. 2007). Once suspended, fine sediments can be transported long distances due to their low settling velocities (Lee & Mehta 1997), and transport velocities are generally much lower than required for sediment erosion (Postma 1961). Coupled with wind-driven surface flows and mass transport, these high-concentration suspensions are preferentially transported onshore during flood tides to mangrove forests fringing the intertidal flats (Bird 1986, Gratiot et al. 2007).

The role of mangroves in trapping sediments

The influence of temperate and tropical mangroves on sedimentation processes and geomorphic evolution of estuaries and coasts has been the focus of research since the early 1900s (Vaughan 1909, Davis 1940, Chapman & Ronaldson 1958, Stephens 1962, Scholl 1968, Scoffin 1970, Bird 1971, Carlton 1974). The question is "whether mangroves promote sedimentation, and thereby the evolution of depositional landforms, or whether they simply occupy sites that have become ecologically suitable, moving in to colonise (and possibly thereafter to stabilise and protect) an intertidal morphology that would have formed independently in their absence" (Bird 1986).

Reconstructions of the evolution of tidal flats/mangrove forests based on analysis of sediment cores and historical records have demonstrated the strong dependence of mangrove forest ecology on coastal geomorphology (Walsh & Nittrouer 2004, Swales et al. 2007b, J.C. Ellison 2008). In temperate and tropical mangrove forests, changes in habitat extent are closely linked to substratum elevation relative to sea level. Mangrove habitat expansion occurs on accreting tidal flats when the bed elevation has increased sufficiently for mangrove seedlings to colonise the substratum (Chapman & Ronaldson 1958, Thom 1967, Bird 1986, Panapitukkul et al. 1998, Bedin 2001, Swales et al. 2002, 2007b, Walsh & Nittrouer 2004, Carvalho do Amaral et al. 2006). Mangrove habitat loss has followed relative declines in surface elevation due to factors such as decreased sediment supply, tidal flat erosion, subsidence and relative SLR (Semeniuk 1980, Bird 1986, Ellison 1993, Lebigre 1999). These observations reflect the present consensus that mangroves are not in themselves 'land builders' (Mitsch et al. 2009).

Few physical process studies have been undertaken in temperate mangrove forests, and the following descriptions include studies done in tropical systems. Mangrove trees enhance the settling and accumulation of fine suspended sediments delivered by river plumes, tidal currents and waves in a number of ways.

In tidal rivers and creeks, suspended sediments are transported into mangrove forests by tidal currents and river plumes. Where the volume of flow through the mangrove forest is similar to or exceeds the tidal channel volume, mangrove forests can substantially influence creek hydrodynamics (Wolanski 1995). At low current velocities (i.e., less than about 5 cm s^{-1}) laminar flow prevails in mangrove forests. Turbulent flow is generated as current velocities increase, with the trunks, stems, leaves and root structures of mangrove trees and seedlings enhancing friction through pressure (form) drag and vegetation-induced viscous drag (i.e., eddy viscosity) (Wolanski et al. 1980, Mazda et al. 1995, Kobashi & Mazda 2005, Mazda et al. 2005, Mazda & Wolanski 2009). Pressure drag is generated by flow separation around the irregular-shaped structural elements of mangrove trees. The total drag force F_D induced by mangrove trees can be described as a function of the projected area of obstacles within the flow and a representative drag coefficient C_D for the particular mangrove species (Struve et al. 2003, Mazda et al. 2005). The F_D will also vary with tide level due to the changes in the projected area of trees with height above the bed. The eddy-viscosity coefficient f encompasses the effects of small-scale turbulence (eddies) on energy dissipation in the flow. Both F_D and f are enhanced by the presence of mangrove trees, the net effect of which is to reduce current velocities within mangrove forests. Current velocities within mangrove forests are typically on the order of 1–10 cm s^{-1} due to this drag-induced current dampening (Furukawa et al. 1997, Kitheka et al. 2002), in comparison with current velocities of 10–100 cm s^{-1} in tidal channels.

Tidal pumping is a key mechanism controlling the flux of suspended sediment to mangrove forests in riverine and tidal creek environments. Tidal pumping describes the asymmetry between the peak flood- and ebb-tide current velocities that develops in estuarine channels due to frictional deformation of the tide as it propagates in shallow water. Flood-tide durations are appreciably shorter, so current velocities are higher than for ebb tides. The degree of tidal asymmetry also varies over the spring–neap cycle (Dyer 1986). Bryce et al.'s (2003) multiyear study of a mangrove creek system demonstrated that changes in flood- and ebb-tide dominance over the spring–neap cycle controlled sediment delivery to mangrove forests. During neap tides, flows were contained with the channel with net flood-tide transport of suspended sediments to the head of the creek, where deposition occurred. These fine-sediment deposits were subsequently resuspended from the channel bed and transported into the mangrove during overbank spring tides.

In systems where mangrove forests occupy a substantial proportion of the tidal prism, current asymmetry in channels is reversed during overbank high spring tides. Under these conditions, water surface gradients induced by vegetation-enhanced friction result in shorter ebb tides with peak current velocities substantially higher than during flood tides (Wolanski et al. 1980, Woodroffe 1985b, Lessa & Masselink 1995). This ebb-tide dominance provides a mechanism to maintain a deep tidal channel with net export of creek sediments (Wolanski et al. 1980). In degraded mangrove systems, with reduced vegetation density, flood-tide dominance in channels is maintained, with net landward transport of suspended sediment (Kitheka et al. 2002). Baroclinic circulation developed during periods of relatively high freshwater discharge also enhances the landward transport of flocs in the near-bottom saline water (Wolanski 1995).

Sedimentation in riverine and tidal creek mangrove forests during overbank tides is dominated by the settling of clay-rich flocs. Settling is also enhanced by the stagnation zones of tree trunks and other flow obstructions (Furukawa & Wolanski 1996, Furukawa et al. 1997, Kitheka et al. 2002). Sedimentation rapidly declines with distance from distributory creeks due to the combined effects of current dampening and flocculation. Furukawa et al. (1997) found that about 40% of the suspended sediment advected into the forest was deposited within tens of metres of the creek edge, and 80% of the suspended sediment imported from coastal waters was trapped in the mangrove forest. In tidal creek systems at catchment outlets, stormwater may displace estuarine water from channels. Under these conditions, suspended silts are deposited as levees in mangroves fringing the channel banks (Swales et al. 2002).

On intertidal flats with sufficient fetches for wave generation, sediment trapping in fringing mangrove forests is enhanced by wave attenuation (Othman 1994, Brinkman et al. 1997, Massel 1999, Massel et al. 1999, Phuoc & Massel 2006, Quartel et al. 2007). Wave attenuation by plants has similarities with the physical mechanisms of vegetation drag-induced current dampening previously described for mangroves; the degree of wave attention varies with the submerged projected area of trees, and the drag profile is species dependent because of differences in tree morphology.

Although the spectral characteristics of waves propagating into mangrove forests are documented, little is known about sedimentation under attenuating waves. Suspended sediment influxes to mangrove forests typically increase with incident wave height (Phuoc & Massel 2006), which is consistent with wave-driven sediment resuspension on tidal flats (Green et al. 1997, Christie et al. 1999). Flocculation is also likely to be important (Furukawa et al. 1997), and the bulk of sedimentation will occur in the wave attenuation zone at the seaward margins of mangrove forests. This is consistent with sediment trap, marker bed and optical sensor data (Young & Harvey 1996, Ellis et al. 2004, Van Santen et al. 2007) and long-term sedimentation patterns derived from cores for mangrove forests in wave-dominated environments (Bird 1972, 1986, Lynch et al. 1989, Walsh & Nittrouer 2004, Swales et al. 2007b).

Moreover, hydroperiod (i.e., frequency and duration of inundation) also rapidly declines with surface elevation in the mangrove forest, so that sediment delivery is also modulated by the spring–neap tidal cycle. In mature mangrove forests where surface elevations are close to the upper tidal limit, delivery of this wave-driven suspended sediment influx only occurs episodically during high spring or storm tides (Swales et al. 2007b).

Sedimentation along the margins of mangrove forests may also be enhanced by the aerial roots of mangrove trees. Studies have included measurements of sedimentation rates in pneumatophore fields for several mangrove species, including *Avicennia marina*, under natural conditions as well as experiments using artificial pneumatophore arrays of various densities (10^2–10^5 m^{-2}). Environments have included wave-exposed mudflat/forest fringes and sheltered sites within forests (Bird 1971, Spenceley 1977, 1987, Bird 1986, Young & Harvey 1996). The results of these studies indicated differences in the pattern and rate of sedimentation that depended on the environmental conditions. Spenceley (1977) undertook experiments using artificial pneumatophore arrays with densities similar to the mangrove trees (400–1600 m^{-2}). His data suggested that local scour by waves occurred on mudflats and forest fringe during episodic storms, with local deposition occurring between these events. Bird (1986) mimicked the radial network of *A. marina* pneumatophore on a wave-exposed sand flat using pegs (density > 400 m^{-2}). Mud deposition was observed, and erosion followed the removal of the pegs. Similar experiments on a wave-cut platform and open mudflat did not induce sedimentation, which Bird (1986) attributed to local variations in sediment supply.

Manipulative experiments done within the sheltered interiors of mangrove forests also suggested that the influence of root structures on sedimentation depends on factors other than root density. Young & Harvey (1996) measured sedimentation rates over 3 mo around pneumatophore arrays of varying densities (100–350 m^{-2}) within an *A. marina* forest. Sedimentation was strongly and positively correlated with pneumatophore density. Differences between Young & Harvey's (1996) and Spenceley's (1977) results likely reflect differences in wave exposure (forest interior vs. fringe) and density of the artificial pneumatophore arrays. Krauss et al. (2003) extended this approach by considering the effect of root structure (i.e., pneumatophores, prop roots and root knees) on sedimentation and surface elevation changes in a Micronesian mangrove forest. Their 2.5-year field experiment included fringing, riverine and basin forests composed of *Rhizophora* sp., *Bruguiera gymnorrhiza* and *Sonneratia alba*. Treatments were prepared by removal of natural roots rather than the addition of artificial arrays, with the specific root area (cm^2 m^{-2}) used to account for differences in root density. Measurements enabled the contribution of subsurface processes, such as root biomass changes and sediment compaction, on net surface elevation changes to be constrained. The results indicated that annual sedimentation rates were significantly higher within the prop root treatments than for pneumatophore treatments or bare substrata controls in the riverine forest. By contrast, there were no significant differences in elevation changes between root types in all three forest types. Unlike Young & Harvey's (1996) study, Krauss et al. (2003) did not find a strong relationship between root density and sedimentation. This difference may reflect the greater 3-dimensional complexity of the natural root structure in the Micronesian forest and resulting hydrodynamic conditions.

The overall impression gained from these studies is that physical processes exert a strong control on sediment trapping in mangrove forests along with structural differences in the forest that relate to species composition and sedimentary environment. Present understanding of sediment dynamics and their role in the long-term development of temperate mangrove forests is limited.

Mangrove forest sediment budgets

Sediment budget studies of riverine mangrove forests have sought to quantify the role these systems play in sequestering terrigenous sediments in coastal and estuarine environments. Small-scale or short-term (i.e., tidal cycle or months) measurements of suspended sediment fluxes (Woodroffe 1985b, Furukawa et al. 1997, Kitheka et al. 2002) may not be representative of longer-term conditions. Over timescales of weeks to months, the direction of net suspended sediment transport in mangrove creek systems can be highly variable (Bryce et al. 2003). Historical data, reconstructions using dated sediment cores that integrate longer timescales (i.e., years to millennia) and modelling enable the geomorphic evolution of mangrove systems to be considered (Walsh & Nittrouer 2004, Swales et al. 2007b, J.C. Ellison 2008).

Sedimentation rates in temperate mangrove forests

Despite the importance of mangrove forests as sinks for terrigenous sediments, few detailed studies of sedimentation processes have been undertaken in modern mangrove systems (Woodroffe 1992, Walsh & Nittrouer 2004). By comparison, studies of mainly tropical autochthonous mangrove systems on sediment-starved oceanic low islands are more numerous (Lynch et al. 1989, Ellison & Stoddart 1991, Woodroffe 1992, Ellison 1993, Parkinson et al. 1994, Snedaker 1995, Cahoon & Lynch 1997, Valiela et al. 2001, Cahoon et al. 2006, McKee et al. 2007). This research interest in part reflects the vulnerability of these remote island mangrove systems to SLR associated with climate warming.

Sediment accumulation rates (SARs) have been estimated for temperate mangrove forests using a variety of techniques: marker beds (Chapman & Ronaldson 1958, Bird 1971, 1986), sedimentation pegs, artificial pneumatophores and plates (Spenceley 1977, Young & Harvey 1996, Coleman 1998, Perry 2007) and sediment-core geochronology. The radioisotopes lead-210 (^{210}Pb) and caesium-137 (^{137}Cs) have proved particularly useful to quantify SAR over annual-to-decadal timescales (Ellis et al. 2004, Rogers et al. 2005b, Perry 2007, Swales et al. 2007b). Radiocarbon (^{14}C) and pollen dating have also been used to estimate sedimentation rates in temperate mangrove forests over hundreds to thousands of years (Nichol et al. 2000, Carvalho do Amaral et al. 2006).

Short-term measurements (i.e., weeks to months) of sedimentation are unlikely to be representative of longer-term conditions in temperate mangrove forests. This is because large-scale ecosystem processes, such as mangrove forest development, occur over annual-to-decadal timescales. Morphological reconstructions of mangrove forest development based on long-term records provided by dated sediment cores, aerial photography and historical archives can overcome limitations of short-term studies (Dahdouh-Guebas & Koedam 2008, J.C. Ellison 2008). These data integrate the effects of biological and physical processes operating over annual-to-decadal timescales, which include the effects of episodic infrequent high-magnitude events, such as storms, that perturb the system. The temporal resolution of sediment cores is a potential limitation of these reconstructions, which depends mainly on sediment-mixing characteristics and SAR. Sediment-mixing effects become less pronounced as SAR increase (Valette-Silver 1993). High-resolution

Table 10 Summary of sedimentation rates in modern temperate mangrove forests from short- and long-term measurements (approximately last 100 yr)

Location	Environment	SAR (mm yr^{-1})	Method	Duration	Reference (species)
Waitemata Harbour, Auckland, New Zealand	Basin	~1.7	mb	14 mo	Chapman & Ronaldson (1958) (*A. marina* subsp. *australasica*)
Westernport Bay, Victoria, Australia	Fringe	1.3–15	mb	3 yr	Bird (1986) (*A. marina* subsp. *australasica*)
	Basin	3–8			
	High basin	0.7–2.3			
Firth of Thames, New Zealand	Fringe/basin	16–100	ap	3 mo	Young & Harvey (1996) (*A. marina* subsp. *australasica*)
		5.5	pegs	5 mo	
		6.4	tfs	~50 yr	
Pakuranga Creek, New Zealand	Tidal creek	3.5–26	^{137}Cs	~35 yr	Swales et al. (2002) (*A. marina* subsp. *australasica*)
		3.3–33	pollen		
Whitford Bay, New Zealand	Tidal creek	1.1–23	^{137}Cs	~50 yr	Ellis et al. (2004) (*A. marina* subsp. *australasica*)
Westernport Bay, Victoria, Australia	Fringe/basin	5–9	mb	3 yr	Rogers et al. (2005b) (*A. marina* subsp. *australasica*)
	Mangrove in salt marsh	1.4–2.5	^{210}Pb	~100 yr	
Bayou Larfourche, Louisiana, USA	Basin with salt marsh	0–17.7	mb	1 yr	Perry (2007) (*A. germinans*)
		5.3	^{137}Cs	~40 yr	
Firth of Thames, New Zealand	Fringe	30–100	^{210}Pb	~50 yr	Swales et al. (2007) (*A. marina* subsp. *australasica*)
	High basin	7–12	^{210}Pb		
	Average	21–36	^{137}Cs		

Note: Types of environment generally follow the classification of Lugo et al. (1976). High basin denotes mangroves near the upper-tidal limit. Sediment accumulation rates (SARs) from radioisotopes are time-averaged values and average annual values from upscaling of short-term (<1 yr) rates. Methods: marker beds (mb); artificial pneumatophores (ap); measuring pegs (pegs); pollen dating (pollen); tidal flat slope and historical aerial photography (tfs); caesium-137 (^{137}Cs); lead-210 (^{210}Pb). Radioisotope SARs are time-averaged values.

sediment cores are preserved in modern mangrove forests that are rapidly accumulating terrigenous sediments (i.e., 10–100 mm yr^{-1}) near large rivers and in systems with enhanced sediment supply following catchment disturbance (Allison et al. 1995, Augustinus 1995, Swales et al. 2002, 2007b, Walsh & Nittrouer 2004).

Table 10 summarises sedimentation rates in modern temperate mangrove forests and includes data from short-term experiments as well as longer-term SAR estimates derived from cores. With one exception (Louisiana; Perry 2007), these studies solely relate to the estuarine temperate mangrove forests (*Avicennia marina* subsp. *australasica*) of northern New Zealand and south-eastern Australia. Estimates of short-term sedimentation rates (0–18 mm yr^{-1}) over 1- to 3-yr timescales integrate some seasonal variability. Longer-term SARs derived from dated cores indicate differences based on geomorphic setting, system maturity or sediment supply. In relatively sediment-poor systems, sedimentation rates in mangrove forests are of the order of several millimetres per year (Rogers et al. 2005b, Perry 2007). High SAR measured in New Zealand mangrove forests (10–100 mm yr^{-1}) reflect large terrigenous sediment supply or close proximity to catchment outlets (e.g., tidal creeks). Sedimentation rates decrease over time as mangrove forests mature due to a progressive reduction in hydroperiod and sediment delivery (Swales & Bentley 2008). Patterns and long-term rates of sedimentation in tropical mangrove forests are similar to those reported for temperate systems (Lynch et al. 1989, Cahoon & Lynch 1997, Smoak & Patchineelam 1999, Walsh & Nittrouer 2004, Van Santen et al. 2007, Kamaruzzaman & Ong 2008).

The ecological significance of sedimentation in temperate mangrove systems primarily relates to the process of tidal flat accretion as a precursor to mangrove habitat expansion (Bird 1986, Bedin

2001, Roy et al. 2001, Swales et al. 2007b) and maintenance of surface elevation relative to sea level (Cahoon et al. 2006, McKee et al. 2007). The delivery of nutrients associated with sediment inputs to mangrove forests is a secondary factor (Saintilan & Williams 1999, Lovelock et al. 2007a). Mangroves and saltmarsh systems are particularly vulnerable to the effects of relative SLR because they occupy a relatively narrow elevation zone in the mid- to upper intertidal zone. The vulnerability of mangrove forests to inundation by rising sea levels has been evaluated based on long-term SAR data, with forest stability assumed to depend on sedimentation keeping pace with relative SLR (Parkinson et al. 1994, Alongi 2008, J.C. Ellison 2008). However, this approach does not account for the effects of *in situ* processes such as sediment compaction and subsurface root production, which also influence local surface elevation changes in mangrove forests (Cahoon et al. 2006, McKee et al. 2007).

The surface elevation table (SET) and marker bed technique (Boumans & Day 1993, Cahoon et al. 1995) enable substratum elevation changes to be apportioned to sedimentation and subsurface processes. This method has been applied to temperate (Rogers et al. 2005a,b, 2006, Rogers & Saintilan 2008, Stokes et al. 2009) and tropical mangrove forests (Cahoon & Lynch 1997, McKee et al. 2007). Cahoon et al. (2006) analysed SET data from a wide range of temperate and tropical mangrove forests in a range of geomorphic settings characterised by terrigenous and organic sediments. Sedimentation rates exceeded relative SLR at all sites, but net elevation changes were mostly negative due to shallow subsidence. Similar trends were observed in *Avicennia* and *Rhizophora* mangrove forests. Subsidence was also highest at sites with the highest sedimentation rates. These types of studies have highlighted the complex biotic and physical feedbacks that drive surface elevation dynamics in mangrove forests. However, records of surface elevation changes are relatively short and as yet do not provide a long-term perspective. Swales and Bentley (2008) reconstructed the morphodynamics of an *Avicennia marina* forest over the prior 50 yr based on high-resolution ^{210}Pb profiles preserved in low-permeability, rapidly depositing muds. The effects of sediment compaction were negligible, and SAR could be used to estimate surface elevation changes. Ultimately, the time resolution of stratigraphic records declines due to sediment compaction and lithification (J.C. Ellison 2008). However, under high-SAR regimes it would appear that detailed reconstructions of modern mangrove forest development can be obtained from sediment cores (Walsh & Nittrouer 2004, Swales & Bentley 2008).

Capacity of mangroves to mitigate coastal hazards

The presence of mangrove forests along low-lying shorelines has been credited with the mitigation of erosion and inundation hazards caused by local wind and swell waves (Othman 1994, Brinkman et al. 1997, Massel 1999, Massel et al. 1999, Phuoc & Massel 2006, Quartel et al. 2007, Alongi 2008), storms (Granek & Ruttenberg 2007, Alongi 2008) and tsunami (Harada & Kawata 2004, Dahdouh-Guebas et al. 2005, Danielsen et al 2005, Kathiresan & Rajendran 2005, Alongi 2008).

Mangrove forests are effective at attenuating the heights of wind waves and swell (wave periods < 30 s) due to vegetation-induced drag. Brinkman et al. (1997) measured a 25–50% reduction in wave energy within about 200 m of the seaward edge of a *Rhizophora* forest. Wave attenuation was also pronounced in a mixed *Avicennia* and *Rhizophora* forest, with a 50–70% reduction in wave energy occurring within 20 m of the forest edge (Phuoc & Massel 2006). The capacity of mangrove forests to attenuate waves depends on tree density, tree morphology, bed slope, spectral characteristics of the waves and water depth (Massel et al. 1999, Alongi 2008). The relative effect of these factors varies with mangrove species. For example, the drag induced by mangroves varies with water depth due to vertical differences in the submerged projected area of trees. The drag profile of *Avicennia* sp., with their peg-like pneumatophores, differs markedly from *Rhizophora* sp., with their large prop roots, so that wave attenuation by *Rhizophora* is more effective when the prop roots are partially submerged (Massel et al. 1999). Unlike *Rhizophora* sp., *Kandelia* sp. lack prop roots or pneumatophores, so that the largest flow obstruction is the leaf canopy, and wave attenuation is less effective when the canopy is exposed (Quartel et al. 2007).

Although mangrove forests effectively attenuate wind and swell waves and thereby protect soft-sediment shorelines from erosion, this may not be the case during severe storms (Massel et al. 1999, Alongi 2008). The erosive capacity of storm waves is much greater due to the quadratic increase in total energy with wave height. Penetration of storm waves into shallow-water coastal and estuarine environments is enhanced by elevated sea levels (storm tides) related to meteorological drivers (i.e., inverse barometric effect and wind setup) and spring tides. Important attributes of mangrove forests that mitigate storm erosion and inundation hazards include forest width, degree of sediment compaction, tree density and tree morphology (height, root structure, ratio of above- to below-ground biomass) (Alongi 2008). The capacity of mangrove trees to withstand bed erosion varies between species largely due to differences in root structure. For example, *Avicennia* spp. are anchored by a radial network of horizontal cable roots and vertical anchor roots within about the top 0.5 m of the substratum (Janssen-Stelder et al. 2002). Mudflat erosion during storms can detach these shallow-rooted mangrove trees, resulting in tree loss on the exposed seaward edge of mangrove forest (Othman 1994, Swales et al. 2007a). Bed erosion will also depend on the degree of substratum compaction, so that substrata in older forest stands will be more resistant to wave erosion (Othman 1994). Mangrove forests that occupy a wide band across the intertidal zone will also be more resilient to damage by episodic storms and may also reduce the risk of inundation of low-lying coastal land by protecting coastal defence structures from direct wave attack and dynamic run-up (Swales et al. 2007a).

The capacity of mangrove forests to mitigate tsunami hazard will depend on the tsunami characteristics, environmental setting and mangrove forest characteristics. Tsunami characteristics include source type (tectonic, volcanic, subsidence, underwater landslide); ocean volume displaced; size and speed; distance from source (remote, regional, local) and approach angle to the coast (de Lange 2003, Alongi 2008). The transformation of tsunamis as they propagate into the near shore will also differ markedly between open coasts and estuarine environments due to differences in shoreline bathymetry (i.e., seabed slope) and estuary shape, tidal volume, intertidal flat area and elevation. Tsunamis have unique hydraulic characteristics due to their much longer periods (0.1–1 h; de Lange 2003). Tsunamis propagate into estuaries in a similar way to tidal bores, with a large water mass behind the wave crest and momentum increasing as shoaling occurs (de Lange 2003, Alongi 2008). Transformations of a tsunami in estuaries are largely controlled by the tidal inlet characteristics, basin shape and volume, proportion of intertidal area, bed elevation and slope. For example, amplification of a tsunami in funnel-shaped estuaries occurs due to landward reduction in basin volume, whereas substantial attenuation in estuaries with extensive intertidal flats is due to friction.

Attributes of mangrove forests that determine their value in tsunami hazard mitigation are similar to those described for storm waves. The degree of forest modification by humans may also be a factor (Dahdouh-Guebas et al. 2005, Danielsen et al. 2005, Kathiresan & Rajendran 2005). In the aftermath of the 2004 Indian Ocean tsunami, several thousand hectares of tropical mangrove forest were uprooted due to bed erosion or died due to prolonged inundation (Alongi 2008). Mangrove species with wide prop roots or knee roots, such as *Rhizophora* and *Bruguiera* sp., withstood the tsunami surge, and forests with *Rhizophora* along their seaward fringes experienced less damage. Mangrove species with shallow, subsurface cable roots, such as *Avicennia* sp., were less effective at withstanding the tsunami (Kathiresan & Rajendran 2005). Modelling of tsunami flow attenuation by mangroves also indicated that species-related differences in drag coefficient are important (Tanaka et al. 2007, Alongi 2008).

Temperate mangrove forests are composed of relatively few species (dominated by *A. marina*), so that their capacity to mitigate tsunami hazard will be less than reported for tropical mangroves. Monospecific stands of *A. marina* occur in northern New Zealand, Victoria, South Australia and

South Africa's Eastern Cape Province, which are susceptible to bed erosion and will provide minimal protection in many cases. In northern and central NSW and South Africa, mangrove forests include more robust *Rhizophora* and *Bruguiera* species. These mixed-species forests are likely to be more effective at mitigating tsunami hazard (Alongi 2008). However, the protective function and resilience of *Avicennia marina* will be enhanced where forests occupy wide intertidal zones that have the capacity to provide an erosion buffer as well as attenuate the tsunami flow. The recovery time of mangrove forests from large-scale disturbances will vary from years to decades depending on event magnitude (Alongi 2008). Thus, large forests will generally have the highest capacity to mitigate storm and tsunami hazards.

The role of mangroves in the ageing of temperate estuaries

The role of biology in long-term landscape evolution is an emerging theme in geomorphology. The concept of 'biomorphodynamics' encapsulates the two-way couplings between biological processes and the physical processes of sediment transport and morphological evolution (Murray et al. 2009). Dietrich & Perron (2006) posed the following question in relation to landscape evolution: "If life had not arisen, would the tectonic and climatic processes that drive uplift and erosion of landscapes be significantly different?" In the context of the present review, it also is apparent that the physical processes that control sediment transport are fundamental drivers of temperate mangrove ecology. Here, we ask the more specific question: What is the role of temperate mangroves in the natural ageing of estuaries?

As has already been seen, estuaries are long-term sinks for terrigenous and marine sediments. How rapidly estuaries have infilled or 'aged' has mainly depended on the original shape and volume of their tidal basins, the rate of sediment supply and their ability to flush sediment to the sea. These factors largely explain observed regional differences in estuarine maturity (Roy et al. 2001).

The geomorphic evolution of estuaries exerts a direct control on temperate mangrove ecology through the process of sedimentation and tidal flat development. Mangroves colonise intertidal flats only after they have become "ecologically suitable" (Bird 1986). More specifically, the physical process of estuarine sedimentation builds intertidal flats that provide potential habitat for mangroves. On intertidal flats in temperate regions, a lower elevation threshold for growth of mangrove forests occurs at about MSL. This threshold primarily relates to the physiological requirement of mangroves, particularly seedlings, for regular emersion (Clarke & Hannon 1970). Although tidal flat accretion provides the opportunity for mangrove forest development or expansion, the actual pattern of seedling recruitment also depends on physical factors, such as wave energy at the site and dispersal of propagules by currents, in addition to biotic factors, such as predation of propagules (Clarke & Kerrigan 2002, and see discussion on p. 124).

Thus, rapid expansion of temperate and tropical mangrove forests has occurred mainly in estuaries and deltas with large terrigenous sediment supply and rapidly accreting intertidal flats (Thom 1967, Panapitukkul et al. 1998, Bedin 2001, Walsh & Nittrouer 2004, Carvalho do Amaral et al. 2006, Swales et al. 2007b). These patterns of mangrove forest expansion are also consistent with long-term reconstructions of estuarine development over centuries or millennia. These reconstructions showed that, as estuaries infill with fluvial sediments, tidal flats build seaward and mangroves initially colonise tidal flats in the upper reaches of the estuary. As the accommodation space is filled, tidal flats expand into the central basin, where the most extensive mangrove forests occur. Eventually, the estuary becomes largely intertidal, and mangrove forests occupy the entire tidal flat area save for areas drained by narrow, sinuous, fluvial channels (Swales et al. 1997, 2002, Roy et al. 2001, Hume 2003, Carvalho do Amaral et al. 2006).

Humans have accelerated the natural process of estuary infilling by increasing terrigenous sediment delivery to estuaries. Average SARs are typically an order of magnitude higher today than prior to catchment deforestation (Wasson & Galloway 1986, Martin 1987, Wasson 1994, Wilmshurst

1997, Morant & Quinn 1999, Prosser et al. 2001, Erskine et al. 2002, Healy 2002, Swales et al. 2002, Kakembo & Rowntree 2003, Olley & Wasson 2003, Adams et al. 2004, Foster et al. 2009). Estuarine sedimentation has also been exacerbated by engineering structures that reduce the sediment accommodation space (e.g., reclamations) and restrict tidal flows and wave fetch (e.g., causeways). It can be argued that the accelerated ageing of estuaries due to human activities largely explains the rapid expansion of temperate mangrove forests that has occurred in many New Zealand, south-eastern Australian and South African estuaries.

Are temperate mangrove forests therefore merely a symptom of estuarine maturity rather than agents of geomorphic change, or do they exert other, subtle effects on the natural process of estuarine ageing? Mangrove forests are highly effective at dampening currents (e.g., Wolanski et al. 1980, Furukawa et al. 1997, Mazda & Wolanski 2009) and attenuating waves (e.g., Brinkman et al. 1997, Massel et al. 1999, Phuoc & Massel 2006), so that they preferentially accumulate suspended fine particles and flocs composed of silt and clay particles (Woodroffe 1992, Kathiresan & Bingham 2001, Swales et al. 2002, 2007b, Ellis et al. 2004, Walsh & Nittrouer 2004) delivered by river plumes and tidal currents or resuspended from tidal flats. In doing so, temperate mangrove forests may mitigate some of the adverse effects of fine terrigenous sediments on estuarine and coastal ecosystems (Thrush et al. 2004). For instance, this sequestration function may add to the fine-sediment budget of large, infilled, wave-dominated estuaries (e.g., Swales et al. 2007b) that would otherwise export a large fraction of their terrigenous sediment load to the coast. In doing so, the mangrove forests enhance the sediment-trapping function of estuaries, even in relatively mature systems. Ultimately, this sediment trapping will be limited by the available accommodation space for sediment in an estuary, with sedimentation rates proportional to relative SLR (Woodroffe & Davies, 2009).

Patterns and causes of changes in the distribution of temperate mangroves

The rapid deforestation of terrestrial ecosystems over the last century has been mirrored in coastal marine ecosystems with large-scale loss of mangrove habitat. An estimated 75% of the world's tropical coasts were originally fringed by mangrove forests compared with 25% today. About one-third of this deforestation has occurred since the 1980s (Chapman 1976, Rönnbäck et al. 1999, Valiela et al. 2001). The current global rate of mangrove habitat destruction is estimated at 2.1%, which exceeds the rate for tropical rainforest. Major causes of tropical mangrove habitat loss associated with human activities include reclamations for industrial, residential and tourism developments, aquaculture and salt production (United Nations Environment Program, World Conservation Monitoring Centre [UNEP-WCMC] 2006). Despite this global trend of net mangrove habitat loss, expansion of tropical mangrove forests has occurred in some systems, particularly in forests growing on river deltas (Neil 1998, Panapitukkul et al. 1998, Lebigre 1999, Lacerda et al. 2007).

Historical loss of temperate mangroves in New Zealand and south-eastern Australian estuaries has followed the construction of causeways and structures that restrict tidal flows or elevate water levels, marina development, stock grazing, stormwater pollution, dredging, reclamations for ports, waste landfills, airports, agriculture, industrial and urban development, harvesting for timber and charcoal manufacture and excessive sedimentation (Chapman & Ronaldson 1958, Nature Conservation Council 1984, Thorogood 1985, Bird 1986, Crisp et al. 1990, Thomas 1993, Williams & Watford 1997, Wright et al. 1997, Steinke 1999, Adams et al. 2004). Large-scale loss of mangrove habitat occurred in New Zealand and south-eastern Australia prior to the 1960s (Glanville 1947, Morrisey et al. 2007). The introduction of new legislation, such as New Zealand's Harbours Amendment Act 1977, made it illegal to reclaim seabed for agricultural purposes, so that mangrove habitat loss has substantially reduced since that time. More recently, New Zealand coastal communities have lobbied regional and central government agencies for the controlled removal of mangroves to restore tidal flat habitats and recreational amenities. In other estuaries, mangrove removal has occurred illegally (Morrisey et al. 2007). In South Africa, extensive mangrove habitat loss during the 1960s–1970s was related to harbour development, bridge construction and land development impacts. Natural events such as lagoon-mouth closures and tidal flat erosion by storm flows in river-dominated estuaries have also resulted in loss of mangrove habitat (Cooper et al. 1999, Steinke 1999). Long-term habitat loss has occurred in Bermuda due to relative increases in sea level that have outpaced peat sediment accretion in mangrove stands (Ellison 1993). The total extent of temperate mangrove habitat loss in New Zealand, Australia and South Africa cannot be accurately quantified because much of this loss occurred before aerial photographic surveys began in the 1930s.

Despite these historical losses, increases in temperate mangrove distribution have occurred in New Zealand, south-eastern Australian (*Avicennia marina*) and South African (*A. marina*, *Bruguiera gymnorrhiza*, *Rhizophora mucronata*) estuaries during the last 50–70 years. Mangrove colonisation of tidal flats as well as encroachment into saltmarsh habitats has been documented (Burton 1982, Burns & Ogden 1985, Mitchell & Adam 1989, Coleman 1998, Creese et al. 1998, Saintilan 1998, Saintilan & Hashimoto 1999, Saintilan & Williams 1999, Bedin 2001, Evans & Williams 2001, Saintilan & Wilton 2001, Wilton 2001, Adams et al. 2004, Ellis et al., 2004, Rogers et al. 2005b, Morrisey et al. 2007, Swales et al. 2007a,b, 2009). The black mangrove (*Avicennia germinans*) has also re-established in the *Spartina* salt marshes of Louisiana following dieback due to severe winter frosts in the late 1980s (Perry 2007, Saintilan et al. 2009).

Historical records also indicate a longer-term pattern of mangrove habitat expansion in south-eastern Australian estuaries since the time of European settlement (McLoughlin 1987, Saintilan & Williams 1999, McLoughlin 2000). In New Zealand, estuaries with relatively large catchments infilled with terrigenous sediment and had been colonised by mangroves by the early twentieth century. This process of estuary infilling was accelerated by large-scale catchment deforestation in the mid- to late 1800s (e.g., Swales et al. 1997, 2002). Extensive areas of mature mangrove forest, infrequently inundated by high spring tides, had developed in the Kaipara Harbour (Northland) before the 1920s (Ferrar 1934). However, in other estuaries with large sediment supply, such as the Firth of Thames, mangrove habitat expansion has only occurred in recent decades. Captain James Cook, who visited the Firth in 1769, recorded that mangroves were present on the delta of the Waihou River (Beaglehole 1968). Aerial photographs from the 1940s showed that these deltaic mangrove forests had not substantially increased their distribution since Cook's time. Large-scale mangrove habitat expansion did not occur until the 1950s (Swales et al. 2007b).

Mangrove habitat expansion

Causes of expansion

Recent expansion of temperate mangrove habitat observed in New Zealand and south-eastern Australian estuaries has been attributed to estuary infilling and vertical accretion of tidal flats (Chapman & Ronaldson 1958, Bird 1986, Young & Harvey 1996, Creese et al. 1998, Saintilan & Williams 1999, Ellis et al. 2004, Swales et al., 2007b), increased nutrient inputs (Saintilan & Williams 1999), climate warming (Burns & Ogden 1985), changes in relative sea level due to sedimentation or subsidence (Burton 1982, Rogers et al. 2005a,b, 2006) or a combination of all or some of the these factors. Seaward expansion of mangrove habitat onto accreting intertidal flats is a feature of New Zealand estuaries (Burns & Ogden 1985, Deng et al. 2004, Morrisey et al. 2007, Swales et al. 2007a), whereas landward encroachment into salt marshes is a notable trend in south-eastern Australian estuaries (Saintilan & Williams 1999, 2000, Wilton 2002, Williams & Meehan 2004). Mangrove encroachment of salt marshes in NSW and Victoria is correlated with declines in tidal flat surface elevations and resulting increases in tidal inundation (Rogers et al. 2005b, 2006). Tidal creeks and drainage channels provide conduits for mangrove propagules to penetrate into saltmarsh habitats (Saintilan & Williams 1999, Rogers et al. 2005b). Mangrove encroachment into salt marsh is not well documented in New Zealand estuaries (Morrisey et al. 2007). Temperate mangroves have also increased their distribution in some South Africa estuaries in recent decades. This change has been attributed to increased sediment delivery to estuaries and tidal flat accretion, although increases in mangrove habitat have been modest in most cases. Future increases in mangrove habitat are also likely to be constrained by the limited extent of suitable habitat, cyclic erosion of river-dominated estuaries and limited number of permanently open barrier estuaries (Wright et al. 1997, Cooper et al. 1999, Steinke 1999, Bedin 2001, Adams et al. 2004). In southern Brazil (e.g., Baia da Iiha Grande), mudflat accretion and seaward progradation of mangrove forests has been limited by low sediment supply (Vann 1980).

Patterns and extent of expansion

Table 9 summarises information on changes in the extent of mangrove habitat in New Zealand, south-eastern Australian and South African estuaries compiled from journal articles and published reports. The studies included data from small mangrove stands as well as large forests (10^0–10^3 ha) and major estuary types (i.e., drowned river valleys, barriers, embayments and coastal lagoons). Mangrove habitat mapping is primarily based on analysis of time series of aerial photographs taken since the 1940s–1950s. The majority of studies came from New Zealand and south-eastern Australia and related to monospecific stands of the *Avicennia marina* subsp. *australasica*. South African studies included mixed-species forests, although these are also predominantly composed of *A. marina* stands. The reliability of the habitat change data varied from study to study due to the methods employed, image scale and quality, habitat classification and accuracy of habitat boundary digitization. The historical periods covered by these studies also varied in length and timing. Few, if any, of the studies satisfied recent protocols for mangrove habitat mapping (Wilton & Saintilan 2000). Although the dataset is not exhaustive, it is sufficient to enable the general patterns and scale of changes in temperate mangrove habitat over the last several decades to be identified.

Rate of mangrove habitat expansion in south-eastern Australian estuaries (average 2.1% yr^{-1}, range 0.7–9.1% yr^{-1}) are substantially lower and less variable than occur in New Zealand estuaries (average 4.1% yr^{-1}, range −0.2 to 20.2% yr^{-1}; Table 9). In South Africa's Eastern Cape Province, the total area of mangrove habitat in estuaries was relatively stable during the period 1982–1999 (−0.02% yr^{-1}). This statistic masks a pattern of habitat expansion and declines for individual estuaries (Adams et al. 2004). Many of these mangrove forests are also small, with 60% being less than 10 ha in size (Table 9). In Kwazulu-Natal, rapid mangrove habitat expansion (5.9% yr^{-1}) in Umhlatuze Estuary (Richards Bay) during 1974–1999 followed the construction of a berm to reduce sedimentation in the port. The berm isolated the Umhlatuze River from the northern half of the estuary and initiated a sequence of large-scale deltaic sedimentation, rapid vertical tidal flat accretion and mangrove habitat expansion in the estuary. The Umhlatuze forest represents about 50% of the temperate mangrove habitat in South Africa.

In northern New Zealand, rapid mangrove habitat expansion in many estuaries reflects high rates of sediment delivery from relatively large catchments. For example, the Wairoa Estuary (high-tide area 3 km^2) represents a mature end member of drowned river valley estuaries on Auckland's eastern coast. The sediment load delivered by its 311-km^2 steep-land catchment had formed extensive intertidal flats that were colonised by mangroves before the 1940s (Swales et al. 2009). A regional study of Auckland estuaries confirmed that the largest increases in mangrove habitat over the last 50–60 years have occurred in the smallest (i.e., <5-km^2) systems (Swales et al. 2009). During the same time, there were virtually no increases in mangrove habitat in the largest estuaries, such as the 65-km^2 Waitemata Harbour, which accounts for 30% of the 2700 ha of mangrove habitat in these estuaries today. In fact, substantial habitat loss (−8%; Table 9) occurred in the Waitemata

Harbour due to reclamations associated with motorway construction, industrial development and refuse landfills in the 1950s–1970s.

Controls on expansion

Temperate mangrove habitats in New Zealand, south-eastern Australia and South Africa are dominated by the genus *Avicennia*, which displays the widest tolerance to environmental factors, such as water salinity, low air and water temperatures, frost frequency and severity and day length (Chapman 1976, Duke 1990, Augustinus 1995, Stuart et al. 2007, Krauss et al. 2008, Woodroffe & Davies 2009). Within its latitudinal range, factors controlling mangrove habitat expansion primarily relate to tidal flat elevation and seedling dispersal, establishment and survival. In this section, the physical processes that influence the spatial distribution of temperate mangroves within estuaries are reviewed.

Tidal amplitude and intertidal flat slope exert first-order controls on the spatial distribution and extent of intertidal flat habitat above MSL elevation. Tides in northern New Zealand are mesotidal (range 2–4 m), whereas those in south-eastern Australia and along South Africa's eastern coast are microtidal (range <2 m) (Bird 1984, Schumann et al. 1999, de Lange et al. 2003). The most extensive intertidal flats suitable for mangroves occur in mature estuaries with large tidal amplitudes and terrigenous sediment supply, such as occur in northern New Zealand. The relationship between relative catchment size and degree of estuary infilling has been demonstrated for the large drowned valley systems of NSW (Roy et al. 2001) and the drowned river valley and barrier estuaries of Auckland's eastern coast (Swales et al. 2009). In the New Zealand study, estuaries with relatively large catchments, which are most at risk of infilling, have also experienced the largest increases in mangrove habitat over the last 50 years (Swales et al. 2009).

Temperate mangrove species occupy the mid- to upper intertidal zone between high tide and MSL elevation (Galloway 1982, Bird 1986, Clarke & Myerscough 1993, Ellison 1993, Steinke 1999, Schaeffer-Novelli et al. 2002), although the exact elevation limits of temperate mangroves species have not been adequately determined (Clarke & Myerscough 1993, Ellison 2009). An important distinction to make in evaluating information on the lower elevation of temperate mangrove forests is between dynamic sea level and MSL attributed to a fixed vertical datum. The latter is typically defined on the basis of historical sea-level records from tide gauges. For example, the fixed MSL datum at Auckland (Auckland Vertical Datum 1946, AVD-46) is based on sea-level measurements during the 1920s–1930s. Likewise, the Australian Height Datum (AHD) is based on MSL measured during the period 1966–1968. By contrast, the dynamic or actual MSL is a varying level that accounts for the effects of long-period fluctuations in sea level. These include the annual heating and cooling cycle, multiyear El Niño-Southern Oscillation (ENSO) cycle, longer-term 20- to 30-yr Interdecadal Pacific Oscillation (IPO) and progressive SLR associated with climate warming. These annual–decadal cycles result in decimetre-scale variations in MSL from year to year (Goring & Bell 1999, Hannah 2004) and in doing so may influence seedling recruitment in a given year by elevating or depressing sea levels. In the long term, SLR associated with climate warming also has ecological significance because of the potential for mangrove habitat loss. For example, relative SLR at Auckland has averaged 1.4 mm yr^{-1} over the last century (Hannah 2004), so that actual MSL today is now about 0.13 m higher than in the 1920s–1930s. This increase in relative SLR translates into a potential 3–250 m landward retreat of the MSL elevation contour for the range of tidal flat slopes in Auckland estuaries. This predicted retreat does not take into account increases in tidal flat elevations due to estuary sedimentation, which has averaged 3.8 mm yr^{-1} over the last 50 years (Swales et al. 2009). The relative importance of short-term sea-level variations and progressive long-term relative SLR on the LEL of present-day temperate mangrove forests is not known.

The LEL for temperate mangroves at about MSL elevation primarily reflects the fact that mangrove seedlings are intolerant to continuous submersion (Clarke & Hannon 1970). Regular daily exposure enables seedlings to maintain an adequate oxygen supply to their tissues, particularly as mangroves typically grow in anaerobic muddy substrata. Laboratory experiments to determine the influence of submergence on the growth and development of *Avicennia marina* seedling indicated a statistically significant effect of inundation time on root mass (Curran et al. 1986, Hovenden et al. 1995). Although aerobic respiration in roots can be maintained throughout a 6-h period of tidal inundation (Curran et al. 1986), a large reduction in root growth rates occurred for inundation periods in excess of about 4 h (Hovenden et al. 1995). Semidiurnal tides with periods of 12.4 h prevail in northern New Zealand, south-eastern Australia and South Africa's eastern coast (Schumann et al. 1999, de Lange et al. 2003), so that tidal flats above MSL are submerged for no more than about 6 h per tidal cycle.

The distribution of *A. marina* was surveyed by Clarke and Myerscough (1993) along four transects in Botany Bay and Jervis Bay (NSW), with mangroves observed down to MSL (AHD). In Tauranga Harbour (Bay of Plenty, New Zealand), grey mangroves extend down to MSL in sheltered creeks and bays and 0.2 m above MSL on open tidal flats in the harbour (Park 2004). Swales et al. (2009) surveyed the LEL for *Avicennia* forests in terms of actual MSL (2007) along 81 transects in 17 Auckland estuaries. The average LEL for adult mangrove trees varied between estuaries (−0.05 to 0.76 m MSL), with an overall average of 0.35 m MSL. For seedlings recruited during the summer of 2007/2008, the LEL varied between −0.41 and 0.21 m MSL, with an overall average of −0.15 m MSL. Mapping of the MSL elevation contour from aerial photography using the waterline method (George & Gulliard 2003) also indicated that the seaward edge of mangrove forests occurred down to −0.33 m MSL in several estuaries (Swales et al. 2009).

In the fetch-limited, infilled estuaries that characterise temperate mangrove habitats, sediment transport on intertidal flats is largely driven by small short-period waves (Green et al. 1997, Roy et al. 2001, Hume 2003, Green & Coco 2007). Thus, these estuarine waves influence substratum stability, mangrove seedling recruitment and the lower elevation of mangroves on intertidal flats (Chapman & Ronaldson 1958, Clarke & Allaway 1993, Clarke & Myerscough 1993, Augustinus 1995, Osunkoya & Creese 1997, Park 2004, Swales et al. 2007b, 2009), although few studies have considered the ecological significance of these physical processes in detail.

Clarke & Myerscough (1993) studied *A. marina* propagule and seedling establishment in Botany Bay and Jervis Bay (NSW). Mangrove seedlings occurred above and below the elevation limits of adult trees. However, seedlings growing on the mudflats displayed substantially higher mortality after 2 yr than seedlings growing in the forest. Less than 5% of seedlings remained on the mudflats after 3.5 yr in comparison with 50% of seedlings in the mangrove forest. The low rate of seedling recruitment on the mudflats as well as the low density of seedlings on mudflats in other south-eastern Australian estuaries was attributed to "the mechanical effects of tides and currents on establishment". Osunkoya & Creese (1997) evaluated the survival and growth of self-established and transplanted *A. marina* seedlings in three New Zealand estuaries (Bay of Islands, Whangateau and Tauranga). Seedlings on lower intertidal flats had disproportionately (but not significantly) higher mortality rates after 18 mo, although higher growth rates, than seedlings on mid- to high intertidal flats. Seedling density declined with decreasing substratum elevation, which Osunkoya and Creese attributed to increased substratum erosion by tides and waves. The survival of recently settled *A. marina* propagules and seedlings on an energetic wave-exposed mudflat was also monitored by Swales et al. (2007b). Propagule and seedling numbers declined rapidly and exponentially, with fewer than 10% remaining after 2 mo. Seedling mortality was not significantly influenced by site or distance from the forest fringe, and surviving seedlings were actively growing. Loss of propagules and seedlings was due to frequent and deep erosion (~7 cm) of the mudflat by waves. Swales et al. (2007b) hypothesized that major recruitment events were likely to coincide with infrequent periods of calm weather lasting 3–5 wk, which is the time required for *A. marina* propagules to strike roots and establish (Clarke 1993). Apart from the realisation that waves influence mangrove seedling recruitment in estuaries, present understanding of this process is largely qualitative.

Regional-scale and long-term effects of wave exposure on mangrove seedling recruitment in estuaries were considered by Swales et al. (2009). Overall, mangrove forests occupied only 58% (2710 ha) of their potential habitat above actual MSL. Within individual estuaries, the area above MSL occupied by mangroves varied from 22% to 74% and was generally higher in small estuaries (high-tide area, $A < 5$ km^2) with large catchments ($A \geq 10$ km^2). Substantial increases in mangrove habitat have occurred in these estuaries since the 1950s (28–400%). However, the historical record suggests substantial time lags (i.e., decades) between tidal flat accretion and subsequent colonisation by mangroves. Modelling of long-term wave climate and sediment entrainment indicated that seedling establishment was more likely to occur in smallest estuaries ($A < 5$ km^2), which was consistent with the historical patterns of mangrove habitat expansion.

In contrast to the dominant role of physical processes influencing the lower elevation of temperate mangrove forests, factors influencing the upper elevation limit (UEL) are more varied. Maximum tide height represents a first-order control on the UEL. Tidal flows control propagule delivery to the upper intertidal zone (Saintilan & Williams 1999, Rogers et al. 2005b) and maintain substratum porewater salinity, preventing establishment of freshwater plants (Chapman 1976, Gillanders & Kingsford 2002, Mitsch et al. 2009). Porewater salinities in mangrove forest sediments are also enhanced by evapotranspiration, with salinities of about 50 or more being substantially higher than seawater (Galloway 1982, Swales et al. 2007b, Mitsch et al. 2009). In NSW estuaries, the upper limit of *A. marina* stands occurs at about mean high-water neap (MHWN) tide elevation. Mixed stands of *A. marina* and the river mangrove *A. corniculatum* occur at higher elevations in salt marsh (Clarke & Myerscough 1993). In Westernport Bay (Victoria), the upper limit of *A. marina* occurs between mean high-water spring (MHWS) and MHWN tide levels (Bird 1986). In the estuaries of northern New Zealand and South Africa's eastern coast, mangrove forests generally occur up to MHWS tide elevation (Chapman & Ronaldson 1958, Steinke 1999, Swales et al. 2007b). Mature forests of *A. marina* also occur in New Zealand estuaries above MHWS elevation, and episodic storm tides can substantially increase the hydroperiod in these forests (Swales et al. 2007b).

In south-eastern Australia, the pattern of mangrove encroachment into saltmarsh habitat is not ubiquitous, and in many estuaries the boundaries between saltmarsh and mangrove habitats have remained stable over the last 50 years or more (Saintilan & Williams 1999). Where landward expansion of mangroves has occurred, propagules have used tidal creeks and artificial drainage channels as conduits to enter saltmarsh habitats (Saintilan & Williams 1999, Rogers et al. 2005b). At elevated saltmarsh sites, *A. marina* propagules may fail to establish due to desiccation after settlement (Clarke & Myerscough 1993). In Westernport Bay (Victoria), mangrove encroachment was strongly correlated with decreases in saltmarsh surface elevation because mangroves generally establish at lower tidal elevations (Rogers et al. 2005b). Declines in marsh surface elevation coincided with El Niño drought conditions, as was also observed in NSW estuaries, so that groundwater recharge may play a significant role in controlling marsh surface elevation (Rogers et al. 2005a, 2006). The effects of progressive SLR on mangrove encroachment into salt marshes may also be exacerbated during droughts. However, subsidence rates in salt marshes and the exact causal mechanisms vary from site to site (Cahoon et al. 2006, Rogers et al. 2006).

In south-eastern Louisiana, the observed south-to-north expansion of *A. germinans* into *Spartina alterniflora* (cordgrass) salt marsh has coincided with two decades of mild winter air temperatures (Perry 2007, Saintilan et al. 2009). Mangrove and saltmarsh zonation differs from south-eastern Australia in that *Avicennia germinans* generally occupies the upper intertidal zone, whereas *Spartina* salt marsh occurs at lower elevations. Patterson et al. (1993) did greenhouse and field-transplant experiments to study factors controlling mangrove seedling establishment in *Spartina* salt marsh. The survival and growth of mangrove seedlings in salt marsh were reduced in comparison with the mangrove forest. Seedling mortality in the lower salt marsh followed submergence and sediment deposition on leaves. Sulphide concentrations were also about eight times higher in saltmarsh sediments. Patterson et al. (1993) attributed the lower success of mangrove seedling recruitment in salt marsh to less-than-optimal physicochemical conditions as well as competition. Where mangrove encroachment has occurred, substratum physicochemical conditions, long-term (^{137}Cs) sedimentation rates and above- and below-ground productivity are not significantly different from pure saltmarsh habitats. Environmental changes may emerge as larger mangrove stands and forests develop in these saltmarsh systems (Perry 2007).

In many estuaries, engineering structures restrict the landward expansion of mangrove forests by physical exclusion, restricting tidal flows and controlling water levels (Williams & Watford 1997). Structures that exclude mangroves include embankments, reclamations and sea walls (Burton 1982, Thorogood 1985, Coleman 1998, Saintilan 1998, Saintilan & Williams 1999, Steinke 1999, Bedin 2001, Wilton 2001, Rogers et al. 2005a, Swales et al. 2007b, 2009). Structures that restrict or enhance tidal flows or control water levels include causeways, navigation, drainage and access canals, floodgates, culverts and weirs (Thorogood 1985, Evans & Williams 2001, Rogers et al. 2005a, Perry 2007).

Future changes in the distribution of temperate mangroves

Environmental stressors

The historical record of temperate mangrove habitat loss is closely related to human activities in estuaries and their catchments. These activities include reclamation, modification of tidal flows and water levels associated with dredging and flow control structures, wood harvesting and sedimentation. Environmental legislation and management practices now curtail many of these earlier practices. However, the potential effects of climate warming and increasing human population in the coastal zone are likely to increase pressure on temperate mangrove habitats. Key stressors include catchment urbanisation, armouring of shorelines to mitigate erosion and inundation hazards associated with SLR, increasing stormwater and sewage contamination and sediment loads (Crisp et al. 1990, Morant & Quinn 1999, Steinke 1999, Morrisey et al. 2003).

The quality of temperate mangrove habitat is also likely to deteriorate as a consequence of future land-use intensification, particularly in estuaries downstream of urban and urbanising catchments. Environmental changes associated with urbanisation may occur gradually, and the ecological consequences are often poorly perceived (Pearce 1995). Over time, mangrove forests accumulate stormwater contaminants, such as trace metals, due to preferential trapping of fine sediments (Ellis et al. 2004). However, field and laboratory studies showed no clear link between trace metal concentrations and mangrove growth or mortality rates (Tam & Wong 1997, Wong et al. 1997a,b, Duke 2008). The effects of earlier management practices, such as reclamations, landfills and flow control structures, will also continue to degrade mangrove habitat. For example, landfill leachates may locally affect the diversity of benthic communities in mangrove forest sediments (Blom 1992). Herbicide accumulation in estuarine sediments may also adversely affect mangrove health, as documented for *Avicennia marina* seedlings and trees (Duke 2008). Despite the protected status of mangroves in New Zealand, illegal reclamations and structures, removal of trees to enhance visual and recreational amenity, dumping of waste and stock grazing still occur (Kronen 2001, Morrisey et al. 2007). Wood harvesting and stock grazing also continue to threaten mangroves in South Africa's Eastern Cape Province (Steinke 1999).

Mangroves are vulnerable to excessive and rapid sedimentation due to smothering of seedlings and the aerial roots of trees. Effects of sedimentation on mangroves include reduced vigour and growth rates and tree loss (Ellison 2009). Sedimentation induced die-off events have been associated with catchment floods, hurricanes, changes in deltaic sedimentation patterns, dredge spoil, reclamations and mining (Terrados et al. 1997, Ellison 1999, 2009). The sensitivity of mangrove species to burial depends on root structure because adult trees die when pneumatophores

(*Avicennia*) and knee roots (*Bruguiera*) are rapidly buried. Adverse effects are also more likely to occur in anaerobic muddy sediments than in sandy substrata. Death of *Avicennia* sp. trees occurs when sedimentation depths exceed 10 cm (Ellison 1999), although the burial rate also appears to be a determining factor. For example, large-scale seaward expansion of *A. marina* forests occurs on rapidly accreting (50–100 mm yr^{-1}) tidal flats (Swales et al. 2007b). In high-sedimentation environments, mangroves may respond by upward extension of pneumatophores or development of higher root arches or knee roots (Ellison 1999).

Climate change and sea-level rise

Changes in the distribution of tropical and temperate mangroves over geological timescales have been reconstructed from sedimentary records of mangrove peat deposits and pollen (Ellison 2009). Mangrove sediments can also provide reliable sea-level markers because they occupy a relatively narrow elevation band in the intertidal zone. At high latitudes, changes in their distribution inferred from sedimentary records also indicate range extension during periods of climate warming. Such retrospective studies also provide a basis to inform predictions of future changes in mangrove habitat distribution associated with the rapid climate warming and SLR that is expected to occur this century and beyond.

The long-term fate of mangrove forests depends on surface (i.e., substratum) elevations increasing at a rate equal to or exceeding SLR so that they maintain their position in the tidal frame (Cahoon et al. 2006, McKee et al. 2007, Alongi 2008, Woodroffe & Davies 2009). Mangrove forest response to sea-level fluctuations can be complex depending on local relative SLR (including vertical landmass movement), regional departures from global mean eustatic SLR, climate change effects on storm surges and waves, and tidal flat accretion and subsidence (Alongi 2008). Paleoenvironmental studies have been used to reconstruct how mangrove forests have responded to SLR over geological timescales (Woodroffe & Davies 2009). Early Holocene mangrove forests were inundated by rapid SLR (5–15 mm yr^{-1}), and the former existence of these forests is preserved in shelf sediments (Pocknall et al. 1989, Woodroffe 1990, McKee et al. 2007, J.C. Ellison 2008, Woodroffe & Davies 2009). Where rates of SLR were slightly lower, mangroves re-established at higher landward positions on the shelf. As the rate of SLR slowed, mangrove forests were able to keep pace with sea level. In the Southern Hemisphere, sea levels stabilised about 6500 years ago, with decimetre variations since that time (Gibb 1986, Roy et al. 2001, Ellison 2009). Temperate mangrove forests subsequently developed in estuaries as they progressively infilled with sediment.

The response of modern mangrove forests to historical sea-level changes has been commonly inferred from dated sediment cores, with SARs used as a surrogate measure of surface elevation change (Cahoon et al. 2006). For example, Alongi (2008) compared relative SLR data with mangrove forest SAR. The analysis indicated a linear relationship between SLR and SAR, with sedimentation exceeding SLR in most cases. Furthermore, sedimentation rates in mangrove forests with large terrigenous sediment supply have exceeded SLR by an order of magnitude or more (Walsh & Nittrouer 2004, Swales et al. 2007b). In south-eastern Australian estuaries, sedimentation rates in mangrove forests, measured over several years, generally exceeded rates of actual surface elevation change due to factors such as sediment compaction, root production and groundwater hydrology (Saintilan & Williams 1999, Rogers et al. 2006). Despite these local and regional differences in drivers, the general pattern of mangrove habitat expansion suggests that over the long term surface elevations in modern temperate forests have kept pace with rates of relative SLR of 0.9–1.4 mm yr^{-1} over the last century (Schumann et al. 1999, Hannah 2004, Rogers et al. 2005b, Saintilan & Williams, 1999). This is not the case in Bermuda, where long-term loss of temperate mangrove habitat has occurred. Rates of peat sediment accretion have not compensated for relative SLR of 2.8 mm yr^{-1} since the 1930s (Ellison 1993).

The effects of climate warming are now evident from increases in global average atmospheric and ocean temperatures over the last century, widespread glacier ice and snow melt and rising eustatic MSL (Pfeffer et al. 2008). These observed effects are very likely due to increases in anthropogenic greenhouse gas concentrations in the atmosphere (IPCC 2007). Global surface temperatures have risen by 0.74 ± 0.18°C during the last century, and the likely range of projected increase this century is 1.1–6.4°C for different emission scenarios. Global mean (eustatic) sea levels have increased by 1.7 ± 0.5 mm yr^{-1} during the twentieth century. Sea levels will continue to rise primarily due to thermal expansion effects and loss of ice sheets and glaciers on land. Global eustatic rates of SLR are projected to be between 2 and 6 mm yr^{-1} by the 2090s (2090–2099) relative to the 1980–1999 average for the basic set of six future emission scenarios (IPCC 2007). A further sea-level increase of 0.1–0.2 m would arise from increased ice flow from Greenland and Antarctica if its contribution grew linearly with global surface temperature change. This effect would increase the projected rate of SLR up to 8 mm yr^{-1} by the 2090s. Actual rates of SLR could be even higher if discharges from the Greenland and West Antarctic ice sheets occur more rapidly than projected, with a possible increase in sea level of 1 m (i.e., 10 mm yr^{-1}) or more by 2100 (Hansen 2007, Rahmstorf 2007, Pfeffer et al. 2008, Rignot et al. 2008). Furthermore, sea level will continue to rise for several centuries due to the long time lag in the response of the deep ocean to climate warming, as well as future greenhouse gas emissions (IPCC 2007).

The future effects of climate warming on temperate mangrove forests will vary due to local differences in climate, relative SLR, increases in water temperatures, tidal regimes, sediment supply and species-dependent tolerance to environmental stressors (e.g., Alongi 2008). Climate warming effects on temperate mangroves include changes in seedling recruitment and tree growth, maintenance of surface elevation relative to sea level and potential for habitat expansion to higher-latitude environments. Climate warming has the potential to alter the distribution of temperate mangroves because these systems are sensitive to climate-related drivers such as increasing air, ocean and estuary temperatures, reduced frost frequency, increased storm frequency or intensity, changing rainfall patterns, river discharges and terrigenous sediment and nutrient loads and accelerated SLR (Field 1995, McKee & Rooth 2008, Ellison 2009).

How will temperate mangrove forests respond to accelerated SLR during the twenty-first century? To avoid submergence, surface elevation increases in mangrove forests will need to equal future rates of relative SLR. Eustatic SLR rates of 2–8 mm yr^{-1} and potentially as high as about 10 mm yr^{-1} projected to the end of this century are within the low to midrange of SLR experienced during the early Holocene. The regional effects of tectonics, postglacial isostatic adjustments and sediment loading of continental margins will locally offset or exacerbate SLR. For example, average relative SLR of 1.4 mm yr^{-1} in northern New Zealand over the last century was about 0.45 mm yr^{-1} lower than the eustatic rate due to isostatic adjustment (Hannah 2004).

Mangrove forests that occupy oceanic low-relief islands with human habitation are most vulnerable to inundation by rising sea levels. Causal factors include subsidence, low rates of sediment supply and engineering structures that prevent landward migration of mangrove forests (Alongi 2008). Based on these criteria, the temperate mangrove stands of Bermuda are unlikely to survive in the long term, with accelerated SLR exacerbating the historical trend of forest loss (Ellison 1993). The temperate mangrove forests of Australasia and South Africa that exist in sediment-rich infilled estuaries are likely to be among the most resilient to the future effects of climate change (Schaeffer-Novelli et al. 2002, Alongi 2008). Terrigenous and marine sediments that have accumulated in estuaries during the Holocene provide a buffer against the potential inundation by rising sea levels. Mangrove forests in rapidly infilling meso–macrotidal drowned river valley estuaries are particularly resilient (Schaeffer-Novelli et al. 2002) and will provide refuges for temperate mangroves.

The relative vulnerability of temperate mangrove forests can be evaluated by considering the likelihood of intertidal flat inundation by rising sea levels using SAR as a proxy for surface elevation change. This approach recognises that estuary inundation is a precursor to mangrove forest retreat (Ellison 1993). Sedimentation data also provide a long-term perspective, and where indicated by uniform bulk-density profiles, sediment compaction effects are negligible (Hancock & Pietsch

2006, Swales et al. 2007b). Recent sedimentation rates in New Zealand and south-eastern Australian estuaries have typically averaged 1–5 mm yr^{-1} over the last 50–100 years (Barnett 1994, Chenhall et al. 1995, Hancock & Hunter 1999, Hancock 2000, Hancock et al. 2001, Jones & Chenhall 2001, Swales et al. 2002, 2009, Ellis et al. 2004, Rogers et al. 2005b, Hancock & Pietsch 2006). These sediment records suggest that increases in tidal flat elevation have outpaced historical rates of relative SLR of less than 1.5 mm yr^{-1} along the temperate mangrove coasts of northern New Zealand, south-eastern Australia and South Africa. This net increase in elevation is consistent with the seaward expansion of mangrove forests observed in New Zealand estuaries over the last 50–70 years. Estuarine sedimentation rates are similar to the range of eustatic SLR (2–8 mm yr^{-1}) projected to occur this century, so that temperate mangrove forests are likely to persist in most estuaries, assuming similar rates of sediment delivery to estuaries, which may not be valid if the trend towards more stringent controls on sediment run-off continues. Under present worst-case SLR scenarios, a 2- to 5-fold increase in estuary sedimentation rates would be required to keep pace with about a 10 mm yr^{-1} average rate of eustatic SLR or more if subsidence is occurring. Such an increase in sedimentation has not occurred since the early Holocene. The implied increase in sediment delivery to estuaries is unlikely to occur unless there are major shifts in rainfall patterns or land use that drastically increase catchment soil erosion. A large sediment deficit means that mangrove forests are likely to retreat landwards towards the end of this century and beyond as SLR continues (Swales et al. 2009). Temperate mangrove forests with low rates of sediment delivery (e.g., estuarine bays with small catchments) or high rates of sediment compaction are unlikely to be sustainable (Rogers et al. 2005b). High-sedimentation environments, such as tidal creeks (e.g., Swales et al. 2002), could provide refuge for mangroves.

In many estuaries, artificial structures such as embankments, reclamations, rock revetments and sea walls will limit the landward retreat of mangrove forests as sea levels rise. Similar restrictions will also occur on estuarine shorelines backed by steep bedrock cliffs. This process, referred to as *coastal squeeze* (French 1997), will affect mangrove forests in many New Zealand, south-eastern Australia and South African estuaries, with their long history of coastal development (Crisp et al. 1990, Williams & Watford 1997, Morant & Quinn 1999). Coastal squeeze will particularly affect highly modified urban estuaries and estuaries with low-lying shorelines that are already vulnerable to inundation by storm tides. The effects of coastal squeeze on temperate mangrove forests are already evident in some estuaries. For example, in the Firth of Thames (New Zealand), rapid vertical accretion of mangrove sediments seaward of a stop bank (levee) has raised tidal flat surface elevations well above land levels (Swales et al. 2007a).

Temperate mangrove forests occur at the latitudinal limits of mangroves globally, the most southern of which are composed of monospecific stands of *Avicennia marina*. The distribution of *Avicennia* appears to be constrained by its physiological limitations to low temperatures and freezing (Steinke & Naidoo 1991, Walbert 2002, Beard 2006, Stuart et al. 2007). Geological evidence indicates that temperate mangroves have extended beyond their latitudinal range in the past. For example, *Avicennia* pollen is preserved in early Holocene sediments at Poverty Bay (New Zealand) about 150 km south of their present-day extent and coincides with a period of warmer climate (Mildenhall & Brown 1987, Mildenhall 1994). Thus, future climate warming may also enable temperate mangroves to extend their present distribution.

Extension of temperate mangrove forests to higher latitudes also depends on propagule dispersal between estuaries and the suitability of intertidal habitats. The buoyancy of *Avicennia* propagules is limited to a few days after shedding of the pericarp on exposure to seawater (Steinke 1975, 1986, Burns 1982, de Lange & de Lange 1994). The hydrodynamic characteristics of an estuary, such as degree of tidal asymmetry, will also determine the distance and direction of net transport (de Lange & de Lange 1994) and thus the likelihood that propagules are exported to the open coast. The propagules of trees fringing tidal channels are also less likely to be stranded in the immediate vicinity of their parent tree (Clarke & Myerscough 1991). In south-eastern Australia, *Avicennia* propagules may be transported up 50 km along shore but most propagules stranded on beaches occur within 1 km of estuaries with *Avicennia* forests (Clarke 1993). In northern New Zealand, longshore dispersal of propagules is limited by the coastal current velocities and alongshore wave drift, so that net transport distances for propagules are no more than ~175 km over several days. Most viable propagules establish in the immediate vicinity of their parent tree (de Lange & de Lange 1994). In the Southern Hemisphere, the potential for temperate mangrove forests to extend their latitudinal range is also limited by the small number of estuaries south of their present distributions. In Louisiana, the potential for increases in *A. germinans* distribution to higher latitudes appears to be less dependent on propagule viability as propagules remain buoyant for long periods (Rabinowitz 1978). Viable *A. germinans* propagules stranded on beaches along the Gulf coast of Texas have been found many kilometres from potential source populations (Gunn & Dennis 1973). However, as observed for *A. marina*, most *A. germinans* propagules establish in the immediate vicinity of their parent trees, with a small fraction dispersing large distances (Sousa et al. 2007). This limited dispersal pattern of propagules is consistent with the considerable genetic variability observed between local *Avicennia* populations (Duke et al. 1998, Dodd et al. 2002).

Management of temperate mangroves

Background

Attitudes towards mangroves in the temperate regions considered in this review have undergone a number of changes, principally since the arrival of Europeans. Pre-European inhabitants generally held the mangrove, and its associated habitat, in high regard as a source of food, fuels and medicines (Crisp et al. 1990, Tomlinson 1986). Following European settlement, however, mangroves were generally considered of little use and with little in the way of aesthetic or economic value. More recently, the value of mangroves and the services that they provide has again been recognised (Duke et al. 2007). In developed countries, these services often relate to their role in promoting biodiversity, supporting fisheries and providing coastal protection rather than more traditional, artisanal uses (A.M. Ellison 2008). Nevertheless, some clearance continues and, in Australia, tends to affect small areas in subtropical or temperate regions or involves concentrated clearance for infrastructure projects (Bridgewater & Cresswell 1999).

Even in the absence of clearance, chronic, low-intensity human disturbance (e.g., trampling, dumping of rubbish and diffuse inputs of contaminants) continues to affect temperate mangroves, particularly around urban areas. In mangrove stands in Sydney, trampling resulted in alteration of the structure of the benthic habitat (decreased numbers and size of pneumatophores and reduced algal biomass) and loss of macrofaunal species associated with these structures (Ross 2006). More generally, however, Lindegarth and Hoskin (2001) failed to detect differences in benthic macrofaunal assemblages between urban and non-urban mangrove areas around Sydney. Human activities may affect mangrove assemblages even when their intention is protective management, as exemplified by changes in benthic assemblages around boardwalks (Kelaher et al. 1998a,b).

The following discussion uses New Zealand as a case study of recent management issues. In New Zealand, adverse attitudes to mangroves post-European settlement were particularly prevalent where mangrove occupied potential areas for new farmland or where they had encroached and transformed the environment into vegetated swamplands. Consequently, little or no consideration was given to the conservation of mangroves, and there were few restrictions preventing the widespread and large-scale destruction of these plants that followed in many regions. Clearance and reclamation of intertidal areas continued for almost a century, and in some harbours (e.g., the Hokianga), approximately 34% of mangrove were destroyed (Chapman 1978).

By the late 1970s, perceptions of mangrove in New Zealand changed again, a move championed largely by Professor V.J. Chapman. Chapman's work, along with that of others, emphasised the unique ecological and economical values of mangrove based largely on work done on mangroves overseas because there was little supporting evidence from New Zealand at that time. A subsequent shift occurred to preserve mangrove, and several reserves (e.g., Waitangi National Reserve in the Bay of Islands) were established on the basis of their recommendations. At the present time, a total of 16 mangrove reserve areas have been established in New Zealand, covering approximately 2000 ha (or about 10% of total mangrove cover) (Mom 2005).

New Zealand's principal environmental legislation, the Resource Management Act (1991), allows governing bodies to uphold protection of mangroves against indiscriminate destruction or reclamation. However, concerns over recent expansion of mangrove areas, coupled with a push to preserve the ecology of adjacent habitats (e.g., salt marsh, seagrass beds and open mudflats), have resulted in increased pressure on regional councils and environmental agencies to provide information about the causes of, and possible resolutions to, this perceived problem.

Meanwhile, the public view of mangroves remains polarised, with some groups advocating protection at all costs, while others see mangroves as a nuisance and a loss to the economic and aesthetic values of the harbours and estuaries in which they grow. In some cases, management initiatives have been put in place with governing agencies, research scientists, community groups and traditional Māori owners (iwi) working closely to find a balance between mangrove and other estuarine habitats. One such programme in the Waikaraka Estuary in Tauranga Harbour has been very successful (Wildland Consultants 2003). However, despite these initiatives, protective legislation and due process, several groups and private individuals in other parts of New Zealand have removed mangroves from estuaries in protest at controls and perceived inaction.

Management initiatives

The concept of 'mangrove management' in New Zealand is increasingly associated with some form of control measure involving mangrove removal. However, management actually encompasses a broader range of possible actions and corresponding outcomes.

At one end of this range, a low-impact 'non-intervention' approach to mangrove management may be taken, allowing mangroves to remain intact and natural processes to take their course. This approach does not necessarily result in expansion of areas occupied by mangroves, but it does infer that people need to adapt to, and accept, the changes that take place in the mangrove habitat over time. This style of management may be more suited to relatively stable mangrove areas where little change has occurred in the populations over several decades (Mom 2005).

A similar approach may also be applied in preserving mangrove areas. In New Zealand, preservation has largely been achieved through the formation of a number of marine reserves that encompass areas of the ocean and foreshore, including mangroves, and are managed for scientific and preservation reasons. Examples of such marine reserves in New Zealand where mangroves form a significant component of the protected foreshore vegetation are Motu Manawa (Pollen Island) marine reserve in the Waitemata Harbour, Auckland, and Te Matuku marine reserve, Waiheke Island, in the nearby Hauraki Gulf; both are managed by the New Zealand Department of Conservation. Reserves have added advantages in that they provide opportunities to enhance appreciation of the mangrove ecosystem and ecology through education (by way of access and interpretative signage) and recreation. For instance, at Waitangi and Paihia in the Bay of Islands and Waikareo Estuary in the Bay of Plenty, mangroves are being managed in a way that allows people access right into the tidal forest habitat by way of boardwalks and tracks.

A middle-road approach to mangrove management, and one that also allows adult plants to remain intact, is the prevention of their further expansion into areas where they have been identified as potentially decreasing or removing existing values (aesthetic, ecological or economic). This approach involves the annual removal of first-year seedlings and requires ongoing and active management, often coupled with large-scale participation by local community groups. Recent consents have been granted by Bay of Plenty and Waikato regional councils to allow such activity in Whangamata and Tauranga Harbours, by which seedling mangrove plants may be removed from newly colonised mudflats (a *seedling* being defined as a mangrove plant with 2–12 leaves and one stem and between 5 and about 55 cm tall) (Maxwell 2006). Removal must be undertaken by hand to avoid unnecessary disturbance of the estuarine sediments.

In contrast, a relatively high-impact control measure, and one that is increasingly being considered as a method of mangrove management in New Zealand, is the large-scale removal of all adult plants, saplings and seedlings back to a predetermined baseline. The main aims of this approach are to preserve the ecology of habitats threatened by mangrove encroachment (e.g., salt marsh, eelgrass beds, open mudflat), to restore aesthetic values in an estuary (i.e., to open up views and to allow built-up sediment to shift following removal of the binding and accumulation properties provided by mangrove roots and stems) and to maintain access ways to, and throughout, a harbour or estuary.

A number of different approaches to large-scale removal have been trialled to date, including removal of all above- and below-ground mangrove material (including crowns, stems, roots and pneumatophores), removal of above-ground material only (also including pneumatophores) and cutting all to the level of the substratum surface, and removing above-ground crowns and stems but leaving pneumatophores and roots intact (Coffey 2001, 2002, 2004, Wildland Consultants 2003). Mangrove debris is either stockpiled, dried and eventually burned within the intertidal area or removed and disposed of outside the coastal marine boundaries.

Management focus has now moved towards catchments because there is a general acceptance that mangrove expansion is a response to increased sediment input into harbours and estuaries, and this perspective on mangrove management is also being adopted in other temperate regions (e.g., Harty & Cheng 2003). Many catchment areas have been greatly modified over the last 200 years, and the native vegetation that would have once slowed the flow of water from hillsides and helped to prevent erosion has been cleared for agriculture, forestry and urban development. These activities have resulted in significant changes in sediment quantities within the coastal marine environment. River and catchment programmes of the regional councils are focused on providing physical works, services and advice to landowners to reduce the risk of soil erosion and flooding, reduce the amount of sediment getting into waterways, and improve water quality, river stability and river environments. Reducing sediment and nutrient inputs will ultimately limit growth and expansion of mangroves in New Zealand harbours and estuaries (Nichol et al. 2000, Mom 2005).

Effects of mangrove removal

Removal may be considered an effective management option for mangroves in some harbours or estuaries in New Zealand, although relatively little is known of the short- and long-term effects of these activities on the immediate and wider environment. In other regions, research indicated that anthropogenic disturbance to the structure of mangrove forests alters physical processes and has ongoing effects on the associated assemblages of plants and animals (Gladstone & Schreider 2003, Prosser 2004, Ross 2006). For example, a study of damaged mangrove habitats in northern Queensland, Australia, revealed that changes linked to human disturbance were largely due to the loss of biological function and to other physical effects. A decline in abundance and diversity of associated mangrove fauna (such as sediment-dwelling crabs) was evident in areas where mangroves had been removed (Kaly et al. 1997). Losses of this nature may have negative effects, such as reduced soil aeration and bioturbation, which in turn can affect productivity and reproductive outputs of mangroves (if they remain) and other organisms. Use of vehicles, machinery and human traffic during the process of mangrove removal inevitably results in mechanical perturbation or compaction of soft sediments. These processes affect the ability of organisms to re-establish in the substratum following disturbance (Kaly et al. 1997).

Mangrove clearance has very significant impacts on vegetation communities and habitats for some fauna. For example, removal of mangrove cover radically alters the habitat for birds. For some species, such as the banded rail, a species commonly associated with mangroves in New Zealand, this removal results in loss of a major part of their foraging, feeding and breeding habitat. However, other species may benefit from mangrove clearance, particularly those that feed over open mudflats (e.g., white-faced heron, reef heron, pied stilt and oystercatcher). Areas cleared of mangroves in Panama developed higher algal biomass and diversity than uncleared areas, and the algal communities in the cleared areas included species that were rare within mangrove stands (Granek & Ruttenberg 2008).

Sediment grain size may also be altered following mangrove removal as a result of changes to run-off and current and tidal flows brought about by the absence of the trees and pneumatophores. Clearance of mangroves in Panama did not affect rates of sedimentation, but the sediments that accumulated in the mangrove habitat contained more organic matter than that accumulating in nearby cleared areas (Granek & Ruttenberg 2008). Sediments in highly altered mangrove areas in northern Australia showed smaller fractions of clay and a higher index of compaction compared with mangrove forests where no human disturbance had occurred (Kaly et al. 1997). Changes in forest nutrient status also occurred via altered processes of run-off and leaching and resulted in decreases of phosphorus and clay particles in disturbed areas.

Removal or slow physical breakdown of root material in the substratum following mangrove clearance may increase the possibility of erosion and transport of sediments to other areas, which in turn could have potentially significant impacts on water circulation, drainage patterns and flooding within an estuary. Removal may also result in the remobilisation not only of previously bound sediments but also of sediment-associated contaminants, thus increasing the potential for bioaccumulation and other effects of chemical contaminants in organisms.

Ongoing monitoring of mangrove areas before and after removal in two New Zealand harbours (Tauranga and Whangamata) has revealed trends similar to overseas studies, with measurable effects of tree removal on the composition and movement of sediment, benthic infauna, mobile epibenthos (crustaceans and gastropods) and birds. In addition, activities associated with mangrove removal, such as physical access, use of vehicles and machinery, trampling and disposal of mangrove debris, also contribute to disturbance of existing plant and animal communities and to some physical changes within and adjacent to mangrove habitat (Coffey 2001, 2002, 2004, Stokes & Healy 2005, Wildland Consultants 2005).

Mangrove restoration and enhancement

Mangrove habitats around the world have long been exploited for fuel, fishing and construction purposes and have also been subject to various forms of pollution from industrial waste, mining, oil exploration and eutrophication. From a worldwide standpoint, they are now counted as one of the most threatened natural community types, with approximately 50% of their global area destroyed or degraded since 1900 (Gilman et al. 2006). Widespread recognition of this global decline, and a growing appreciation of mangrove values in coastal protection, water quality, wildlife or fisheries habitat and tourism, has led to increasing efforts in many countries to restore, conserve and sustainably manage mangrove areas (Field 1999, Saenger 2002, Lewis 2005, Walton et al. 2006, Bosire et al. 2008). Of the approximately 90 countries that have mangrove vegetation, around 20 have undertaken rehabilitation initiatives (Field 1999), establishing nurseries and attempting aforestation of previously uncolonised mudflats and replanting in degraded areas (Erftemeijer & Lewis 1999).

Rehabilitation, restoration and planting of mangrove areas is not, and has not been, common practice in New Zealand. As recently as 1970, the preferred option for many mangrove areas was actually reclamation for various types of land development, including marinas, roading, oxidation ponds, agriculture and tip sites. This practice still continues, albeit on a much smaller scale and under the control of the Resource Management Act (Crisp et al. 1990). Even though mangroves continue to support ecological, community and traditional Māori values in New Zealand and despite historical losses, the recent and ongoing expansion of mangrove in many harbours and the lack of any major industry based on this vegetation has encouraged management initiatives that focus largely on removal rather than restoration.

Mangroves have been introduced to a few areas in New Zealand with a view to controlling erosion (e.g., Mohakatino, Mokau and Urenui River mouths at 38°59′ to 38°44′S, slightly beyond their natural latitudinal limit), but these attempts were largely unsuccessful due to plant mortality (Crisp et al. 1990). Successful establishment of mangroves, or enhancement of degraded areas, can only be achieved if the stresses (or actions) that initially caused their decline or absence are removed or discontinued. In some cases, mangrove wetlands will then repair themselves if the necessary natural processes, such as seedling recruitment and hydrology, are still intact. Otherwise, given appropriate environmental conditions (e.g., wave energy, salinity, pH, nutrient concentrations, substratum composition, inundation), successful rehabilitation may be a long-term process dependent on human assistance and ongoing active management (including replanting and weed control) (Gilman et al. 2006).

Effectiveness of mangrove management initiatives

Thus far, few conclusions have been reached regarding the most effective or ecologically sound method of mangrove removal in terms of sediment remobilization and impacts on other organisms, including other vegetation types, benthic fauna, shellfish, fishes and birds. However, in a number of New Zealand coastal areas, ongoing monitoring and research of both intact mangrove systems, and those where mangroves have been removed, are helping to answer some of these questions. Conclusions have also yet to be drawn in regard to economics because large-scale clearance of this nature can be costly in terms of equipment and labour and require ongoing and active management to prevent seedlings re-establishing.

Research has established that, regardless of which approach is decided on, sustainable management can only be achieved if evaluation of mangrove areas is undertaken on a site-by-site basis. Processes and effects vary according to the type of mangrove community, whether it is stable or dynamic and site-specific physical and ecological characteristics defined by a range of factors, including geomorphology, climate, sediment input, nutrient status and hydrodynamics.

Thorough research, provision of information and communication are crucial components of any management initiative. The recent debate about values of New Zealand mangrove, particularly their ecological role in coastal ecosystems, has highlighted the need for more comprehensive information than has been available up to very recent times. Much of the information on which New Zealand mangrove values were based was gleaned from a small number of isolated studies, anecdotal evidence and comparisons with overseas mangrove systems. This information proved inadequate not only for communities seeking guidance or action on mangrove management but also for the governing agencies responsible for providing those services.

Conclusions and directions for future research

Public interest in mangroves in temperate regions has waxed and waned over time and with it the pressure to manage them. Current concern is relatively high, but there are markedly conflicting viewpoints. Much of the basic information required to address concerns and manage mangroves is lacking. This review has identified variation in ecological values of temperate mangroves, such as levels of litter production and decomposition, faunal abundance or importance to fishes, at a range of scales among studies and among locations. This in turn highlights the need to assess the appropriate management actions for a given area of mangroves or a given estuary on a case-by-case basis.

The information that would allow us to make the assessments is, however, often lacking. The usefulness of applying general conclusions from the wider body of mangrove research, dominated as it is by studies in tropical regions, needs to be treated with caution. Important differences between the ecology of tropical and temperate mangroves, such as the roles played by crabs in processing mangrove material and the relative importance of mangroves as fish habitat, have been identified in the discussion. A critical eye is needed even when comparing information from studies of different temperate regions, as illustrated by the differing patterns of mangrove spread between eastern Australia and New Zealand. There is therefore a strong need for local studies to provide information that will allow understanding and management.

Current work addressing some of the issues has been discussed, but there are many other aspects that still need to be investigated. For example, our present knowledge of relative productivity of mangroves across the range of latitude, estuarine characteristics, tidal elevation, tree size and age indicates that there is considerable variation but is not sufficient to allow us to predict productivity at a particular site based on these factors. Systematic studies of productivity and incorporation of mangrove material into local food webs along these gradients are needed. Similarly, although we have a reasonably good knowledge of the benthic fauna of mangroves and how it varies with stand age and height on the shore, our knowledge of other components of faunal and floral diversity (particularly terrestrial invertebrates) is extremely limited.

Subsequent work has addressed some of the sampling deficiencies identified by Faunce and Serafy (2006) in earlier studies of fishes in mangroves, including not sampling alternative habitats or measuring environmental conditions beyond the basics of water temperature and salinity (e.g., structural complexity and landscape measures). However, many fundamental issues remain unresolved in both the sampling of fishes in mangrove habitats and in assessing the role of mangroves for fishes relative to alternative habitats. Some of these gaps in our knowledge are related to funding cycles, practical constraints and issues of scale rather than lack of awareness of the issues. Limitations include the use of gears that do not provide estimates of density per unit area (e.g., fyke and gill nets), the short timescale of most studies (generally only 1 or 2 yr at most), sampling of only mangroves and immediate adjacent habitats rather than the spectrum of habitats present in estuarine systems and not accounting for where mangroves are located in the wider habitat landscape mosaic. Of the four measures of nursery function proposed by Beck et al. (2001), no work has been done to date on whether mangrove habitats enhance fish growth relative to other habitats or whether they ultimately contribute more to final adult populations on a habitat area basis than alternative nursery habitats. As with work on other habitat types, such as seagrass meadows and coral reefs, future work will need to be directed towards larger-scale studies that include mangroves as one of a number of habitat types contributing to the support and production of fish populations in estuarine and coastal ecosystems.

Description of patterns and mechanisms of change in the distribution of mangroves themselves are hampered by lack of physical process studies of temperate mangrove forests, and this review has had to draw on studies done in tropical mangrove systems. There is a general paucity of information on sedimentation in temperate regions, including present rates of sediment accumulation in mangrove forests (see Walsh & Nittrouer 2004, p. 228), and sedimentation processes within fringing mangroves in wave-dominated environments. Furthermore, there have been few long-term physical studies and none in temperate mangrove systems, so the extent to which the information currently available is representative is not known. Precise elevation limits have not been adequately described for most species, including *Avicennia marina* (Clarke & Myerscough 1993, p. 307). The influence of wave exposure on elevation limits and the relative effects of short-term sea-level variations versus progressive, long-term relative SLR on the LEL of present-day temperate mangrove forests is not known. Apart from recognition that waves influence mangrove seedling recruitment in estuaries, our present understanding of this process is largely qualitative.

Our ability to predict the long-term development of mangrove forests is limited by the lack of deterministic morphodynamic models to simulate these systems. However, models have been developed to improve understanding of the dynamics of mangrove forests themselves (Berger et al. 2008). Furthermore, morphodynamic models have been developed to predict the effects of sediment supply, subsidence and SLR on saltmarsh ecosystems (e.g., Allen 1990, French 1993, van Wijnen & Bakker 2001, Morris et al. 2002, Temmerman et al. 2004, French 2006, Kirwan et al. 2008, Craft et al. 2009). The absence of similar morphodynamic models for mangrove systems is surprising given the similarity of the physical drivers and dynamics of mangrove and saltmarsh communities. The need for morphodynamic models of estuaries that incorporate mangrove ecosystems will become pressing as the combined environmental effects of burgeoning human populations in the coastal zone and climate change, such as SLR and changes in terrigenous sediment supply, become apparent (probably within the present century). Such models should explicitly incorporate the feedbacks among hydrodynamics, sediment processes, geomorphology and mangrove ecology and be underpinned by process measurements at a wide range of temporal and spatial scales.

As our understanding of different estuarine habitats and their assemblages (plants, invertebrates, fishes, birds) increases, the next obvious step is to start assessing how changes in the spatial habitat landscape (including the pelagic environment) might influence the overall biological/ecological functioning of the estuary. This information is especially relevant to the potential influence of human activities, which speed up the 'ageing' and infilling of estuaries. For instance, Saintilan (2004) showed that as NSW (Australia) estuaries infill and 'age', the relative proportion of different habitats change (e.g., seagrasses decline, mangroves expand), and the production of many fish species valuable to humans declines. However, in addition to the total habitat extents, 'habitat landscape' factors are also important. These factors include spatial configuration (e.g., the ratio of area to edge, the proximity of habitat patches to each other and distance from the harbour mouth) and habitat quality (e.g., age, health). Mangroves are part of the landscape dynamics of this estuarine habitat and need to be assessed in this context as new information becomes available.

Acknowledgements

We are very grateful to the NIWA librarians, in particular Hannah Russell, for library services and for compiling the list of references, Max Oulton for the map of mangrove distribution, the Auckland Regional Council (particularly Dominic McCarthy and Megan Stewart) for the original impetus for the study, Terry Hume and Giovanni Coco (NIWA) for reviewing parts of the text, and to Atsuko Fukunaga for translating information in Japanese. We thank Gary Hancock of the Commonwealth Scientific and Industrial Research Organisation (CSIRO; Land and Water Division) for information on sedimentation rates in south-eastern Australian estuaries, Jacquie Reed (Northland Regional Council, New Zealand), Grant Barnes (Auckland Regional Council) and Stephen Park (Environment Bay of Plenty) for providing access to reports and data. We particularly thank Rob Bell (NIWA) for his careful review of the discussion of climate change effects.

Information for the original New Zealand study was kindly provided by numerous people, and some of it has been included in the present report: Andrea Alfaro (Auckland University of Technology), Oliver Ball (Northland Polytechnic), Phil Battley (Massey University), Tony Beauchamp (Department of Conservation), Bruce Burns (Landcare Research), John Dugdale (Landcare Research, retired), Bruce Howse (Northland Regional Council), Joe Lee (Griffith University), David Melville, Stephen Park (Environment Bay of Plenty), Ray Pierce (Eco Oceania Ltd.), Greg Skilleter (University of Queensland), Brian Sorrell (NIWA), Debra Stokes (University of Waikato), Gillian Vaughan (Miranda Naturalists Trust), Robert Williams (NSW Department of Primary Industries), Kylee Wilton (NSW Department of Natural Resources) and Rosalind Wilton (Environment Waikato).

Any errors, omissions or misinterpretations contained in this review, despite the best efforts of those named, remain our responsibility. Finally, given the breadth of the published and unpublished information on temperate mangroves, we apologise to any authors whose contributions may have been omitted.

D.M., M.M. and A.S. were partly funded by NIWA Capability Fund Contract CRBE094 during the preparation of this review.

References

Adams, J.B., Colloty, B.M. & Bate, G.C. 2004. The distribution and state of mangroves along the coast of Transkei, Eastern Cape Province, South Africa. *Wetlands Ecology and Management* **12**, 531–541.

Albright, L.J. 1976. *In situ* degradation of mangrove tissues. *New Zealand Journal of Marine and Freshwater Research* **10**, 385–389.

Alfaro, A.C. 2006. Benthic macro-invertebrate community composition within a mangrove/seagrass estuary in northern New Zealand. *Estuarine Coastal and Shelf Science* **66**, 97–110.

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. *Estuarine Coastal and Shelf Science* **70**, 271–286.

Allen, J.R.L. 1990. Salt-marsh growth and stratification: a numerical model with special reference to the Severn Estuary, southwest Britain. *Marine Geology* **95**, 77–96.

Allison, M.A., Nittrouer, C.A. & Faria, L.E.C., Jr. 1995. Rates and mechanisms of shoreface progradation and retreat downdrift of the Amazon river mouth. *Marine Geology* **125**, 373–392.

Alongi, D.M. 1987a. Intertidal zonation and seasonality of meiobenthos in tropical mangrove estuaries. *Marine Biology* **95**, 447–458.

Alongi, D.M. 1987b. The influence of mangrove-derived tannins on intertidal meiobenthos in tropical estuaries. *Oecologia* **71**, 537–540.

Alongi, D.M. 1987c. Inter-estuary variation and intertidal zonation of free-living nematode communities in tropical mangrove systems. *Marine Ecology Progress Series* **40**, 103–114.

Alongi, D.M. 2008. Mangrove forests: resilience, protection from tsunamis, and responses to global climate change. *Estuarine Coastal and Shelf Science* **76**, 1–13.

Alongi, D.M. 2009. *The Energetics of Mangrove Forests*. Berlin: Springer.

Alongi, D.M. & Christoffersen, P. 1992. Benthic infauna and organism-sediment relations in a shallow, tropical coastal area: influence of outwelled mangrove detritus and physical disturbance. *Marine Ecology Progress Series* **81**, 229–245.

Alongi, D.M., Tirendi, E. & Clough, B.F. 2000. Below-ground decomposition of organic matter in forests of the mangroves *Rhizophora stylosa* and *Avicennia marina* along the arid coast of Western Australia. *Aquatic Botany* **68**, 97–122.

Alongi, D.M., Trott, L.A., Wattayakorn, G. & Clough, B.F. 2002. Below-ground nitrogen cycling in relation to net canopy production in mangrove forests of southern Thailand. *Marine Biology* **140**, 855–864.

Andersen, T.J. 2001. Seasonal variation in erodibility of two temperate, microtidal mudflats. *Estuarine Coastal and Shelf Science* **53**, 1–12.

Araújo da Silva, C., Souza-Filho, P.W.M. & Rodrigues, S.W.P. 2009. Morphology and modern sedimentary deposits of the macrotidal Marapanim Estuary (Amazon, Brazil). *Continental Shelf Research* **29**, 619–631.

Armenteros, M., Martin, I., Williams, J.P., Creagh, B., Gonzalez-Sanson, G. & Capetillo, N. 2006. Spatial and temporal variations of meiofaunal communities from the western sector of the Gulf of Batabano, Cuba. I. Mangrove systems. *Estuaries and Coasts* **29**, 124–132.

Armonies, W. 1988. Active emergence of meiofauna from intertidal sediment. *Marine Ecology Progress Series* **43**, 151–159.

Arnaud-Haond, S., Teixeira, S., Massa, S.I., Billot, C., Saenger, P., Coupland, G., Duarte, C.M. & Serrao, E.A. 2006. Genetic structure at range edge: diversity and high inbreeding in southeast Asian mangrove (*Avicennia marina*) populations. *Molecular Ecology* **15**, 3515–3525.

Augustinus, P. 2002. Biochemical factors influencing deposition and erosion of fine grained sediment. In *Muddy Coasts of the World: Processes, Deposits and Function,* T. Healy et al. (eds). Amsterdam: Elsevier Science, 203–228.

Augustinus, P.G.E.F. 1995. Geomorphology and sedimentology of mangroves. In *Geomorphology and Sedimentology of Estuaries*, G.M.E. Perillo (ed.). Amsterdam: Elsevier Science, 333–357.

Ball, M.C. 1988. Salinity tolerance in the mangroves *Aegiceras corniculatum* and *Avicennia marina*. I. Water use in relation to growth, carbon partitioning, and salt balance. *Australian Journal of Plant Physiology* **15**, 447–464.

Ball, M.C. 1998. Mangrove species richness in relation to salinity and waterlogging: a case study along the Adelaide River floodplain, northern Australia. *Global Ecology and Biogeography Letters* **7**, 73–82.

Barnett, E.J. 1994. A Holocene paleoenvironmental history of Lake Alexandria. *Journal of Paleolimnology* **12**, 259–268.

Bartsch, I. 1989. Marine mites (*Halacaroidea: Acari*): a geographical and ecological survey. *Hydrobiologia* **178**, 21–42.

Bayliss, D.E. 1982. Switching by *Lepsiella vinosa* (Gastropoda) in South Australian mangroves. *Oecologia* **54**, 212–226.

Bayliss, D.E. 1993. Spatial distribution of *Balanus amphitrite* and *Elminius adelaidae* on mangrove pneumatophores. *Marine Biology* **116**, 251–256.

Beaglehole, J.C. 1968. *The Journals of Captain James Cook on His Voyages of Discovery. The Voyage of the Endeavour 1968–1771*. Cambridge, United Kingdom: Cambridge University Press.

Beanland, W.R. & Woelkerling, W.J. 1982. Studies on Australian mangrove algae: II. Composition and geographic distribution of communities in Spencer Gulf, South Australia. *Proceedings of the Royal Society of Victoria* **94**, 89–106.

Beanland, W.R. & Woelkerling, W.J. 1983. *Avicennia* canopy effects on mangrove algal communities in Spencer Gulf, South Australia. *Aquatic Botany* **17**, 309–313.

Beard, C.M. 2006. *Physiological constraints on the latitudinal distribution of the mangrove Avicennia marina (Forsk.) Vierh. subsp. australasica (Walp.) J. Everett (Avicenniaceae) in New Zealand*. PhD thesis, University of Waikato, Hamilton, New Zealand.

Beauchamp, A.J. & Parrish, G.R. 1999. Bird use of the sediment settling ponds and roost areas at Port Whangarei. *Notornis* **46**, 470–483.

Beauchamp, T. (n.d.). Statement of evidence in the matter of the Resource Management Act 1991 and in the matter of submissions and further submissions by the Director General of Conservation on proposed Plan Change No. 3 (Mangrove Management) to the Regional Coastal Plan for Northland. Whangarei, New Zealand: Department of Conservation. 13 p.

Beck, M.W., Heck, K.L., Jr., Able, K.W., Childers, D.L., Eggleston, D.B., Gillanders, B.M., Halpern, B., Hays, G.G., Hoshino, K., Minello, T.J., Orth, R.J., Sheridan, P.F. & Weinstein, M.P. 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *BioScience* **51**, 633–641.

Bedin, T. 2001. The progression of a mangrove forest over a newly formed delta in the Umhlatuze Estuary, South Africa. *South African Journal of Botany* **67**, 433–438.

Bell, J.D., Pollard, D.A., Burchmore, J.J., Pease, B.C. & Middleton, M.J. 1984. Structure of a fish community in a temperate tidal mangrove creek in Botany Bay, New South Wales. *Australian Journal of Marine and Freshwater Research* **35**, 33–46.

Berger, U., Rivera-Monroy, V.H., Doyle, T.W., Dahdouh-Guebas, F., Duke, N.C., Fontalvo-Herazo, M.L., Hildenbrandt, H., Koedam, N., Mehlig, U., Piou, C. & Twilley, R.R. 2008. Advances and limitations of individual-based models to analyze and predict dynamics of mangrove forests: a review. *Aquatic Botany* **89**, 260–274.

Bhat, N.R., Suleiman, M.K. & Shahid, S.A. 2004. Mangrove, *Avicennia marina*, establishment and growth under the arid climate of Kuwait. *Arid Land Research and Management* **18**, 127–139.

Bird, E.C.F. 1971. Mangroves as land builders. *Victorian Naturalist* **88**, 189–197.

Bird, E.C.F. 1972. Mangroves and coastal morphology in Cairns Bay, North Queensland. *Journal of Tropical Geography* **35**, 11–16.

Bird, E.C.F. 1984. *Coasts. An Introduction to Coastal Geomorphology*. Oxford, United Kingdom: Blackwell, 3rd edition.

Bird, E.C.F. 1986. Mangroves and intertidal morphology in Westernport Bay, Victoria, Australia. *Marine Geology* **69**, 251–271.

Blom, C.M. 1992. *Anthropogenic impacts on the benthic fauna and forest structure of the New Zealand mangrove Avicennia marina var.* resinifera. MSc thesis, University of Auckland, Auckland, New Zealand.

Bloomfield, A.L. & Gillanders, B.M. 2005. Fish and invertebrate assemblages in seagrass, mangrove, saltmarsh, and nonvegetated habitats. *Estuaries* **28**, 63–77.

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

Bordignon, M.O. 2006. Diet of the fishing bat *Noctilio leporinus* (Linnaeus) (Mammalia, Chiroptera) in a mangrove area of southern Brazil. *Revista Brasileira de Zoologia* **23**, 256–260.

Bosire, J.O., Dahdouh-Guebas, F., Walton, M., Crona, B.I., Lewis, R.R., III, Field, C., Kairo, J.G. & Koedam, N. 2008. Functionality of restored mangroves: a review. *Aquatic Botany* **89**, 251–259.

Bouillon, S., Borges, A.V., Castaneda-Moya, E., Diele, K., Dittmar, T., Duke, N.C., Kristensen, E., Lee, S.Y., Marchand, C., Middelburg, J.J., Rivera-Monroy, V.H., Smith, T.J., III & Twilley, R.R. 2008. Mangrove production and carbon sinks: a revision of global budget estimates. *Global Biogeochemical Cycles* **22**, GB2013.

Boumans, R. & Day, J.W. 1993. High precision measurements of sediment elevation in shallow coastal areas using a sedimentation-erosion table. *Estuaries* **16**, 375–380.

Branch, G.M. & Branch, M.L. 1980. Competition in *Bembicium auratum* (Gastropoda) and its effect on microalgal standing stock in mangrove muds. *Oecologia* **46**, 106–114.

Branch, G.M. & Grindley, J.R. 1979. Ecology of southern African estuaries. Part XI. Mgazana: a mangrove estuary in Transkei. *South African Journal of Zoology* **14**, 149–170.

Brejaart, R. & Brownell, B. 2004. Mangroves: the cornerstone of a dynamic coastal environment. In *Muddy Feet: Firth of Thames Ramsar Site Update 2004*, B. Brownell (ed.). Pokeno, New Zealand: Ecoquest Education Foundation, 34–52.

Bridgewater, P. & Cresswell, I.D. 1999. Biogeography of mangrove and saltmarsh vegetation: implications for conservation and management in Australia. *Mangroves and Salt Marshes* **3**, 117–125.

Briggs, S.V. 1977. Estimates of biomass in a temperate mangrove community. *Australian Journal of Ecology* **2**, 369–373.

Brinkman, R.M., Massel, S.R., Ridd, P.V. & Furukawa, K. 1997. *Surface wave attenuation in mangrove forests*. Christchurch, New Zealand: Centre for Advanced Engineering, University of Canterbury.

Brownell, B. 2004. *Muddy Feet: Firth of Thames Ramsar Site Update 2004*. Kaiaua, New Zealand: Ecoquest Education Foundation.

Bryce, S., Larcombe, P. & Ridd, P.V. 2003. Hydrodynamic and geomorphological controls on suspended sediment transport in mangrove creek systems, a case study: Cocoa Creek, Townsville, Australia. *Estuarine Coastal and Shelf Science* **56**, 415–431.

Bunt, J.S. 1995. Continental scale patterns in mangrove litter fall. *Hydrobiologia* **295**, 135–140.

Burchett, M.D., Field, C.D. & Pulkownik, A. 1984. Salinity, growth and root respiration in the grey mangrove, *Avicennia marina*. *Physiologia Plantarum* **60**, 113–118.

Burns, B.R. 1982. *Population biology of Avicennia marina var.* resinifera. MSc thesis, University of Auckland, Auckland, New Zealand.

Burns, B.R. & Ogden, J. 1985. The demography of the temperate mangrove (*Avicennia marina* (Forsk.) Vierh.) at its southern limit in New Zealand. *Australian Journal of Ecology* **10**, 125–133.

Burrows, D.W. 2003. *The role of insect leaf herbivory on the mangroves Avicennia marina and Rhizophora stylosa*. PhD thesis, James Cook University, Townsville, Australia.

Burton, T. 1982. Mangrove development north of Adelaide. *Transactions of the Royal Society of South Australia* **106**, 183–189.

Butler, A.J., Depers, A.M., McKillup, S.C. & Thomas, D.P. 1977a. Distribution and sediments of mangrove forests in South Australia. *Transactions of the Royal Society of South Australia* **101**, 35–44.

Butler, A.J., Depers, A.M., McKillup, S.C. & Thomas, D.P. 1977b. A survey of mangrove forests in South Australia. *South Australian Naturalist* **51**, 34–49.

Cahoon, D.R., Hensel, P.F., Spencer, T., Reed, D.J., McKee, K.L. & Saintilan, N. 2006. Coastal wetland vulnerability to relative sea-level rise: wetland elevation trends and process controls. In *Wetlands and Natural Resource Management*, J.T.A. Verhoeven et al. (eds). Berlin: Springer-Verlag, 271–292.

Cahoon, D.R. & Lynch, J.C. 1997. Vertical accretion and shallow subsidence in a mangrove forest of southwestern Florida, USA. *Mangroves and Salt Marshes* **1**, 173–186.

Cahoon, D.R., Reed, D.R. & Day, J.W. 1995. Estimating shallow subsidence in microtidal salt marshes of the southeastern United States: Kaye and Barghoorn revisited. *Marine Geology* **128**, 1–9.

Cannicci, S., Burrows, D., Fratini, S., Smith, T.J., III, Offenberg, J. & Dahdouh-Guebas, F. 2008. Faunal impact on vegetation structure and ecosystem function in mangrove forests: a review. *Aquatic Botany* **89**, 186–200.

Carlton, J.M. 1974. Land-building and stabilization by mangroves. *Environmental Conservation* **1**, 285–294.

Carvalho do Amaral, P.G., Ledru, M.P., Branco, F.R. & Giannini, P.C.F. 2006. Late Holocene development of a mangrove ecosystem in southeastern Brazil (Itanhaem, state of Sao Paulo). *Palaeogeography Palaeoclimatology Palaeoecology* **241**, 608–620.

Chafer, C.J. 1998. A spatio-temporal analysis of estuarine vegetation change in the Minnamurra River 1938–1997. Report prepared for the Minnamurra Estuary Management Committee, Kiama, New South Wales, Australia.

Chant, R.J. & Stoner, A.W. 2001. Particle trapping in a stratified flood-dominated estuary. *Journal of Marine Research* **59**, 29–51.

Chapman, M.G. 1998. Relationships between spatial patterns of benthic assemblages in a mangrove forest using different levels of taxonomic resolution. *Marine Ecology Progress Series* **162**, 71–78.

Chapman, M.G., Michie, K. & Lasiak, T. 2005. Responses of gastropods to changes in amounts of leaf litter and algae in mangrove forests. *Journal of the Marine Biological Association of the United Kingdom* **85**, 1481–1488.

Chapman, M.G. & Tolhurst, T.J. 2004. The relationship between invertebrate assemblages and bio-dependent properties of sediment in urbanized temperate mangrove forests. *Journal of Experimental Marine Biology and Ecology* **304**, 51–73.

Chapman, M.G. & Tolhurst, T.J. 2007. Relationships between benthic macrofauna and biogeochemical properties of sediments at different spatial scales and among different habitats in mangrove forests. *Journal of Experimental Marine Biology and Ecology* **343**, 96–109.

Chapman, M.G. & Underwood, A.J. 1995. Mangrove forests. In *Coastal Marine Ecology of Temperate Australia*, A.J. Underwood & M.G. Chapman (eds). Sydney: University of New South Wales Press, 187–204.

Chapman, V.J. (ed.). 1976. *Mangrove Vegetation*. Lehre, Germany: J. Cramer Verlag.

Chapman, V.J. (ed.). 1977. *Wet Coastal Ecoystems*. Amsterdam: Elsevier.

Chapman, V.J. 1978. *Mangroves and Salt Marshes of the Herekino, Whangape and Hokianga Harbours: A Study with Proposals for Preservation of Areas Supporting the Harbour Ecosystem*. Auckland, New Zealand: Department of Lands and Survey.

Chapman, V.J. & Ronaldson, J.W. 1958. The mangrove and saltmarsh flats of the Auckland isthmus. New Zealand Department of Scientific and Industrial Research Bulletin No. 125. Wellington, New Zealand.

Chenhall, B.E., Yassini, I., Depers, A.M., Caitcheon, G., Jones, B.G., Batley, G.E. & Ohmsen, G.S. 1995. Anthropogenic marker evidence for accelerated sedimentation in Lake Illawarra, New South Wales, Australia. *Environmental Geology* **26**, 124–135.

Christie, M.C., Dyer, K.R. & Turner, P. 1999. Sediment flux and bed level measurements from a macrotidal mudflat. *Estuarine Coastal and Shelf Science* **49**, 667–688.

Clarke, L.D. & Hannon, N.J. 1970. The mangrove swamp and salt marsh communities of the Sydney district. III. Plant growth in relation to salinity and waterlogging. *Journal of Ecology* **58**, 351–369.

Clarke, P.J. 1992. Predispersal mortality and fecundity in the grey mangrove (*Avicennia marina*) in southeastern Australia. *Australian Journal of Ecology* **17**, 161–168.

Clarke, P.J. 1993. Dispersal of grey mangrove (*Avicennia marina*) propagules in southeastern Australia. *Aquatic Botany* **45**, 195–204.

Clarke, P.J. 1994. Baseline studies of temperate mangrove growth and reproduction: demographic and litterfall measures of leafing and flowering. *Australian Journal of Botany* **42**, 37–48.

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

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

Clarke, P.J., Kerrigan, R.A. & Westphal, C.J. 2001. Dispersal potential and early growth in 14 tropical mangroves: do early life history traits correlate with patterns of adult distribution? *Journal of Ecology* **89**, 648–659.

Clarke, P.J. & Myerscough, P.J. 1991. Buoyancy of *Avicennia marina* propagules in south-eastern Australia. *Australian Journal of Botany* **39**, 77–83.

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. *Australian Journal of Ecology* **18**, 307–315.

Clough, B.F. 1984. Growth and salt balance of the mangroves *Avicennia marina* (Forsk.) Vierh. and *Rhizophora stylosa* Griff. in relation to salinity. *Australian Journal of Plant Physiology* **11**, 419–430.

Clough, B.F., Dixon, P. & Dalhaus, O. 1997. Allometric relationships for estimating biomass in multi-stemmed mangrove trees. *Australian Journal of Botany* **45**, 1023–1031.

Clynick, B. & Chapman, M.G. 2002. Assemblages of small fish in patchy mangrove forests in Sydney Harbour. *Marine and Freshwater Research* **53**, 669–677.

Coffey, B.T. 2001. Resource Consent 103475: trial clearance of mangroves Patiki Place Reserve, Whangamata Harbour. Final monitoring report—January 2001. Hamilton, New Zealand: Environment Waikato (Waikato Regional Council).

Coffey, B.T. 2002. *Resource Consent 102475: Trial Clearance of Mangroves Patiki Place Reserve, Whangamata Harbour*. Hamilton, New Zealand: Environment Waikato (Waikato Regional Council).

Coffey, B.T. 2004. *Mangrove Clearance Whangamata Harbour, October 2004: Sediment Monitoring Programme to Meet Condition 10 of Resource Consent 107665*. Hamilton, New Zealand: Environment Waikato (Waikato Regional Council).

Coleman, P.S.J. 1998. Changes in a mangrove/samphire community, North Arm Creek, South Australia. *Transactions of the Royal Society of South Australia* **122**, 173–178.

Cooper, A., Wright, I. & Mason, T. 1999. Geomorphology and sedimentology. In *Estuaries of South Africa*, B.R. Allanson & D. Baird (eds). Cambridge, United Kingdom: Cambridge University Press, 5–26.

Coull, B.C. 1990. Are members of the meiofauna food for higher trophic levels? *Transactions of the American Microscopical Society* **109**, 233–246.

Coull, B.C. 1999. Role of meiofauna in estuarine soft-bottom habitats. *Australian Journal of Ecology* **24**, 327–343.

Coull, B.C. & Chandler, G.T. 1992. Pollution and meiofauna: field, laboratory and mesocosm studies. *Oceanography and Marine Biology An Annual Review* **30**, 191–271.

Coull, B.C., Greenwood, J.G., Fielder, D.R. & Coull, B.A. 1995. Subtropical Australian juvenile fish eat meiofauna: experiments with winter whiting *Sillago maculata* and observations on other species. *Marine Ecology Progress Series* **125**, 13–19.

Cox, G.J. 1977. *Utilization of New Zealand mangrove swamps by birds*. MSc thesis, University of Auckland, Auckland, New Zealand.

Craft, C., Clough, J., Ehman, J., Jove, S., Park, R., Pennings, S., Guo, H. & Machmuller, M. 2009. Forecasting the effects of accelerated sea-level rise on tidal marsh ecosystem services. *Frontiers in Ecology and the Environment* **7**, 73–78.

Creese, B., Nichol, S., Gregory, M., Augustinus, P., Horrocks, M. & Mom, B. 1998. *Siltation of Whangape Harbour, Northland. Implications for local iwi*. Auckland, New Zealand: James Henare Maori Research Centre, University of Auckland/Foundation for Research, Science and Technology.

Crisp, P., Daniel, L. & Tortell, P. 1990. *Mangroves in New Zealand—Trees in the Tide*. Wellington, New Zealand: GP Books.

Cunha, S.R., Tognella-De Rosa, M.M.P. & Costa, C.S.B. 2006. Structure and litter production of mangrove forests under different tidal influences in Babitonga Bay, Santa Catarina, southern Brazil. *Journal of Coastal Research* **Special Issue 39**, 1169–1174.

Curran, M., Cole, M. & Allaway, W.G. 1986. Root aeration and respiration in young mangrove plants (*Avicennia marina* (Forsk.) Vierh.). *Journal of Experimental Botany* **37**, 1225–1233.

Dahdouh-Guebas, F., Jayatissa, L.P., Di Nitto, D., Bosire, J.O., Lo Seen, D. & Koedam, N. 2005. How effective were mangroves as a defence against the recent tsunami? *Current Biology* **15**, R443–R447.

Dahdouh-Guebas, F. & Koedam, N. 2008. Long-term retrospection on mangrove development using transdisciplinary approaches: a review. *Aquatic Botany* **89**, 80–92.

Dakin, W.J. 1966. *Australian Seashores*. Sydney, Australia: Angus & Robertson Ltd., revised edition.

Dalgren, C.P., Kellison, G.T., Adams, A.J., Gillanders, B.M., Kendall, M.S., Layman, C.A., Ley, J.A., Nagelkerken, I. & Serafy, J.E. 2006. Marine nurseries and effective juvenile habitats: concepts and applications. *Marine Ecology Progress Series* **312**, 291–295.

Danielsen, F., Sorensen, 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.

Davey, A. & Woelkerling, W.J. 1985. Studies on Australian mangrove algae. III. Victorian communities: structure and recolonization in Western Port Bay. *Journal of Experimental Marine Biology and Ecology* **85**, 177–190.

Davis, J.H. 1940. Ecology and geologic role of mangroves in Florida. Carnegie Institution of Washington Publication No. 517. Carnegie Institute of Washington, Washington, D.C., USA.

Dawes, C.J., Siar, K. & Marlett, D. 1999. Mangrove structure, litter and macroalgal productivity in a northernmost forest of Florida. *Mangroves and Salt Marshes* **3**, 259–267.

de Lange, W.P. 2003. Tsunamis and storm-surge hazard in New Zealand. In *The New Zealand Coast: Te Tai O Aotearoa*, J.R. Goff et al. (eds). Palmerston North, New Zealand: Dunmore Press, 79–95.

de Lange, W.P., Bell, R.G., Gorman, R. & Reid, S. 2003. Physical oceanography of New Zealand waters. In *The New Zealand Coast: Te Tai O Aotearoa*, J.R. Goff et al. (eds). Palmerston North, New Zealand: Dunmore Press, 59–78.

de Lange, W.P. & de Lange, P.J. 1994. An appraisal of factors controlling the latitudinal distribution of mangrove (*Avicennia marina* var. *resinifera*) in New Zealand. *Journal of Coastal Research* **10**, 539–548.

Delgado, P., Hensel, P.F., Jimenez, J.A. & Day, J.W. 2001. The importance of propagule establishment and physical factors in mangrove distributional patterns in a Costa Rican estuary. *Aquatic Botany* **71**, 157–178.

Deng, Y., Ogden, J., Horrocks, M., Anderson, S.H. & Nichol, S.L. 2004. The vegetation sequence at Whangapoua Estuary, Great Barrier Island, New Zealand. *New Zealand Journal of Botany* **42**, 565–588.

Department of Medical Entomology, University of Sydney. (n.d.). *Saltwater wetlands*. Online. Available HTTP: http://www.medent.usyd.edu.au/fact/saltwet.htm (accessed 2 September 2009).

Dick, T.M. & Osunkoya, O.O. 2000. Influence of tidal restriction floodgates on decomposition of mangrove litter. *Aquatic Botany* **68**, 273–280.

Dietrich, W.E. & Perron, J.T. 2006. The search for a topographic signature of life. *Nature* **439**, 411–418.

Dodd, R.S. & Afzal Rafii, Z. 2002. Evolutionary genetics of mangroves: continental drift to recent climate change. *Trees Structure and Function* **16**, 80–86.

Dodd, R.S., Afzal-Rafii, Z., Kashini, N. & Budrick, J. 2002. Land barriers and open oceans: effects on gene diversity and population structure in *Avicennia germinans* L. (*Avicenniaceae*). *Molecular Ecology* **11**, 1327–1338.

Dor, I. & Levy, I. 1984. Primary productivity of the benthic algae in the hard-bottom mangal of Sinai. In *Hydrobiology of the Mangal: The Ecosystem of the Mangrove Forests*, F.D. Por & I. Dor (eds). The Hague: Dr. W. Junk, 179–191.

Downton, W.J.S. 1982. Growth and osmotic relations of the mangrove *Avicennia marina*, as influenced by salinity. *Australian Journal of Plant Physiology* **9**, 519–528.

Dugdale, J.S. 1990. Reassessment of *Ctenopseustis* Meyrick and *Planotortrix* Dugdale with descriptions of two new genera (Lepidoptera: Tortricidae). *New Zealand Journal of Zoology* **17**, 437–465.

Duke, N.C. 1990. Phenological trends with latitude in the mangrove tree *Avicennia marina*. *Journal of Ecology* **78**, 113–133.

Duke, N.C. 1991. A systematic revision of the mangrove genus *Avicennia* (Avicenniaceae) in Australia. *Australian Systematic Botany* **4**, 299–324.

Duke, N.C. 2006. *Australia's Mangroves. The Authoritative Guide to Australia's Mangrove Plants*. Brisbane: MER.

Duke, N.C. 2008. Corrections and updates to the article by Duke et al. (2005) reporting on the unusual occurrence and cause of dieback of the common mangrove species, *Avicennia marina*, in NE Australia. *Marine Pollution Bulletin* **56**, 1668–1670

Duke, N.C., Benzie, J.A.H., Goodall, J.A. & Ballment, E.R. 1998. Genetic structure and evolution of species in the mangrove genus *Avicennia* (Avicenniaceae) in the Indo-West Pacific. *Evolution* **52**, 1612–1626.

Duke, N.C., Meynecke, J.O., Dittmann, S., Ellison, A.M., Anger, K., Berger, U., Cannicci, S., Diele, K., Ewel, K.C., Field, C.D., Koedam, N., Lee, S.Y., Marchand, C., Nordhaus, I. & Dahdouh-Guebas, F. 2007. A world without mangroves? *Science* **317**, 41–42.

Dye, A.H. 1983a. Composition and seasonal fluctuations of meiofauna in a southern African mangrove estuary. *Marine Biology* **73**, 165–170.

Dye, A.H. 1983b. Vertical and horizontal distribution of meiofauna in mangrove sediments in Transkei, southern Africa. *Estuarine Coastal and Shelf Science* **16**, 591–598.

Dyer, K. 1986. *Coastal and Estuarine Sediment Dynamics*. Chichester, United Kingdom: Wiley.

Dyer, K.R. 1997. *Estuaries—Physical Introduction*. Chichester, United Kingdom: Wiley, 2nd ed.

Elliot, A.H., Shaanker, U., Hicks, D.M., Woods, R.A. & Dymonds, J.R. 2009. SPARROW regional regression for sediment yields in New Zealand rivers. In *Sediment Dynamics in Changing Environments (Proceedings of a Symposium Held in Christchurch, New Zealand, December 2008),* J. Schmidt et al. (eds). Wallingford, U.K.: IAHS Press, 242–249.

Ellis, J., Nicholls, P., Craggs, R., Hofstra, D. & Hewitt, J. 2004. Effects of terrigenous sedimentation on mangrove physiology and associated macrobenthic communities. *Marine Ecology Progress Series* **270**, 71–82.

Ellison, A.M. 2002. Macroecology of mangroves: large-scale patterns and processes in tropical coastal forests. *Trees Structure and Function* **16**, 181–194.

Ellison, A.M. 2008. Managing mangroves with benthic biodiversity in mind: moving beyond roving banditry. *Journal of Sea Research* **59**, 2–15.

Ellison, J.C. 1993. Mangrove retreat with rising sea-level, Bermuda. *Estuarine Coastal and Shelf Science* **37**, 75–87.

Ellison, J.C. 1999. Impacts of sediment burial on mangroves. *Marine Pollution Bulletin* **37**, 420–426.

Ellison, J.C. 2008. Long-term retrospection on mangrove development using sediment cores and pollen analysis: a review. *Aquatic Botany* **89**, 93–104.

Ellison, J.C. 2009. Geomorphology and sedimentology of mangroves. In *Coastal Wetlands—An Integrated Ecosystem Approach*, G.M.E. Perillo et al. (eds). Amsterdam: Elsevier, 565–591.

Ellison, J.C. & Stoddart, D.R. 1991. Mangrove ecosystem collapse during predicted sea-level rise: Holocene analogues and implications. *Journal of Coastal Research* **7**, 151–165.

Emmerson, W.D. & McGwynne, L.E. 1992. Feeding and assimilation of mangroves leaves by the crab *Sesarma meinerti* de Man in relation to leaf-litter production in Mgazana, a warm-temperate southern African mangrove swamp. *Journal of Experimental Marine Biology and Ecology* **157**, 41–53.

Emmerson, W.D. & Ndenze, T.T. 2007. Mangrove tree specificity and conservation implications of the arboreal crab *Parasesarma leptosoma* at Mngazana, a mangrove estuary in the Eastern Cape, South Africa. *Wetlands Ecology and Management* **15**, 13–25.

Environment Waikato. 2009. *Estuarine Vegetation Survey, Extent of Coastal Habitats*. Hamilton, New Zealand: Environment Waikato (Waikato Regional Councl). Online. Available HTTP: http://www.ew.govt.nz/Environmental-information/REDI/628521/ (accessed 6 July 2009).

Erftemeijer, P.L.A. & Lewis, R.R., III. 1999. Planting mangroves on intertidal mudflats: habitat restoration or habitat conversion? In *Enhancing Coastal Ecosystem Restoration for the 21st Century. Proceedings of Regional Seminar for East and Southeast Asian Countries: ECOTONE VIII, Ranong and Phuket, Thailand, 23–28 May 1999*, V. Sumantakul (ed.). Bangkok, Thailand: Royal Forest Department of Thailand, 156–165.

Erskine, W.D., Mahmoudzadeh, A. & Myers, C. 2002. Land use effects on sediment yields and soil loss rates in small basins of Triassic sandstone near Sydney, NSW, Australia. *Catena* **49**, 271–287.

Eston, V.R., Braga, M.R.A., Cordeiro-Marinao, M., Fujii, M.T. & Yokoya, N.S. 1992. Macroalgal colonization patterns on artificial substrates inside southeastern Brazilian mangroves. *Aquatic Botany* **42**, 315–325.

Evans, M.J. & Williams, R.J. 2001. Historical distribution of estuarine wetlands at Kurnell Peninsula, Botany Bay. *Wetlands (Australia)* **19**, 61–71.

Farnsworth, E.J. 1998. Issues of spatial, taxonomic and temporal scale in delineating links between mangrove diversity and ecosystem function. *Global Ecology and Biogeography Letters* **7**, 15–25.

Farnsworth, E.J. & Ellison, A.M. 1997. Global patterns of pre-dispersal propagule predation in mangrove forests. *Biotropica* **29**, 318–330.

Farnsworth, E.J. & Farrant, J.M. 1998. Reductions in abscisic acid are linked with viviparous reproduction in mangroves. *American Journal of Botany* **85**, 760–769.

Faunce, C.H. & Serafy, J.E. 2006. Mangroves as fish habitat: 50 years of field studies. *Marine Ecology Progress Series* **318**, 1–18.

Faust, M.A. & Gulledge, R.A. 1996. Associations of microalgae and meiofauna in floating detritus at a mangrove island, Twin Cays, Belize. *Journal of Experimental Marine Biology and Ecology* **197**, 159–175.

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

Fenchel, T.M. 1978. The ecology of micro- and meiobenthos. *Annual Review of Ecology and Systematics* **9**, 99–121.

Ferrar, H.T. 1934. The geology of the Dargaville—Rodney Subdivision, Hokianga and Kaipara Divisions. Wellington, New Zealand: Geology Survey Branch, Department of Scientific and Industrial Research, Bulletin No. 34.

Field, C.D. 1995. Impact of expected climate change on mangroves. *Hydrobiologia* **295**, 75–81.

Field, C.D. 1999. Rehabilitation of mangrove ecosystems: an overview. *Marine Pollution Bulletin* **37**, 383–392.

Foster, I.D.L., Boardman, J. & Gates, J.B. 2009. Reconstructing historical sediment yields from the infilling of farm reservoirs, Eastern Cape, South Africa. In *Sediment Dynamics in Changing Environments (Proceedings of a Symposium Held in Christchurch, New Zealand, December 2008),* J. Schmidt et al. (eds). Wallingford, U.K.: IAHS Press, 440–447.

Fratini, S., Vannini, M., Cannicci, S. & Schubart, C.D. 2005. Tree-climbing mangrove crabs: a case of convergent evolution. *Evolutionary Ecology Research* **7**, 219–233.

French, J. 2006. Tidal marsh sedimentation and resilience to environmental change: exploratory modelling of tidal, sea-level and sediment supply forcing in predominantly allochthonous systems. *Marine Geology* **235**, 119–136.

French, J.R. 1993. Numerical simulation of vertical marsh growth and adjustment to accelerated sea-level rise, north Norfolk, UK. *Earth Surface Processes and Landforms* **18**, 63–81.

French, P.W. 1997. *Coastal and Estuarine Management*. London: Routledge.

Friedrichs, C.T. & Aubrey, D.G. 1988. Non-linear tidal distortion in shallow well-mixed estuaries: a synthesis. *Estuarine Coastal and Shelf Science* **27**, 521–545.

Fugate, D.C. & Chant, R.J. 2005. Near-bottom shear stresses in shallow well-mixed estuaries: a synthesis. *Journal of Geophysical Research* **110**, C03022, doi:03010.01029/02004JC002563.

Furukawa, K. & Wolanski, E. 1996. Sedimentation in mangrove forests. *Mangroves and Salt Marshes* **1**, 3–10.

Furukawa, K., Wolanski, E. & Mueller, H. 1997. Currents and sediment transport in mangrove forests. *Estuarine Coastal and Shelf Science* **44**, 301–310.

Galloway, R.W. 1982. Distribution and physiographic patterns of Australian mangroves. In *Mangrove Ecosystems in Australia: Structure, Function and Management*, B.F. Clough (ed.). Townsville, Australia: Australian Institute of Marine Science, 31–54.

Gee, J.M. 1989. An ecological and economic review of meiofauna as food for fish. *Zoological Journal of the Linnean Society* **96**, 243–261.

Gee, J.M. & Somerfield, P.J. 1997. Do mangrove diversity and leaf litter decay promote meiofaunal diversity? *Journal of Experimental Marine Biology and Ecology* **218**, 13–33.

George, K. & Gulliard, F. 2003. Application of the waterline method to the bathymetry of a drying macrotidal bay. *Hydrographic Journal* **108**, 3–9.

Geyer, W.R., Beardsley, R.C., Candela, J., Castro, B.M., Legeckis, R.V., Lentz, S.J., Limeburner, R., Miranda, L.B. & Trowbridge, J.H. 1991. The physical oceanography of the Amazon outflow. *Oceanography* **4**, 8–14.

Gibb, J.G. 1986. A New Zealand regional Holocene eustatic sea-level curve and its application to determination of vertical tectonic movements. A contribution to IGCP-Project 200. *Royal Society of New Zealand Bulletin* **24**, 377–395.

Giere, O. 2009. *Meiobenthology. The Microscopic Motile Fauna of Aquatic Sediments.* Berlin: Springer.

Gillanders, B.M. & Kingsford, M.J. 2002. Impact of changes in flow of freshwater on estuarine and open coastal habitats and the associated organisms. *Oceanography and Marine Biology An Annual Review* **40**, 233–309.

Gilman, E., Van Lavieren, H., Ellison, J., Jungblut, V., Wilson, L., Areki, F., Brighouse, G., Bungitak, J., Dus, E., Henry, M., Kilman, M., Matthews, E., Sauni, I., Teariki-Ruatu, N., Tukia, S. & Yuknavage, K. 2006. Pacific island mangroves in a changing climate and rising sea. Nairobi: United Nations Environment Programme, Regional Seas Programme, Regional Seas Report and Studies No. 179.

Gladstone, W. & Schreider, M.J. 2003. Effects of pruning a temperate mangrove forest on the associated assemblages of macroinvertebrates. *Marine and Freshwater Research* **54**, 683–690.

Glanville, E.B. 1947. Reclamation of tidal flats. *New Zealand Journal of Agriculture* **74**, 49–58.

Goring, D.G. & Bell, R.G. 1999. El Niño and decadal effects on sea-level variability in northern New Zealand: a wavelet analysis. *New Zealand Journal of Marine and Freshwater Research* **33**, 587–598.

Goulter, P.F.E. & Allaway, W.B. 1979. Litterfall and decomposition in a mangrove stand, *Avicennia marina* (Forsk.) Vierh., in Middle Harbour, Sydney. *Australian Journal of Marine and Freshwater Research* **30**, 541–546.

Granek, E. & Ruttenberg, B.I. 2008. Changes in biotic and abiotic processes following mangrove clearing. *Estuarine Coastal and Shelf Science* **80**, 555–562.

Granek, E.F. & Ruttenberg, B.I. 2007. Protective capacity of mangroves during tropical storms: a case study from 'Wilma' and 'Gamma' in Belize. *Marine Ecology Progress Series* **343**, 101–105.

Grant, J., Bathmann, U.V. & Mills, E.L. 1986. The interaction between benthic diatom films and sediment transport. *Estuarine Coastal and Shelf Science* **23**, 225–238.

Gratiot, N., Gardel, A. & Anthony, E.J. 2007. Trade-wind waves and mud dynamics on the French Guiana coast, South America: input from ERA-40 wave data and field investigations. *Marine Geology* **236**, 15–26.

Green, M.O., Black, K.P. & Amos, C.L. 1997. Control of estuarine sediment dynamics by interactions between currents and waves at several scales. *Marine Geology* **144**, 97–116.

Green, M.O. & Coco, G. 2007. Sediment transport on an estuarine intertidal flat: measurements and conceptual model of waves, rainfall and exchanges with a tidal creek. *Estuarine Coastal and Shelf Science* **72**, 553–569.

Green, P.S. 1994. *Oceanic Islands*. Canberra: Australian Government Printing Service.

Griffiths, G.A. & Glasby, G.P. 1985. Input of river-derived sediment to the New Zealand continental shelf: I. Mass. *Estuarine Coastal and Shelf Science* **21**, 773–787.

Guest, M.A. & Connolly, R.M. 2004. Fine-scale movement and assimilation of carbon in saltmarsh and mangrove habitat by resident animals. *Aquatic Ecology* **38**, 599–609.

Guest, M.A. & Connolly, R.M. 2006. Movement of carbon among estuarine habitats: the influence of saltmarsh patch size. *Marine Ecology Progress Series* **310**, 15–24.

Gunn, C.R. & Dennis, J.V. 1973. Tropical and temperate stranded seeds and fruits from the Gulf of Mexico. *Contributions in Marine Science* **17**, 111–121.

Gwyther, J. 2000. Meiofauna in phytal-based and sedimentary habitats of a temperate mangrove ecosystem—a preliminary survey. *Proceedings of the Royal Society of Victoria* **112**, 137–151.

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

Gwyther, J. & Fairweather, P.G. 2002. Colonisation by epibionts and meiofauna of real and mimic pneumatophores in a cool temperate mangrove habitat. *Marine Ecology Progress Series* **229**, 137–149.

Gwyther, J. & Fairweather, P.G. 2005. Meiofaunal recruitment to mimic pneumatophores in a cool-temperate mangrove forest: spatial context and biofilm effects. *Journal of Experimental Marine Biology and Ecology* **317**, 69–85.

Hancock, G.J. 2000. Identifying resuspended sediment in an estuary using the 228Th/232Th activity ratio: the fate of lagoon sediment in the Bega River estuary, Australia. *Marine and Freshwater Research* **51**, 659–667.

Hancock, G.J. & Hunter, J.R. 1999. Use of excess 210Pb and 228Th to estimate rates of sediment accumulation and bioturbation in Port Phillip Bay, Australia. *Marine and Freshwater Research* **50**, 533–545.

Hancock, G.J., Olley, J.M. & Wallbrink, P.J. 2001. Sediment transport and accumulation in the Western Port. Report on Phase I of a study to determine the sources of sediment to Western Port. CSIRO Land and Water Technical Report No. 47/01. CSIRO Land and Water, Canberra, Australia.

Hancock, G.J. & Pietsch, T. 2006. Sedimentation in the Gippsland Lakes as determinded from sediment cores. CSIRO Land and Water Science Report No. 40/06. CSIRO Land and Water, Canberra, Australia.

Hannah, J. 2004. An updated analysis of long-term sea level change in New Zealand. *Geophysical Research Letters* **31**, L03307, doi:03310.01029/02003GL019166.

Hansen, J.E. 2007. Scientific reticence and sea level rise. *Environmental Research Letters* **2**, 024002.

Harada, K. & Kawata, Y. 2004. Study on the effect of coastal forest to tsunami reduction. *Annals of the Disaster Prevention Research Institute, Kyoto University* **47C**, 161–166.

Hartnoll, R.G., Cannici, 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 Ecology and Management* **10**, 203–213.

Harty, C. & Cheng, D. 2003. Ecological assessment and strategies for the management of mangroves in Brisbane Water—Gosford, New South Wales, Australia. *Landscape and Urban Planning* **62**, 219–240.

He, B., Lai, T., Fan, H., Wang, W. & Zheng, H. 2007. Comparison of flooding-tolerance in four mangrove species in a diurnal tidal zone in the Beibu Gulf. *Estuarine Coastal and Shelf Science* **74**, 254–262.

Healy, T. 2002. Muddy coasts of mid-latitude oceanic islands on an active plate margin—New Zealand. In *Muddy Coasts of the World: Processes, Deposits and Function,* T. Healy et al. (eds). Amsterdam: Elsevier Science, 347–374.

Hedges, B., Ibene, B., Koenig, S., La Marca, R.I. & Hardy, J. 2008. *Eleutherodactylus johnstonei.* In *IUCN Red List of Threatened Species*. International Union for Conservation of Nature and Natural Resources, Red List Unit, Cambridge, U.K. Online. Available HTTP: http://www.iucnredlist.org (accessed 2 May 2009).

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. *Marine Biology* **144**, 385–395.

Hindell, J.S. & Jenkins, G.P. 2005. Assessing patterns of fish zonation in temperate mangroves, with emphasis on evaluating sampling artefacts. *Marine Ecology Progress Series* **290**, 193–205.

Hodda, M. 1990. Variation in estuarine littoral nematode populations over three spatial scales. *Estuarine Coastal and Shelf Science* **30**, 325–340.

Hodda, M. & Nicholas, W.L. 1985. Meiofauna associated with mangroves in the Hunter River estuary and Fullerton Cove, south-eastern Australia. *Australian Journal of Marine and Freshwater Research* **36**, 41–50.

Hodda, M. & Nicholas, W.L. 1986a. Temporal changes in littoral meiofauna from the Hunter River estuary. *Australian Journal of Marine and Freshwater Research* **37**, 729–741.

Hodda, M. & Nicholas, W.L. 1986b. Nematode diversity and industrial pollution in the Hunter River estuary, NSW, Australia. *Marine Pollution Bulletin* **17**, 251–255.

Hogarth, P.J. 2007. *The Biology of Mangroves*. New York, USA: Oxford University Press.

Horticulture and Food Research Institute of New Zealand Ltd. 1998a. *HortFACT factsheet. Brownheaded leafroller, Ctenopseustis obliquana (Walker).* Plant and Food Research, Auckland, New Zealand. Online. Available HTTP: http://www.hortnet.co.nz/publications/hortfacts/hf401027.htm (accessed 20 July 2009).

Horticulture and Food Research Institute of New Zealand Ltd. 1998b. *HortFACT factsheet. Lemon tree borer, Oemona hirta (Fabricius)*. Plant and Food Research, Auckland, New Zealand. Online. Available HTTP: http://www.hortnet.co.nz/publications/hortfacts/hf401033.htm (accessed 20 July 2009).

Hovenden, M.J., Curran, M., Cole, M.A., Goulter, P.F.E., Skelton, N.J. & Allaway, W.G. 1995. Ventilation and respiration in roots of one-year-old seedlings of grey mangrove *Avicennia marina* (Forsk.) Vierh. *Hydrobiologia* **295**, 23–29.

Hughes, R.H. & Hughes, J.S. 1992. *A Directory of African Wetlands*. Gland, Switzerland/Cambridge, United Kingdom/Nairobi, Kenya: IUCN/UNEP/WCMC.

Hume, T.M. 2003. Estuaries and tidal inlets. In *The New Zealand Coast: Te Tai O Aotearoa*, J.R. Goff et al. (eds). Palmerston North, New Zealand: Dunsmore Press, 191–213.

Hume, T.M., Snelder, T., Weatherhead, M. & Liefting, R. 2007. A controlling factor approach to estuary classification. *Ocean and Coastal Management* **50**, 905–929.

Hutchings, P. & Saenger, P. 1986. *Ecology of Mangroves*. Brisbane, Australia: Queensland University Press.

Hutchings, P.A. & Recher, H.F. 1974. The fauna of Careel Bay with comments on the ecology of mangrove and sea-grass communities. *Australian Zoologist* **18**, 99–128.

Hutchings, P.A. & Recher, H.F. 1982. Fauna of Australian mangroves. *Proceedings of the Linnean Society of New South Wales* **106**, 703–712.

Imgraben, S. & Dittmann, S. 2008. Leaf litter dynamics and litter consumption in two temperate South Australian mangrove forests. *Journal of Sea Research* **59**, 83–93.

IPCC 2007. *Climate change 2007: the physical basis. Contributions of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel for Climate Change*. S. Solomon et al. (eds). Cambridge: Cambridge University Press.

Janssen-Stelder, B.M., Augustinus, P.G.E.F. & van Santen, W.A.C. 2002. Sedimentation in a coastal mangrove system, Red River Delta, Vietnam. In *Fine Sediment Dynamics in the Marine Environment,* J.C. Winterwerp & C. Kranenberg (eds). Amsterdam: Elsevier Science, 455–467.

Jelbart, J.E., Ross, P.M. & Connolly, R.M. 2007. Fish assemblages in seagrass beds are influenced by the proximity of mangrove forests. *Marine Biology* **150**, 993–1002.

Jenkins, G.P., Wheatley, M.J. & Poore, A.G.B. 1996. Spatial variation in recruitment, growth, and feeding of postsettlement King George whiting, *Sillaginoides punctata*, associated with seagrass beds of Port Phillip Bay, Australia. *Canadian Journal of Fisheries and Aquatic Sciences* **53**, 350–359.

Jensen, P. 1987. Feeding ecology of free-living aquatic nematodes. *Marine Ecology Progress Series* **35**, 187–196.

Johnstone, I.M. 1981. Consumption of leaves by herbivores in mixed mangrove stands. *Biotropica* **13**, 252–259.

Jones, B.G. & Chenhall, B.E. 2001. Lagoonal and estuarine sedimentation during the past 200 years. In *Australian Institute of Nuclear Science and Engineering: Environment Workshop on Archives of Human Impact of the Last 200 Years,* H. Heijnis & K. Harle (eds). Lucas Heights, New South Wales, Australia: Australian Institute of Nuclear Science and Engineering, 42–46.

Joye, S.B. & Lee, R.Y. 2004. Benthic microbial mats: important sources of fixed nitrogen and carbon to the Twin Cays, Belize ecosystem. *Atoll Research Bulletin*, 1–24.

Kakembo, V. & Rowntree, K.M. 2003. Relationship between land use and soil erosion in the communal lands near Peddie Town, Eastern Cape, South Africa. *Land Degradation and Development* **14**, 39–49.

Kaly, U.L. 1988. *Distribution, abundance and size of mangrove and saltmarsh gastropods*. PhD thesis, University of Sydney, Sydney, Australia.

Kaly, U.L., Eugelink, G. & Robertson, A.I. 1997. Soil conditions in damaged North Queensland mangroves. *Estuaries* **20**, 291–300.

Kamaruzzaman, B.Y. & Ong, M.C. 2008. Recent sedimentation rate and sediment ages determination of Kemaman-Chukai mangrove forest, Terengganu, Malaysia. *American Journal of Agricultural and Biological Science* **3**, 522–525.

Kangas, P.C. & Lugo, A.E. 1990. The distribution of mangroves and saltmarsh in Florida. *Journal of Tropical Ecology* **31**, 32–39.

Kathiresan, K. & Bingham, B.L. 2001. Biology of mangroves and mangrove ecosystems. *Advances in Marine Biology* **40**, 84–254.

Kathiresan, K. & Rajendran, N. 2005. Coastal mangrove forests mitigated tsunami. *Estuarine Coastal and Shelf Science* **65**, 601–606.

Kelaher, B.P., Chapman, M.G. & Underwood, A.J. 1998a. Changes in benthic assemblages near boardwalks in temperate urban mangrove forests. *Journal of Experimental Marine Biology and Ecology* **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. *Journal of Experimental Marine Biology and Ecology* **227**, 281–300.

King, R.J. 1995. Mangrove macroalgae: a review of Australian studies. *Proceedings of the Linnean Society of New South Wales* **115**, 151–161.

Kirwan, M.L., Murray, A.B. & Boyd, W.S. 2008. Temporary vegetation disturbance as an explanation for permanent loss of tidal wetlands. *Geophysical Research Letters* **35**, L05403.

Kitheka, J.U., Ongwenyi, G.S. & Mavuti, K.M. 2002. Dynamics of suspended sediment exchange and transport in a degraded mangrove creek in Kenya. *Ambio* **31**, 580–587.

Knox, G.A. 1983. *Estuarine Ecology*. Auckland, New Zealand: Auckland Regional Authority.

Kobashi, D. & Mazda, Y. 2005. Tidal flow in riverine-type mangroves. *Wetlands Ecology and Management* **13**, 615–619.

Koch, G.W., Sillet, S.C., Jennings, G.M. & Davis, S. 2004. Limits to tree growth. *Nature* **428**, 851–854.

Krauss, K.W., Allen, J.A. & Cahoon, D.R. 2003. Differential rates of vertical accretion and elevation change among aerial root types in Micronesian mangrove forests. *Estuarine Coastal and Shelf Science* **56**, 251–259.

Krauss, K.W., Lovelock, C.E., McKee, K.L., Lopez-Hoffman, L., Ewe, S.M.L. & Sousa, W.P. 2008. Environmental drivers in mangrove establishment and early development: a review. *Aquatic Botany* **89**, 105–127.

Kristensen, E., Bouillon, S., Dittmar, T. & Marchand, C. 2008. Organic carbon dynamics in mangrove ecosystems: a review. *Aquatic Botany* **89**, 201–219.

Kronen, M. 2001. *Dynamics of mangroves (Avicennia marina) in the Puhoi Estuary, New Zealand*. MSc thesis, University of Auckland, Auckland, New Zealand.

Lacerda, L.D., Menezes, M.O.T. & Molisani, M.M. 2007. Changes in mangrove extension at the Pacoti River estuary, CE, NE Brazil due to regional environmental changes between 1958 and 2004. *Biota Neotropica* **7**, 67–72.

Laegdsgaard, P. & Johnson, C.R. 1995. Mangrove habitats as nurseries: unique assemblages of juvenile fish in subtropical mangroves in eastern Australia. *Marine Ecology Progress Series* **126**, 67–81.

Laegdsgaard, P. & Johnson, C. 2001. Why do juvenile fish utilise mangrove habitats? *Journal of Experimental Marine Biology and Ecology* **257**, 229–253.

Lamb, K.P. 1952. New plant galls: 1—Mite and insect galls. *Transactions of the Royal Society of New Zealand* **79**, 349–362.

Lebigre, J.M. 1999. Natural spatial dynamics of mangals through their margins: diagnostic elements. *Hydrobiologia* **413**, 103–113.

Leduc, D., Probert, P.K. & Duncan, A. 2009. A multi-method approach for identifying meiofaunal trophic interactions. *Marine Ecology Progress Series* **383**, 95–111.

Lee, R.Y. & Joye, S.B. 2006. Seasonal patterns of nitrogen fixation and dentrification in oceanic mangrove habitats. *Marine Ecology Progress Series* **307**, 127–141.

Lee, S.C. & Mehta, A.J. 1997. Problems in characterizing dynamics of mud shore profiles. *Journal of Hydraulic Engineering* **123**, 351–360.

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

Lee, S.Y. 1999. The effect of mangrove leaf litter enrichment on macrobenthic colonization of defaunated sandy substrates. *Estuarine Coastal and Shelf Science* **49**, 703–712.

Lee, S.Y. 2008. Mangrove macrobenthos: assemblages, services, and linkages. *Journal of Sea Research* **59**, 16–29.

Lessa, G. & Masselink, G. 1995. Morphodynamic evolution of a macrotidal barrier estuary. *Marine Geology* **129**, 25–46.

Lester, G.D., Sorensen, S.G., Faulkner, P.L., Reid, C.S. & Maxit, I.E. 2005. *Louisiana Comprehensive Wildlife Conservation Strategy*. Baton Rouge, Louisiana, USA: Louisiana Department of Wildlife and Fisheries.

Lewis, R.R., III. 2005. Ecological engineering for successful management and restoration of mangrove forests. *Ecological Engineering* **24**, 403–418.

Ley, J.A., Montague, C.L. & Mcivor, C.C. 1994. Food habits of mangrove fishes: a comparison along estuarine gradients in northeastern Florida Bay. *Bulletin of Marine Science* **54**, 881–899.

Li, M.S. & Lee, S.Y. 1997. Mangroves of China: a brief review. *Forest Ecology and Management* **96**, 241–259.

Lindegarth, M. & Hoskin, M. 2001. Patterns of distribution of macro-fauna in different types of estuarine, soft sediment habitats adjacent to urban and non-urban areas. *Estuarine Coastal and Shelf Science* **52**, 237–247.

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. *Marine Biology* **130**, 289–300.

Lovelock, C. 1993. *Field Guide to the Mangroves of Queensland*. Townsville, Australia: Australian Institute of Marine Science.

Lovelock, C.E. 2008. Soil respiration and belowground carbon allocation in mangrove forests. *Ecosystems* **11**, 342–354.

Lovelock, C.E., Ball, M.C., Feller, I.C., Engelbrecht, B.M.J. & Ewe, M.L. 2006. Variation in hydraulic conductivity of mangroves: influence of species, salinity, and nitrogen and phosphorus availability. *Physiologia Plantarum* **127**, 457–464.

Lovelock, C.E., Ball, M.C., Martin, K.C. & Feller, I.C. 2009. Nutrient enrichment increases mortality of mangroves. *PLoS One* **4**, e5600.

Lovelock, C.E., Feller, I.C., Ball, M.C., Ellis, J. & Sorrell, B.K. 2007a. Testing the growth rate vs. geochemical hypothesis for latitudinal variation in plant nutrients. *Ecology Letters* **10**, 1154–1163.

Lovelock, C.E., Feller, I.C., Ellis, J., Schwarz, A.M., Hancock, N., Nichols, P. & Sorrell, B. 2007b. Mangrove growth in New Zealand estuaries: the role of nutrient enrichment at sites with contrasting rates of sedimentation. *Oecologia* **153**, 633–641.

Lugo, A.E., Sell, M. & Snedaker, S.C. 1976. Mangrove ecosystem analysis. In *Systems Analysis and Simulation in Ecology*, B.C. Pattern (ed.). New York, USA: Academic Press, 113–145.

Lynch, J.C., Meriwether, J.R., McKee, B.A., Vera-Herrera, F. & Twilley, R.R. 1989. Recent accretion in mangrove ecosystems based on super(137)Cs and super(210)Pb. *Estuaries* **12**, 284–299.

Mackey, A.P. 1993. Biomass of the mangrove *Avicennia marina* (Forssk.) Vierh. near Brisbane, south-eastern Queensland. *Australian Journal of Marine and Freshwater Research* **44**, 721–725.

Mackey, A.P. & Smail, G. 1996. The decomposition of mangrove litter in a subtropical mangrove forest. *Hydrobiologia* **332**, 93–98.

Macnae, W. 1963. Mangroves swamps in South Africa. *Journal of Ecology* **51**, 1–25.

Macnae, W. 1966. Mangroves in eastern and southern Australia. *Australian Journal of Botany* **14**, 67–104.

Macnae, W. 1968. A general account of the fauna and flora of mangrove swamps and forests in the Indo-West-Pacific region. *Advances in Marine Biology* **6**, 73–270.

Maguire, T.L., Edwards, K.J., Saenger, P. & Henry, R. 2000. Characterisation and analysis of microsatellite loci in a mangrove species, *Avicennia marina* (Forsk.) Vierh. (*Avicenniaceae*). *Theoretical and Applied Genetics* **101**, 279–285.

Maguire, T.L., Peakall, R. & Saenger, P. 2002. Comparative analysis of genetic diversity in the mangrove species *Avicennia marina* (Forsk.) Vierh. (*Avicenniaceae*) detected by AFLPs and SSRs. *Theoretical and Applied Genetics* **104**, 388–398.

Marshall, D.J. & Pugh, P.J.A. 2001. Two new species of *Schusteria* (Acari: Oribatida: Ameronothroidea) from marine shores in southern Africa. *African Zoology* **35**, 201–205.

Martin, A.K. 1987. Comparison of sedimentation rates in the Natal Valley, south-west Indian Ocean, with modern sediment yields in east coast rivers of Southern Africa. *South African Journal of Science* **83**, 716–724.

Martin, K.C. 2007. *Interactive effects of salinity and nutrients on mangrove physiology: implications for mangrove forest structure and function*. PhD thesis, Australian National University, Canberra.

Massel, S.R. 1999. *Fluid Mechanics for Marine Ecologists*. Berlin: Springer-Verlag.

Massel, S.R., Furukawa, K. & Brinkman, R.M. 1999. Surface wave propagation in mangrove forests. *Fluid Dynamics Research* **24**, 219–249.

Mathew, J. & Baba, M. 1995. Mudbanks of the southwest coast of India. II: Wave-mud interactions. *Journal of Coastal Research* **11**, 179–187.

Maxwell, G.S. 2006. *The Removal of Mangrove Seedlings from Whangamata Harbour—An Assessment of Environmental Effects*. Hamilton, New Zealand: Environment Waikato (Waikato Regional Council).

May, J.D. 1999. Spatial variation in litter production by the mangrove *Avicennia marina* var. *australasica* in Rangaunu Harbour, Northland, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **33**, 163–172.

Mazda, Y., Kanazawa, N. & Wolanski, E. 1995. Tidal asymmetry in mangrove creeks. *Hydrobiologia* **295**, 51–58.

Mazda, Y., Kobashi, D. & Okada, S. 2005. Tidal-scale hydrodynamics within mangrove swamps. *Wetlands Ecology and Management* **13**, 647–655.

Mazda, Y. & Wolanski, E. 2009. Hydrodynamics and modelling of water flow in mangrove areas. In *Coastal Wetlands—An Integrated Ecosystem Approach*, G.M.E. Perillo et al. (eds). Amsterdam: Elsevier, 231–261.

Mazumder, D., Saintilan, N. & Williams, R.J. 2005. Temporal variations in fish catch using pop nets in mangrove and saltmarsh flats at Towra Point, NSW, Australia. *Wetlands Ecology and Management* **13**, 457–467.

Mazumder, D., Saintilan, N. & Williams, R.J. 2006. Fish assemblages in three tidal saltmarsh and mangrove flats in temperate NSW, Australia: a comparison based on species diversity and abundance. *Wetlands Ecology and Management* **14**, 201–209.

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. *Estuarine Coastal and Shelf Science* **73**, 316–324.

McIvor, C.C. & Smith, T.J., III. 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.

McKee, K.L. 1995a. Interspecific variation in growth, biomass partitioning, and defensive characteristics of neotropical mangrove seedlings: response to light and nutrient availability. *American Journal of Botany* **82**, 299–307.

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

McKee, K.L., Cahoon, D.R. & Feller, I.C. 2007. Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation. *Global Ecology and Biogeography* **16**, 545–556.

McKee, K.L. & Rooth, J.E. 2008. Where temperate meets tropical: multi-factorial effects of elevated CO2, nitrogen enrichment, and competition on a mangrove-salt marsh community. *Global Change Biology* **14**, 971–984.

McKillup, S.C. & Butler, A.J. 1979. Cessation of hole-digging by the crab *Helograpsus haswellianus*: a resource-conserving adaptation. *Marine Biology* **50**, 157–161.

McLoughlin, L. 1987. Mangroves and grass swamps: changes in the shoreline vegetation of the Middle Lane Cover River, Sydney, 1780s–1880s. *Wetlands (Australia)* **7**, 13–24.

McLoughlin, L. 2000. Estuarine wetlands distribution along the Paramatta River, Sydney, 1788–1940: implications for planning and conservation. *Cunninghamia* **6**, 579–610.

McTainsh, G., Iles, B. & Saffinga, P. 1986. Spatial and temporal patterns of mangroves at Oyster Point Bay, South East Queensland. *Proceedings of the Royal Society of Queensland* **99**, 83–91.

Meades, L., Rodgerson, L., York, A. & French, K. 2002. Assessment of the diversity and abundance of terrestrial mangrove arthropods in southern New South Wales, Australia. *Austral Ecology* **27**, 451–458.

Meadows, P.S., Tait, J. & Hussain, S.A. 1990. Effects of estuarine infauna on sediment stability and particle sedimentation. *Hydrobiologia* **190**, 263–266.

Mehta, A.H. 2002. Mud-shore dynamics and controls. In *Muddy Coasts of the World: Processes, Deposits and Function,* T. Healy et al. (eds). Amsterdam, Elsevier Science, 19–60.

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. *Marine Biology* **148**, 363–371.

Melville, F. & Pulkownik, A. 2006. Investigation of mangrove macroalgae as bioindicators of estuarine contamination. *Marine Pollution Bulletin* **52**, 1260–1269.

Melville, F., Pulkownik, A. & Burchett, M. 2005. Zonal and seasonal variation in the distribution and abundance of mangrove macroalgae in the Parramatta River, Australia. *Estuarine Coastal and Shelf Science* **64**, 267–276.

Mendez-Alonzo, R., Lopez-Portillo, J. & Rivera-Monroy, V.H. 2008. Latitudinal variation in leaf and tree traits of the mangrove *Avicennia germinans* (*Avicenniaceae*) in the central region of the Gulf of Mexico. *Biotropica* **40**, 449–456.

Middleton, B.A. & McKee, K.L. 2001. Degradation of mangrove tissues and implications for peat formation in Belizean island forests. *Journal of Ecology* **89**, 818–828.

Mildenhall, D.C. 1994. Early to mid Holocene pollen samples containing mangrove pollen from Sponge Bay, East Coast, North Island, New Zealand. *Journal of the Royal Society of New Zealand* **24**, 219–230.

Mildenhall, D.C. & Brown, L. 1987. An early Holocene occurrence of the mangrove *Avicennia marina* in Poverty Bay, North Island, New Zealand. *New Zealand Journal of Botany* **25**, 281–294.

Miller, P. & Miller, K. 1991. Bitterns using mangroves. *Notornis* **38**, 79.

Milliman, J.D. & Syvitski, J.P.M. 1992. Geomorphic/tectonic control of sediment discharge to the ocean: the importance of small mountainous rivers. *Journal of Geology* **100**, 525–544.

Milward, N.E. 1982. Mangrove-dependent biota. In *Mangrove Ecosystems in Australia: Structure, Function and Management*, B.F. Clough (ed.). Townsville, Australia: Australian Institute of Marine Science, 121–139.

Minchinton, T.E. 2006. Consequences of pre-dispersal damage by insects for the dispersal and recruitment of mangroves. *Oecologia* **148**, 70–80.

Minchinton, T.E. & Dalby-Ball, M. 2001. Frugivory by insects on mangrove propagules: effects on the early life history of *Avicennia marina*. *Oecologia* **129**, 243–252.

Minchinton, T.E. & Ross, P.M. 1999. Oysters as habitats for limpets in a temperate mangrove forest. *Australian Journal of Ecology* **24**, 157–170.

Mitchell, M.L. & Adam, P. 1989. The relationship between mangrove and saltmarsh communities in the Sydney region. *Wetlands (Australia)* **8**, 37–46.

Mitsch, W.J., Gosselink, J.G., Anderson, C.J. & Zhang, L. 2009. *Wetland Ecosystems*. Chichester, United Kingdom: Wiley.

Mom, G.A.T. 2005. *Effects of management on the ecology of mangrove communities in New Zealand*. PhD thesis, University of Auckland, Auckland, New Zealand.

Morant, P. & Quinn, N. 1999. Influence of man and management of South African estuaries. In *Estuaries of South Africa*, B.R. Allanson & D. Baird (eds). Cambridge, United Kingdom: Cambridge University Press, 289–320.

Morris, J.T., Sundareshwar, P.V., Nietch, C.T., Kjerfve, B. & Cahoon, D.R. 2002. Responses of coastal wetlands to rising sea level. *Ecology* **83**, 2869–2877.

Morrisey, D. 1995. Saltmarshes. In *Coastal Ecology of Temperate Australia*, A.J. Underwood & M.G. Chapman (eds). Sydney: University of New South Wales Press, 205–220.

Morrisey, D., Beard, C., Morrison, M., Craggs, R. & Lowe, M. 2007. The New Zealand mangrove: review of the current state of knowledge. Auckland Regional Council Technical Publication No. 325. Auckland, New Zealand: Auckland Regional Council.

Morrisey, D.J., Hill, A.F., Kemp, C.L.S. & Smith, R.K. 1999. Changes in abundance and distribution of coastal and estuarine vegetation in the Auckland region. NIWA Client Report No. ARC90232/1. Hamilton, New Zealand: National Institute of Water and Atmospheric Research Ltd (NIWA).

Morrisey, D.J., Hume, T.M., Swales, A., Hewitt, J.E., Hill, A.F., Ovenden, R., Smith, R.K., Taylor, M.D. & Wilkinson, M.R. 1995. *Ecological monitoring for potential effects of forestry activities on the intertidal habitats of Whangapoua Harbour. Annual report 1991–1995*. Hamilton, New Zealand: NIWA.

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. *Estuarine Coastal and Shelf Science* **56**, 581–592.

Morton, B. 2004. Predator-prey interactions between *Lepsiella vinosa* (Gastropoda : Muricidae) and *Xenostrobus inconstans* (Bivalvia : Mytilidae) in a southwest Australian marsh. *Journal of Molluscan Studies* **70**, 237–245.

Morton, J. & Miller, M. 1968. *The New Zealand Sea Shore*. Auckland, New Zealand: Collins.

Murray, A.B., Lazarus, E., Ashton, A., Baas, A., Coco, G., Coulthard, T., Fonstad, M., Haff, P., McNamara, D., Paola, C., Pelletier, J. & Reinhardt, L. 2009. Geomorphology, complexity and the emerging science of the Earth's surface. *Geomorphology* **103**, 496–505.

Murray, A.L. & Spencer, T. 1997. On the wisdom of calculating annual material budgets in tidal wetlands. *Marine Ecology Progress Series* **150**, 207–216.

Murray, F. 1985. Cycling of fluoride in a mangrove community near a fluoride emission source. *Journal of Applied Ecology* **22**, 277–285.

Nagelkerken, I., Blaber, S.J.M., Bouillon, S., Green, P., Haywood, M., Kirton, L.G., Meynecke, J.O., Pawlik, J., Penrose, H.M., Sasekumar, A. & Somerfield, P.J. 2008. The habitat function of mangroves for terrestrial and marine fauna: a review. *Aquatic Botany* **89**, 155–185.

Nagelkerken, I., Kleijnen, S., Klop, T., van den Brand, R.A., de la Moriniere, E.C. & van der Velde, G. 2001. Dependence of Caribbean reef fishes on mangroves and seagrass beds as nursery habitats: a comparison of fish faunas between bays with and without mangroves/seagrass beds. *Marine Ecology Progress Series* **214**, 225–235.

Nagelkerken, I., van der Velde, G., Gorissen, M.W., Meijer, G.J., vant Hof, T. & den Hartog, C. 2000. Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. *Estuarine Coastal and Shelf Science* **51**, 31–44.

Naidoo, Y., Steinke, T.D., Mann, F.D., Bhatt, A. & Gairola, S. 2008. Epiphytic organisms on the pneumatophores of the mangrove *Avicennia marina*: occurrence and possible function. *African Journal of Plant Science* **2**, 12–15.

Nakasuga, T., Oyama, H. & Haruki, M. 1974. Studies on the mangrove community. 1. The distribution of the mangrove community in Japan. *Japanese Journal of Ecology* **24**, 237–246.

Nature Conservation Council. 1984. *Strategies for the management of mangrove forests in New Zealand, Nature Conservation Council discussion document*. Auckland, New Zealand: Nature Conservation Council.

Neil, D.T. 1998. Moreton Bay and its catchment: seascape and landscape, development and degradation. In *Moreton Bay and Catchment*, I.R. Tibbetts et al. (eds). Brisbane, Australia: University of Queensland, 3–54.

Netto, S.A. & Gallucci, F. 2003. Meiofauna and macrofauna communities in a mangrove from the island of Santa Catarina, South Brazil. *Hydrobiologia* **505**, 159–170.

New South Wales Department of Primary Industries. 2009. *Mud crab Scylla serrata*. Cronulla, Australia: New South Wales Department of Primary Industries. Online. Available HTTP: http://www.dpi.nsw.gov.au/fisheries/recreational/saltwater/sw-species/mud-crab (accessed 13 June 2009).

Nichol, S.L., Augustinus, P.C., Gregory, M.R., Creese, R. & Horrocks, M. 2000. Geomorphic and sedimentary evidence of human impact on the New Zealand coastal landscape. *Physical Geography* **21**, 109–132.

Nicholas, W.L. 1996. *Robustnema fosteri* sp. nov., gen. nov. (Xyalidae, Monhysterida, Nematoda), a common nematode of mangrove mudflats in Australia. *Transactions of the Royal Society of South Australia* **120**, 161–165.

Nicholas, W.L., Elek, J.A., Stewart, A. & Marples, T.G. 1991. The nematode fauna of a temperate Australian mangrove mudflat; its population density, diversity and distribution. *Hydrobiologia* **209**, 13–27.

Nicholas, W.L., Goodchild, D.J. & Stewart, A. 1987. The mineral composition of intracellular inclusions in nematodes from thiobiotic mangrove mud-flats. *Nematologica* **33**, 167–179.

Nicholas, W.L., Stewart, A.C. & Marples, T.G. 1988. Field and laboratory studies of *Desmodora cazca* Gerlach, 1956 (Desmodoridae: Nematoda) from mangrove mud-flats. *Nematologica* **34**, 331–349.

Nichols, M.M. 1977. Response and recovery of an estuary following a river flood. *Journal of Sedimentary Petrology* **47**, 1171–1186.

Ochieng, C.A. & Erftemeijer, P.L.A. 2002. Phenology, litterfall and nutrient resorption in *Avicennia marina* (Forssk.) Vierh in Gazi Bay, Kenya. *Trees Structure and Function* **16**, 167–171.

Olafsson, E. 1995. Meiobenthos in mangrove areas in eastern Africa with emphasis on assemblage structure of free-living marine nematodes. *Hydrobiologia* **312**, 47–57.

Olafsson, E. & Ndaro, S.G.M. 1997. Impact of the mangrove crabs *Uca annulipes* and *Dotilla fenestrata* on meiobenthos. *Marine Ecology Progress Series* **158**, 225–231.

Olley, J.M. & Wasson, R.J. 2003. Changes in the flux of sediment in the Upper Murrumbidgee catchment, Southeastern Australia, since European settlement. *Hydrological Processes* **17**, 3307–3320.

Oñate-Pacalioga, J.A. 2005. *Leaf litter production, retention, and decomposition of Avicennia marina var. australasica at Whangateau Estuary, Northland, New Zealand*. MSc thesis, University of Auckland, Auckland, New Zealand.

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

Osunkoya, O.O. & Creese, R.G. 1997. Population structure, spatial pattern and seedling establishment of the grey mangrove, *Avicennia marina* var. *australasica*, in New Zealand. *Australian Journal of Botany* **45**, 707–725.

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

Panapitukkul, N., Duarte, C.M., Thampanya, U., Kheowvongsri, P., Srichai, N., Geertz-Hansen, O., Terrados, J. & Boromthanarath, S. 1998. Mangrove colonization: mangrove progression over the growing Pak Phanang (SE Thailand) mud flat. *Estuarine Coastal and Shelf Science* **47**, 51–61.

Park, S. 2004. Aspects of mangrove distribution and abundance in Tauranga Harbour. Tauranga, New Zealand: Environmental Bay of Plenty (Bay of Plenty Regional Council) Environmental Publication No. 2004/16.

Parkinson, R.W., DeLaune, R.D. & White, J.R. 1994. Holocene sea-level rise and the fate of mangrove forests within the wider Caribbean region. *Journal of Coastal Research* **10**, 1077–1086.

Patterson, C.S., McKee, K.L. & Mendelssohn, I.A. 1997. Effects of tidal inundation and predation on *Avicennia germinans* seedling establishment and survival in a sub-tropical mangal/salt marsh community. *Mangroves and Salt Marshes* **1**, 103–111.

Patterson, C.S., Mendelssohn, I.A. & Swenson, E.M. 1993. Growth and survival of *Avicennia germinans* seedlings in a mangal/salt marsh community in Louisiana, USA. *Journal of Coastal Research* **9**, 801–810.

Payne, J.L. & Gillanders, B.M. 2009. Assemblages of fish along a mangrove-mudflat gradient in temperate Australia. *Marine and Freshwater Research* **60**, 1–13.

Pearce, J.B. 1995. Urban development and marine and riparian habitat quality. *Marine Pollution Bulletin* **30**, 496–499.

Peel, M.C., Finlayson, B.L. & McMahon, T.A. 2007. Updated world map of the Koppen-Geiger climate classification. *Hydrology and Earth System Sciences* **11**, 1633–1644.

Perry, C.L. 2007. *Ecosystem effects of expanding populations of Avicennia germinans in a southeastern Louisiana Spartina alterniflora saltmarsh*. MSc thesis, Louisiana State University, Baton Rogue, Louisiana.

Perry, C.L. & Mendelssohn, I.A. 2009. Ecosystem effects of expanding populations of *Avicennia germinans* in a Louisiana salt marsh. *Wetlands* **29**, 396–406.

Pfeffer, W.T., Harper, J.T. & O'Neel, S. 2008. Kinematic constraints on glacier contributions to 21st-century sea-level rise. *Science* **321**, 1340–1343.

Phillips, A., Lambert, G., Granger, J.E. & Steinke, T.D. 1994. Horizontal zonation of epiphytic algae associated with *Avicennia marina* (Forssk) Vierh pneumatophores at Beachwood Mangroves Nature Reserve, Durban, South Africa. *Botanica Marina* **37**, 567–576.

Phleger, F.B. 1970. Foraminiferal populations and marine marsh processes. *Limnology and Oceanography* **15**, 522–536.

Phuoc, V.L.H. & Massel, S.R. 2006. Experiments on wave motion and suspended sediment concentration at Nang Hai, CanGio mangrove forest, Southern Vietnam. *Oceanologia* **48**, 23–40.

Pocknall, D.T., Gregory, M.R. & Greig, D.A. 1989. Palynology of core 80/20 and its implications for understanding Holocene sea level changes in the Firth of Thames, New Zealand. *Journal of the Royal Society of New Zealand* **19**, 171–179.

Polz, M.F., Felbeck, H., Novak, R., Nebelsick, M. & Ott, J.A. 1992. Chemoautotrophic, sulfur-oxidizing symbiotic bacteria on marine nematodes: morphological and biochemical characterization. *Microbial Ecology* **24**, 313–329.

Postma, H. 1961. Transport and accumulation of suspended matter in the Dutch Wadden Sea. *Netherlands Journal of Sea Research* **1**, 148–190.

Proches, S. 2004. Ecological associations between organisms of different evolutionary history: mangrove pneumatophore arthropods as a case study. *Journal of the Marine Biological Association of the United Kingdom* **84**, 341–344.

Proches, S. & Marshall, D.J. 2002. Epiphytic algal cover and sediment deposition as determinants of arthropod distribution and abundance on mangrove pneumatophores. *Journal of the Marine Biological Association of the United Kingdom* **82**, 937–942.

Proches, S., Marshall, D.J., Ugrasen, K. & Ramcharan, A. 2001. Mangrove pneumatophore arthropod assemblages and temporal patterns. *Journal of the Marine Biological Association of the United Kingdom* **81**, 545–552.

Proffitt, C.E. & Devlin, D.J. 2005. Grazing by the intertidal gastropod *Melampus coffeus* greatly increases mangrove leaf litter degradation rates. *Marine Ecology Progress Series* **296**, 209–218.

Prosser, A.J. 2004. *Faunal community change following mangrove dieback in Moreton Bay, Australia*. BSc Hons thesis, University of Queensland, Brisbane, Australia.

Prosser, I.P., Rutherfurd, I.D., Olley, J.M., Young, W.J., Wallbrink, P.J. & Moran, C.J. 2001. Large-scale patterns of erosion and sediment transport in river networks, with examples from Australia. *Marine and Freshwater Research* **52**, 81–99.

Quartel, S., Kroon, A., Augustinus, P.G.E.F., Van Santen, P. & Tri, N.H. 2007. Wave attenuation in coastal mangroves in the Red River Delta, Vietnam. *Journal of Asian Earth Sciences* **29**, 576–584.

Rabinowitz, D. 1978. Dispersal properties of mangrove propagules. *Biotropica* **10**, 47–57.

Rahmstorf, S. 2007. A semi-empirical approach to projecting future sea-level rise. *Science* **315**, 368–370.

Raines, J., Youngson, K. & Unno, J. 2000. Use of the Leschenault Inlet estuary by waterbirds. *Journal of the Royal Society of Western Australia* **83**, 503–512.

Rignot, E., Bamber, J.L., Van Den Broeke, M.R., Davis, C., Li, Y., Van De Berg, W.J. & Van Meijgaard, E. 2008. Recent Antarctic ice mass loss from radar interferometry and regional climate modelling. *Nature Geoscience* **1**, 106–110.

Robertson, A.I. 1988. Decomposition of mangrove leaf litter in tropical Australia. *Journal of Experimental Marine Biology and Ecology* **116**, 235–248.

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.

Robertson, A.I., Daniel, P.A. & Dixon, P. 1991. Mangrove forest structure and productivity in the Fly River estuary, Papua New Guinea. *Marine Biology* **111**, 147–155.

Rogers, K. & Saintilan, N. 2008. Relationships between surface elevation and groundwater in mangrove forests of southeast Australia. *Journal of Coastal Research* **24**, 63–69.

Rogers, K., Saintilan, N. & Cahoon, D. 2005a. Surface elevation dynamics in a regenerating mangrove forest at Homebush Bay, Australia. *Wetlands Ecology and Management* **13**, 587–598.

Rogers, K., Saintilan, N. & Heijnis, H. 2005b. Mangrove encroachment of salt marsh in Western Port Bay, Victoria: the role of sedimentation, subsidence, and sea level rise. *Estuaries* **28**, 551–559.

Rogers, K., Wilton, K.M. & Saintilan, N. 2006. Vegetation change and surface elevation dynamics in estuarine wetlands of southeast Australia. *Estuarine Coastal and Shelf Science* **66**, 3–4.

Rönnbäck, P., Troell, M., Kautsky, N. & Primavera, J.H. 1999. Distribution pattern of shrimps and fish among *Avicennia* and *Rhizophora* microhabitats in the Pagbilao mangroves, Philippines. *Estuarine Coastal and Shelf Science* **48**, 223–234.

Ross, P.M. 2001. Larval supply, settlement and survival of barnacles in a temperate mangrove forest. *Marine Ecology Progress Series* **215**, 237–249.

Ross, P.M. 2006. Macrofaunal loss and microhabitat destruction: the impact of trampling in a temperate mangrove forest, NSW Australia. *Wetlands Ecology and Management* **14**, 167–184.

Ross, P.M. & Underwood, A.J. 1997. The distribution and abundance of barnacles in a mangrove forest. *Australian Journal of Ecology* **22**, 37–47.

Roy, P.S., Williams, R.J., Jones, A.R., Yassini, I., Gibbs, P.J., Coates, B., West, R.J., Scanes, P.R., Hudson, J.P. & Nichol, S. 2001. Structure and function of south-east Australian estuaries. *Estuarine Coastal and Shelf Science* **53**, 351–384.

Saenger, P. 1998. Mangrove vegetation: an evolutionary perspective. *Marine and Freshwater Research* **49**, 277–286.

Saenger, P. 2002. *Mangrove Ecology, Silviculture and Conservation*. Dordrecht, The Netherlands: Kluwer.

Saenger, P. & Snedaker, S.C. 1993. Pan-tropical trends in mangrove above-ground biomass and litter fall. *Oecologia* **96**, 293–299.

Saenger, P., Specht, M.M., Specht, R.L. & Chapman, V.J. 1977. Mangal and coastal salt-marsh communities in Australasia. In *Wet Coastal Ecosystems*, V.J. Chapman (ed.). Amsterdam: Elsevier, 293–339.

Saintilan, N. 1997b. Above- and below-ground biomass of mangroves in a sub-tropical estuary. *Marine and Freshwater Research* **48**, 601–604.

Saintilan, N. 1997a. Above- and below-ground biomasses of two species of mangrove on the Hawkesbury River Estuary, New South Wales. *Marine and Freshwater Research* **48**, 147–152.

Saintilan, N. 1998. Photogrammetric survey of the Tweed River wetlands. *Wetlands (Australia)* **17**, 74–82.

Saintilan, N. 2004. Relationships between estuarine geomorphology, wetland extent and fish landings in New South Wales estuaries. *Estuarine Coastal and Shelf Science* **61**, 591–601.

Saintilan, N. & Hashimoto, T.R. 1999. Mangrove-saltmarsh dynamics on a bay-head delta in the Hawkesbury River estuary, New South Wales, Australia. *Hydrobiologia* **413**, 95–102.

Saintilan, N., Hossain, K. & Mazumder, D. 2007. Linkages between seagrass, mangrove and saltmarsh as fish habitat in the Botany Bay estuary, New South Wales. *Wetlands Ecology and Management* **15**, 277–286.

Saintilan, N., Rogers, K. & McKee, K.L. 2009. Salt marsh-mangrove interactions in Australasia and the Americas. In *Coastal Wetlands—An Integrated Ecosystem Approach*, G.M.E. Perillo et al. (eds). Amsterdam: Elsevier, 855–883.

Saintilan, N. & Williams, R.J. 1999. Mangrove transgression into saltmarsh environments in south-east Australia. *Global Ecology and Biogeography* **8**, 117–124.

Saintilan, N. & Williams, R.J. 2000. The decline of saltmarsh in southeast Australia: results of recent surveys. *Wetlands (Australia)* **18**, 49–54.

Saintilan, N. & Wilton, K. 2001. Changes in the distribution of mangroves and saltmarshes in Jervis Bay, Australia. *Wetlands Ecology and Management* **9**, 409–420.

Sakai, A., Paton, D. & Wardle, P. 1981. Freezing resistance of trees of the south temperate zone, especially subalpine species of Australasia. *Ecology* **62**, 563–570.

Sakai, A. & Wardle, P. 1978. Freezing resistance of New Zealand trees and shrubs. *New Zealand Journal of Ecology* **1**, 51–61.

Sasekumar, A. 1994. Meiofauna of a mangrove shore on the west coast of peninsular Malaysia. *Raffles Bulletin of Zoology* **42**, 901–915.

Satumanatpan, S. & Keough, M.J. 1999. Effect of barnacles on the survival and growth of temperate mangrove seedlings. *Marine Ecology Progress Series* **181**, 189–199.

Schaeffer-Novelli, Y., Cintron-Molero, G., Adaime, R.R. & de Camargo, T.M. 1990. Variability of mangrove ecosystems along the Brazilian coast. *Estuaries* **13**, 204–218.

Schaeffer-Novelli, Y., Cintron-Molero, G. & Soares, M.L.G. 2002. Mangroves as indicators of sea level change in the muddy coasts of the world. In *Muddy Coasts of the World: Processes, Deposits and Function,* T. Healy et al. (eds). Amsterdam: Elsevier Science, 245–262.

Schodde, R., Mason, I.J. & Gill, H.B. 1982. The avifauna of the Australian mangroves—a brief review of composition, structure and origin. In *Mangrove Ecosystems in Australia: Structure, Function and Management*, B.F. Clough (ed.). Townsville, Australia: Australian Institute of Marine Science, 141–150.

Scholl, D.W. 1968. Mangrove swamps: geology and sedimentology. In *Encyclopedia of Geomorphology*, F.R. Fairbridge (ed.). New York, USA: Reinhold, 683–688.

Schubel, J.R. & Pritchard, D.W. 1986. Responses of upper Chesapeake Bay to variations in discharge of the Susquehanna River. *Estuaries* **9**, 236–249.

Schumann, E.H., Largier, J.L. & Slinger, J.H. 1999. Estuarine hydrodynamics. In *Estuaries of South Africa*, B.R. Allanson & D. Baird (eds). Cambridge, United Kingdom: Cambridge University Press, 27–52.

Schwarzbach, A.E. & McDade, L.A. 2002. Phylogenetic relationships of the mangrove family Avicenniaceae based on chloroplast and nuclear ribosomal DNA sequences. *Systematic Botany* **27**, 84–98.

Scoffin, T.P. 1970. Trapping and binding of subtidal carbonate sediments by marine vegetation in Bimimi Lagoon, Bahamas. *Journal of Sedimentary Petrology* **40**, 249–273.

Semeniuk, T.A. 2000. Small benthic Crustacea of the Leschenault Inlet estuary. *Journal of the Royal Society of Western Australia* **83**, 429–441.

Semeniuk, V. 1980. Mangrove zonation along an eroding coastline in King Sound, north-western Australia. *Journal of Ecology* **68**, 789–812.

Semeniuk, V. & Wurm, P.A.S. 2000. Molluscs of the Leschenault Inlet estuary: their diversity, distribution, and population dynamics. *Journal of the Royal Society of Western Australia* **83**, 377–418.

Singh, N., Steinke, T.D. & Lawton, J.R. 1991. Morphological changes and the associated fungal colonization during decomposition of leaves of a mangrove, *Bruguiera gymnorrhiza* (Rhizophoraceae). *South African Journal of Botany* **57**, 151–155.

Skilleter, G.A. & Warren, S. 2000. Effects of habitat modification in mangroves on the structure of mollusc and crab assemblages. *Journal of Experimental Marine Biology and Ecology* **244**, 107–129.

Slim, F.J., Hemminga, M.A., Ochieng, C., Jannink, N.T., Cocheret de la Morinière, 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). *Journal of Experimental Marine Biology and Ecology* **215**, 35–48.

Smith, T.J., III. 1987. Effects of light and intertidal position on seedling survival and growth in tropical tidal forests. *Journal of Experimental Marine Biology and Ecology* **110**, 133–146.

Smith, T.M. & Hindell, J.S. 2005. Assessing effects of diel period, gear selectivity and predation on patterns of microhabitat use by fish in a mangrove dominated system in S.E. Australia. *Marine Ecology Progress Series* **294**, 257–270.

Smoak, J.M. & Patchineelam, S.R. 1999. Sediment mixing and accumulation in a mangrove ecosystem: evidence from 210Pb, 234Th and 7Be. *Mangroves and Salt Marshes* **3**, 17–27.

Snedaker, S.C. 1995. Mangroves and climate change in the Florida and Caribbean region: scenarios and hypotheses. *Hydrobiologia* **295**, 43–49.

Solís, F., Ibanez, R., Hammerson, G., Hedges, B., Diesmos, A., Matsui, J.-M.H., Richards, S., Coloma, L.A., Ron, S., La Marca, E., Hardy, J., Powell, R., Bolanos, F. & Chaves, G. 2008. *Rhinella marina.* In: *IUCN Red List of Threatened Species*. Online. Available HTTP: http://www.iucnredlist.org (accessed 2 May 2009).

Sousa, W.P., Kennedy, P.G., Mitchell, B.J. & Ordonez, B.M. 2007. Supply-side ecology in mangroves: do propagule dispersal and seedling establishment explain forest structure? *Ecological Monographs* **77**, 53–76.

Spalding, M., Blasco, F. & Field, C. (eds). 1997. *World Mangrove Atlas*. Okinawa, Japan: International Society for Mangrove Ecosytems.

Spenceley, A.P. 1977. The role of pneumatophores in sedimentary processes. *Marine Geology* **24**: M31–M37.

Spenceley, A.P. 1987. Mangroves and intertidal morphology in Westernport Bay, Victoria, Australia—comment. *Marine Geology* **77**, 327–330.

Steinke, G.W., Naidoo, G. & Charles, L.M. 1983. Degradation of mangrove leaf and stem tissues in situ in Mgeni Estuary, South Africa. In *Biology and Ecology of Mangroves*, H.J. Teas (ed.). The Hague, The Netherlands: Dr. W. Junk, 141–149.

Steinke, T. 1999. Mangroves in South African estuaries. In *Estuaries of South Africa*, B.R. Allanson & D. Baird (eds). Cambridge, United Kingdom: Cambridge University Press, 119–140.

Steinke, T.D. 1975. Some factors affecting the dispersal and establishment of propagules of *Avicennia marina* (forsk.) Vierh. In *Proceedings of the International Symposium on the Biology and Management of Mangroves, University of Gainsville, Florida,* G.E. Walsh et al. (eds), Gainsville, Florida, USA: University of Florida, 404–414.

Steinke, T.D. 1986. A preliminary study of buoyancy behaviour in *Avicennia marina* propagules. *South African Journal of Botany* **52**, 559–565.

Steinke, T.D. 1995. A general review of the mangroves of South Africa. In *Wetlands of South Africa*, G.I. Cowan (ed.). Pretoria, South Africa: South African Wetlands Conservation Programme, Department of Environmental Affairs and Tourism, 53–73.

Steinke, T.D., Barnabas, A.D. & Somaru, R. 1990. Structural changes and associated microbial activity accompanying decomposition of mangrove leaves in Mgeni Estuary. *South African Journal of Botany* **56**, 39–48.

Steinke, T.D. & Charles, L.M. 1986. In vitro rates of decomposition of leaves of the mangrove *Bruguiera gymnorrhiza* as affected by temperature and salinity. *South African Journal of Botany* **52**, 39–42.

Steinke, T.D. & Charles, L.M. 1990. Litter production by mangroves. III. Wavecrest (Transkei) with predictions for other Transkei estuaries. *South African Journal of Botany* **56**, 514–519.

Steinke, T.D. & Naidoo, Y. 1991. Respiration and net photosynthesis of cotyledons during establishment and early growth of propagules of the mangrove, *Avicennia marina*, at three temperatures. *South African Journal of Botany* **57**, 171–174.

Steinke, T.D., Rajh, A. & Holland, A.J. 1993. The feeding behaviour of the red mangrove crab *Sesarma meinerti* de Man, 1887 (Crustacea: Decapoda: Grapsidae), and its effect on the degradation of mangrove leaf litter. *South African Journal of Marine Science* **13**, 151–160.

Steinke, T.D., Ward, C.J. & Rajh, A. 1995. Forest structure and biomass of mangroves in the Mgeni Estuary, South Africa. *Hydrobiologia* **295**, 159–166.

Stephens, W.M. 1962. Trees that make land. *Sea Frontiers* **8**, 219–230.

Stern, M.K., Day, J.W. & Teague, K.G. 1986. Seasonality of materials transport through a coastal freshwater marsh: riverine versus tidal forcing. *Estuaries* **9**, 301–308.

Steyaert, M., Moodley, L., Nadong, T., Moens, T., Soetaert, K. & Vincx, M. 2007. Responses of intertidal nematodes to short-term anoxic events. *Journal of Experimental Marine Biology and Ecology* **345**, 175–184.

Stokes, D. & Healy, T. 2005. Mangrove expansion and their human removal in Tauranga Harbour, New Zealand. In *Proceedings of the 17th Coastal and Ocean Engineering Conference and the 10th Australasian Port and Harbour Conference, Adelaide, Australia*. M. Townsend & D. Walker (eds). Barton, ACT, Australia: Australian Institution of Engineers, 577–582.

Stokes, D.J., Healy, T. & Cooke, P.J. 2009. Surface elevation changes and sediment characteristics of intertidal surfaces undergoing mangrove expansion and mangrove removal, Waikaraka Estuary, Tauranga Harbour, New Zealand. *International Journal of Ecology and Development* **12**, 88–106.

Struve, J., Falconer, R.A. & Wu, Y. 2003. Influence of model mangrove trees on the hydrodynamics in a flume. *Estuarine Coastal and Shelf Science* **58**, 163–171.

Stuart, S., Choat, B., Martin, K., Holbrook, N. & Ball, M. 2007. The role of freezing in setting the latitudinal limits of mangrove forests. *New Phytologist* **173**, 576–583.

Suarez, N. & Medina, E. 2006. Influence of salinity on Na+ and K+ accumulation, and gas exchange in *Avicennia germinans*. *Photosynthetica* **44**, 268–274.

Swales, A., Bell, R.G., Ovenden, R., Hart, C., Horrocks, M., Hermansphan, N. & Smith, R.K. 2007a. Mangrove-habitat expansion in the southern Firth of Thames: sedimentation processes and coastal-hazards mitigation. Environment Waikato Technical Report No. 2008/13. Hamilton, New Zealand: Environment Waikato (Waikato Regional Council).

Swales, A. & Bentley, S.J. 2008. Recent tidal-flat evolution and mangrove-habitat expansion: application of radioisotope dating to environmental reconstruction. In *Sediment Dynamics in Changing Environments (Proceedings of a Symposium Held in Christchurch, New Zealand, December 2008),* J. Schmidt et al. (eds). Wallingford, U.K.: IAHS Press, 76–84.

Swales, A., Bentley, S.J., Lovelock, C. & Bell, R.G. 2007b. Sediment processes and mangrove-habitat expansion on a rapidly-prograding muddy coast, New Zealand. In *Coastal Sediments '07. Proceedings of the Sixth International Conference on Coastal Engineering and Science of Coastal Sediment Processes, New Orleans, May 2007*. Reston, Virginia, USA: American Society of Civil Engineers, 1441–1454.

Swales, A., Gorman, R., Oldman, J.W., Altenberger, A., Hart, C., Bell, R.G., Claydon, L., Wadhwa, S. & Ovenden, R. 2009. Potential future changes in mangrove habitat in Auckland's east-coast estuaries. Auckland, New Zealand: Auckland Regional Council, Technical Report No. 2009/079.

Swales, A., Hume, T.M., Oldman, J.W. & Green, M.O. 1997. Holocene sedimentation and recent human impacts on infilling in a drowned valley estuary. In *Proceedings of the 13th Australasian Coastal and Ocean Engineering Conference and the 6th Australasian Port and Harbour Conference, Christchurch, New Zealand,* J. Lumsden (ed.). Christchurch, New Zealand: Centre for Advanced Engineering, University of Canterbury, 895–900.

Swales, A., MacDonald, I.T. & Green, M.O. 2004. Influence of wave and sediment dynamics on cordgrass (*Spartina anglica*) growth and sediment accumulation on an exposed intertidal flat. *Estuaries* **27**, 225–243.

Swales, A., Williamson, R.B., Van Dam, L.F., Stroud, M.J. & McGlone, M.S. 2002. Reconstruction of urban stormwater contamination of an estuary using catchment history and sediment profile dating. *Estuaries* **25**, 43–56.

Syvitski, J.P.M., Vorosmarty, C.J., Kettner, A.J. & Green, P. 2005. Impact of humans on the flux of terrestrial sediment to the global coastal ocean. *Science* **308**, 376–380.

Tam, N.F.Y. & Wong, Y.-S. 1997. Accumulation and distribution of heavy metals in a simulated mangrove system treated with sewage. *Hydrobiologia* **352**, 67–75.

Tanaka, N., Sasaki, Y., Mowjood, M.I.M., Jindasa, K.B.S.N. & Homchuen, S. 2007. Coastal vegetation structures and their functions in tsunami protection: experience of the recent Indian Ocean tsunami. *Landscape Ecology and Engineering* **3**, 33–45.

Taylor, F.J. 1983. The New Zealand mangrove association. In *Biology and Ecology of Mangroves*, H.J. Teas (ed.). The Hague, The Netherlands: Dr. W. Junk, 77–79.

Teas, H.J. (ed.). 1983. *Biology and Ecology of Mangroves*. The Hague, Netherlands: Dr. W. Junk.

Temmerman, S., Govers, G., Wartel, S. & Meire, P. 2004. Modelling estuarine variations in tidal marsh sedimentation: response to changing sea level and suspended sediment concentrations. *Marine Geology* **212**, 1–19.

Terrados, J., Thampanya, U. & Duarte, C.M. 1997. The effect of increased sediment accretion on the survival and growth of *Rhizophora apiculata* seedlings. *Estuarine Coastal and Shelf Science* **45**, 697–701.

Thom, B.G. 1967. Mangrove ecology and deltaic geomorphology, Tabasco, Mexico. *Journal of Ecology* **55**, 301–343.

Thom, B.G. 1982. Mangrove ecology—a geomorphological perspective. In *Mangrove Ecosystems in Australia: Structure, Function and Management*, B.F. Clough (ed.). Townsville, Australia: Australian Institute of Marine Science, 3–17.

Thom, B.G., Wright, L.D. & Coleman, J.M. 1975. Mangrove ecology and deltaic-estuarine geomorphology: Cambridge Gulf-Ord River, Western Australia. *Journal of Ecology* **63**, 203–232.

Thomas, M.L. & Logan, A. 1992. A guide to the ecology of the shoreline and shallow-water marine communities of Bermuda. Bermuda Biological Station for Research Special Publication No. 30. Bermuda: Bermuda Biological Station for Research.

Thomas, M.L.H. 1993. Mangrove swamps in Bermuda. *Atoll Research Bulletin* **386**, 1–17.

Thorogood, C.A. 1985. Changes in the distribution of mangroves in the Port Jackson-Paramata River Estuary from 1930 to 1985. *Wetlands (Australia)* **5**, 91–93.

Thrush, S.F., Hewitt, J.E., Cummings, V.J., Ellis, J.I., Hatton, C., Lohrer, A. & Norkko, A. 2004. Muddy waters: elevating sediment input to coastal and estaurine habitats. *Frontiers in Ecology and the Environment* **2**, 299–306.

Tolhurst, T.J. & Chapman, M.G. 2007. Patterns in biogeochemical properties of sediments and benthic animals among different habitats in mangrove forests. *Austral Ecology* **32**, 775–788.

Tomlinson, P.B. 1986. *The Botany of Mangroves*. Cambridge, United Kingdom: Cambridge University Press.

Tortoise and Freshwater Turtle Specialist Group 1996. *Malaclemys terrapin.* In *IUCN Red List of Threatened Species*. International Union for Conservation of Nature and Natural Resources, Red List Unit, Cambridge, U.K. Online. Available HTTP: http://www.iucnredlist.org (accessed 2 May 2009).

Traynum, S. & Styles, R. 2007. Flow, stress and sediment resuspension in a shallow tidal channel. *Estuaries and Coasts* **30**, 94–101.

Twilley, R.R., Chen, R.H. & Hargis, T. 1992. Carbon sinks in mangrove forests and their implications to the carbon budget of tropical coastal ecosystems. *Water Air and Soil Pollution* **64**, 265–288.

Uncles, R.J. 2002. Estuarine physical processes research: some recent studies and progress. *Estuarine Coastal and Shelf Science* **55**, 829–856.

Underwood, A.J. & Barrett, G. 1990. Experiments on the influence of oysters on the distribution, abundance and sizes of the gastropod *Bembicium auratum* in a mangrove swamp in New South Wales, Australia. *Journal of Experimental Marine Biology and Ecology* **137**, 25–45.

United Nations Environment Program, World Conservation Monitoring Centre (UNEP-WCMC). 2006. *In the Front Line: Shoreline Protection and Other Ecosystem Services from Mangroves*. Cambridge, United Kingdom: United Nations Environment Program, World Conservation Monitoring Centre.

Valette-Silver, N.J. 1993. The use of sediment cores to reconstruct historical trends in contamination of estuarine and coastal sediments. *Estuaries* **16**, 577–588.

Valiela, I., Bowen, J.L. & York, J.K. 2001. Mangrove forests: one of the world's threatened major tropical environments. *BioScience* **51**, 807–815.

Vance, D.J., Haywood, M.D.E., Heales, D.S., Kenyon, R.A., Loneragan, N.R. & Pendrey, R.C. 1996. How far do prawns and fish move into mangroves? Distribution of juvenile banana prawns *Penaeus merguiensis* and fish in a tropical mangrove forest in northern Australia. *Marine Ecology Progress Series* **131**, 115–124.

Van der Valk, A.G. & Attiwill, P.M. 1984. Decomposition of leaf and root litter of *Avicennia marina* at Westernport Bay, Victoria, Australia. *Aquatic Botany* **18**, 205–221.

Vanhove, S., Vincx, M., van Gansbeke, D., Gijselinck, W. & Schram, D. 1992. The meiobenthos of five mangrove vegetation types in Gazi Bay, Kenya. *Hydrobiologia* **247**, 99–108.

Vann, J.H. 1980. Shoreline changes in mangrove areas (Brazil and Guiana). *Zeitschrift für Geomorphologie Supplementband* **34**, 255–261.

Van Santen, P., Augustinus, P.G.E.F., Janssen-Stelder, B.M., Quartel, S. & Tri, N.H. 2007. Sedimentation in an estuarine mangrove system. *Journal of Asian Earth Sciences* **29**, 566–575.

Van Wijnen, H.J. & Bakker, J.P. 2001. Long-term surface elevation change in salt marshes: a prediction of marsh response to future sea-level rise. *Estuarine Coastal and Shelf Science* **52**, 381–390.

Vaughan, T.W. 1909. Geologic work of mangroves in southern Florida. *Smithsonian Miscellaneous Collection* **52**, 461–464.

Wakamatsu, A. & Tomiyama, K. 2000. Seasonal changes in the distribution of Batillarid snails on a tidal flat near the most northern mangrove forest in Atago River Estuary, Kyushu, Japan. *Japanese Journal of Malacology* **59**, 225–243.

Walbert, K. 2002. *Investigations in the New Zealand mangrove, Avicennia marina var. australasica*. MSc thesis, University of Waikato, Hamilton, New Zealand.

Walling, D.E. 1999. Linking land use, erosion and sediment yields in river basins. *Hydrobiologia* **410**, 223–240.

Walsh, J.P. & Nittrouer, C.A. 2004. Mangrove-bank sedimentation in a mesotidal environment with large sediment supply, Gulf of Papua. *Marine Geology* **208**, 225–248.

Walton, M.E.M., Samonte-Tan, G.P.B., Primavera, J.H., Edwards-Jones, G. & Le Vay, L. 2006. Are mangroves worth replanting? The direct economic benefits of a community-based reforestation project. *Environmental Conservation* **33**, 335–343.

Ward, C.J. & Steinke, T.D. 1982. A note on the distribution and approximate areas of mangroves in South Africa. *South African Journal of Botany* **1**, 51–53.

Warren, J.H. 1987. *Behavioural ecology of crabs in temperate mangrove swamps*. PhD thesis, University of Sydney, Sydney, Australia.

Warren, J.H. 1990. The use of open burrows to estimate abundances of intertidal estuarine crabs. *Australian Journal of Ecology* **15**, 277–280.

Warren, J.H. & Underwood, A.J. 1986. Effects of burrowing crabs on the topography of mangrove swamps in New South Wales. *Journal of Experimental Marine Biology and Ecology* **102**, 2–3.

Wasson, R.J. 1994. Annual and decadal variation of sediment yield in Australia and some global comparisons. In *Variability in Stream Erosion and Sediment Transport (Proceedings of the Canberra Symposium, December 1994),* L.J. Olive et al. (eds). Wallingford, U.K.: IAHS Press, 269–279.

Wasson, R.J. & Galloway, R.W. 1986. Sediment yield in the barrier range before and after European settlement. *Australian Rangeland Journal* **8**, 79–90.

Wells, A.G. 1983. Distribution of mangrove species in Australia. In *Biology and Ecology of Mangroves*, H.J. Teas (ed.). The Hague, The Netherlands: Dr. W. Junk, 57–76.

Wells, J.T. 1983. Dynamics of coastal fluid muds in low-, moderate-, and high-tide-range environments. *Canadian Journal of Fisheries and Aquatic Sciences* **40**, 130–142.

Wells, J.T. & Coleman, J.M. 1981. Physical processes and fine-grained sediment dynamics, coast of Surinam, South America. *Journal of Sedimentary Petrology* **51**, 1053–1068.

West, R.J., Thorogood, C.A., Walford, T.R. & Williams, R.J. 1985. *Estuarine Inventory for New South Wales, Australia*. Sydney: Division of Fisheries, Department of Agriculture New South Wales.

Whitfield, A.K. 1994. An estuary-association classification for the fishes of southern Africa. *South African Journal of Science* **90**, 411–417.

Wieser, W. 1953. Die Beziehung zwischen Mundhoelengestalt, Ernaehrungsweise und Vorkommen bei freilebenden marine Nematoden. *Archiv für Zoologie* **4**, 439–484.

Wildland Consultants. 2003. *Ecological restoration and enhancement of Waikaraka Estuary, Tauranga Harbour. Report prepared for the Waikaraka Estuary Management Group, Tauranga*. Tauranga, New Zealand: Waikaraka Estuary Management Group.

Wildland Consultants. 2005. Extent and effects of mangrove clearance in the Whangamata Harbour. Rotorua, New Zealand: Wildlands Consultants Ltd., Contract report No. 1274.

Wilkie, M.L. & Fortuna, S. 2003. Status and trends in mangrove area extent worldwide. Forest Resources Assessment Working Paper No. 63. Rome, Italy: Forestry Department, Food and Agriculture Organization of the United Nations.

Williams, R.J. & Meehan, A.J. 2004. Focusing management needs at the sub-catchment level via assessments of change in the cover of estuarine vegetation, Port Hacking, NSW, Australia. *Wetlands Ecology and Management* **12**, 499–518.

Williams, R.J. & Watford, F.A. 1997. Identification of structures restricting tidal flow in New South Wales, Australia. *Wetlands Ecology and Management* **5**, 87–97.

Wilmshurst, J.M. 1997. The impact of human settlement on vegetation and soil stability in Hawke's Bay, New Zealand. *New Zealand Journal of Botany* **35**, 97–111.

Wilton, K. 2001. Changes in coastal wetland habitats in Careel Bay, Pittwater, N.S.W. from 1940–1996. *Wetlands (Australia)* **19**, 72–86.

Wilton, K. 2002. *Mangrove and saltmarsh habitat dynamics in selected NSW estuaries*. PhD thesis, Australian Catholic University, Australia.

Wilton, K. & Saintilan, N. 2000. *Protocols for Mangrove and Saltmarsh Habitat Mapping*. Sydney, Australia: Australian Catholic University.

Wolanski, E. 1995. Transport of sediment in mangrove swamps. *Hydrobiologia* **295**, 31–42.

Wolanski, E., Jones, M. & Bunt, J.S. 1980. Hydrodynamics of a tidal creek-mangrove swamp system. *Australian Journal of Marine and Freshwater Research* **31**, 431–450.

Wolanski, E., Moore, K., Spagnol, S., D'Adamo, N. & Pattiaratchi, C. 2001. Rapid, human-induced siltation of the macro-tidal Ord River estuary, Western Australia. *Estuarine Coastal and Shelf Science* **53**, 717–732.

Wolanski, E., Spagnol, S. & Lim, E.B. 2002. Fine sediment dynamics in the mangrove-fringed, muddy coastal zone. In *Muddy Coasts of the World: Processes, Deposits and Function,* T. Healy et al. (eds). Amsterdam: Elsevier Science, 279–292.

Wong, Y.-S., Tam, N.F.Y., Chen, G.-Z. & Ma, H. 1997a. Response of *Aegiceras corniculatum* to synthetic sewage under simulated tidal conditions. *Hydrobiologia* **352**, 89–96.

Wong, Y.S., Tam, N.F.Y. & Lan, C.Y. 1997b. Mangrove wetlands as wastewater treatment facility: a field trial. *Hydrobiologia* **352**, 49–59.

Woodroffe, C.D. 1982. Litter production and decomposition in the New Zealand mangrove, *Avicennia marina* var. *resinifera*. *New Zealand Journal of Marine and Freshwater Research* **16**, 179–188.

Woodroffe, C.D. 1985a. Studies of a mangrove basin, Tuff Crater, New Zealand: I. Mangrove biomass and production of detritus. *Estuarine Coastal and Shelf Science* **20**, 265–280.

Woodroffe, C.D. 1985b. Studies of a mangrove basin, Tuff Crater, New Zealand: III. The flux of organic and inorganic particulate matter. *Estuarine Coastal and Shelf Science* **20**, 447–461.

Woodroffe, C.D. 1990. The impact of sea-level rise on mangrove shorelines. *Progress in Physical Geography* **14**, 483–520.

Woodroffe, C.D. 1992. Mangrove sediment and geomorphology. In *Tropical Mangrove Ecosystems*, A.I. Robertson & D.M. Alongi (eds). Washington, D.C., USA: American Geophysical Union, 7–41.

Woodroffe, C.D., Bardsley, K.N., Ward, P.J. & Hanley, J.R. 1988. Production of mangrove litter in a macrotidal embayment, Darwin Harbour, N.T., Australia. *Estuarine Coastal and Shelf Science* **26**, 581–598.

Woodroffe, C.D. & Davies, G. 2009. The morphology and development of tropical coastal wetlands. In *Coastal Wetlands—An Integrated Ecosystem Approach*, G.M.E. Perillo et al. (eds). Amsterdam: Elsevier, 65–88.

Wright, C.I., Lindsay, P. & Cooper, J.A.G. 1997. The effect of sedimentary processes on the ecology of the mangrove-fringed Kosi estuary/lake system, South Africa. *Mangroves and Salt Marshes* **1**, 79–94.

Wright, I.J. & Westoby, M. 2002. Leaves at low versus high rainfall: coordination of structure, lifespan and physiology. *New Phytologist* **155**, 403–416.

Wright, I.J., Westoby, M. & Reich, P.B. 2002. Convergence towards higher leaf mass per area in dry and nutrient-poor habitats has different consequences for leaf life span. *Journal of Ecology* **90**, 534–543.

Yan, Z., Wang, W. & Tang, D. 2007. Effect of different time of salt stress on growth and some physiological processes of *Avicennia marina* seedlings. *Marine Biology* **152**, 581–587.

Yates, E.J., Ashwath, N. & Midmore, D.J. 2004. Responses to nitrogen, phosphorus, potassium and sodium chloride by three mangrove species in pot culture. *Trees Structure and Function* **16**, 120–125.

Ye, Y., Tam, N.F.Y., Lu, C.Y. & Wong, Y.S. 2005. Effects of salinity on germination, seedling growth and physiology of three salt-secreting mangrove species. *Aquatic Botany* **83**, 193–205.

Young, B.M. & Harvey, L.E. 1996. A spatial analysis of the relationship between mangrove (*Avicennia marina* var. *australasica*) physiognomy and sediment accretion in the Hauraki Plains, New Zealand. *Estuarine Coastal and Shelf Science* **42**, 231–246.