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The New Zealand mangrove: review of the current state of knowledge

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1 Executive Summary

The present review provides a baseline of information on mangroves in New Zealand to inform the debate on their management.

What are mangroves and are they native to New Zealand?

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. The New Zealand mangrove, or Manawa, is one of several taxa within the genus *Avicennia*. *Avicennia* are true mangroves in that their habitat is defined solely by the intertidal zone, and they also possess specialized physiological and reproductive adaptations which allow them to grow there. Manawa is presently ranked as a sub-species (*Avicennia marina* (Forsk.) Vierh subsp. *australasica* (Walp.) J. Everett) within *Avicennia marina* (grey mangrove), a species occurring in both northern and southern hemispheres of the globe.

Avicennia marina subsp. *australasica* qualifies as an indigenous member of the New Zealand flora, given that its existence here can be dated some thousands of years before humans inhabited, or even visited, these islands. Mangroves have inhabited New Zealand coastlines for approximately 19 million years, as indicated by the presence of *Avicennia*-type silicified woods associated with lower Miocene rocks from the Kaipara Harbour. The origin of New Zealand's mangroves remains in question. It has been suggested that some populations may have arisen from sporadic introductions of propagules (the young plantlets) rafting across the Tasman Sea.

Habitat requirements of mangroves

Mangroves in New Zealand are confined to the northern coastlines of the North Island, forming often dense stands along the sheltered littoral margins of most major estuaries, shallow harbours, lagoons, tidal creeks and rivers north of about latitude 38°S. Their southern natural limit occurs at almost identical latitudes on both east (Kutarere, Ohiwa Harbour, latitude 38°03′S) and west (Kawhia Harbour, latitude 38°05′S) coasts of the North Island. Historically, the range of *Avicennia* extended much further south. Pollen in sediment cores from Sponge Bay and Awapuni (Poverty Bay) puts the range of mangrove approximately 140 km south of its present southernmost natural limit.

Frosts play an important, additional and episodic role in defining the range of mangrove in New Zealand, but the main driver enforcing their latitudinal limit appears to be physiological stress. *Avicennia* distribution may be constrained by its physiological limitations under chilling (non-freezing) conditions, or latitudinal limits may be set by constraints on internal water transport as a result of vessel size, and embolism in the xylem vessels following freezing. It is also possible that establishment of plants in suitable microclimates further south of the present limits may be prevented by dispersal barriers (unsuitable coastline) and unfavourable ocean currents.

Shallow, low-energy and gently-shelving shorelines are required not only for mangrove seedlings to anchor, but to allow these plants to persist in an area. Mangroves have significant value in the coastal zone as a buffer against erosion and storm surges. Mangroves themselves require some protection from high-energy waves and currents. In open estuaries in southeastern Australia, the upper and lower limits of *A. marina* distribution lie between mean high water and mean sea level. The seaward limits of mangrove growth in New Zealand have not been examined in great detail, but in locations where they are known mangroves are limited to slightly above mean sea level, possibly because of inhibitory effects of waves on establishment of propagules.

The preferred habitat for mangroves in general is soft, muddy, waterlogged sediment, but some, such as *Avicennia*, will also grow successfully on a wide variety of other substrates including volcanic rock, sand and soil.

Seedlings are only shade-tolerant up to the end of their cotyledon stage and high light intensity is crucial for their ongoing development and survival. Further development from this stage may be arrested if conditions are not suitable, with plants remaining in a 'seedling bank' for several years before progressing to the next size class.

Seedling development is affected by salinity of the substrate in which they grow, with optimum growth occurring between 10 and 50% seawater. Photosynthetic performance of adult plants is also affected by salinity. Despite these limitations, *A. marina* exhibits a wide range of salt-tolerance and an ability to grow in waterlogged soils of salinities ranging from 0 to 90 psu.

Elevated nutrient loadings (particularly nitrogen) have been thought to play a part in the acceleration of mangrove spread in some New Zealand estuaries, by contributing to enhanced growth rates and biomass, and increasing their potential to produce more propagules. As yet, however, there is no conclusive evidence that nutrients are the main causal factor of the observed expansion.

Occasionally ‘natural’ disturbances have severe impacts on mangrove stands, resulting either in severe dieback or death of mangrove. Identified causes of dieback of *A. marina* in New Zealand and overseas include the pathogenic fungus *Phytophthora* and severe winter frosts.

Mangrove productivity

Comparisons of the productivity of mangroves from different latitudes worldwide suggest that productivity and plant biomass decreases with increasing latitude. The species found in New Zealand, *Avicennia marina*, also occurs in the tropics so we can make direct comparisons for this species. From this global pattern we would expect that mangroves in New Zealand, near their southern geographical limit, would have relatively low productivity compared to their tropical equivalents. In fact, although the recorded rates of litter production in New Zealand fall below the maximum values reported from tropical Australia, they are comparable with values from subtropical and temperate regions. This partly reflects the fact that there is large variation among data from different locations and over time within a particular geographical region. This variation is due to a range of factors, including differences in the size of trees and chance events such as storms that cause large amounts of litter to be shed.

The variability in reported rates of litter production and the general lack of information makes it difficult to compare values of biomass or productivity for mangroves in New Zealand with those of other intertidal habitats. Very broad-scale comparisons of rates of primary production suggest that the range of values for New Zealand mangrove forests is within the range of values from temperate Australian and USA saltmarshes (*Juncus* spp.) and northern European and USA seagrass (*Zostera marina*) beds. Mangrove productivity is comparable to or slightly higher than published values for coastal phytoplankton or benthic microalgae. Unfortunately, these broad comparisons conceal large variation among and within locations, making them of little use in assessing the value of individual forests or other habitats.

Primary production by mangroves may enter the surrounding and adjacent food webs by direct grazing or as detritus (dead plant material) but it is likely that the largest proportion enters as detritus. Although it has been assumed for a long time that mangroves export detritus and faunal biomass to adjacent habitats and offshore, this hypothesis has only been tested relatively recently. A study in the Matapouri Estuary, Northland, concluded that the food web 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. Work on the trophic role New Zealand mangroves play in supporting fish production has also shown them to be less critical than traditionally thought.

Intrinsic and unique values of mangroves to the marine environment

Historically, many of the ecological values, physical processes and biological properties commonly associated with tropical and subtropical mangrove forests have been uncritically attributed to New Zealand mangrove stands. These include the assumption that mangroves support a high diversity of species, and are critically important to fish and other estuarine or marine organisms for food and habitat. However, given that many aspects of New Zealand mangrove systems have not yet been sufficiently studied, their importance in relation to marine and estuarine species in New Zealand, and their role in terms of ecosystem structure and function, should be carefully questioned before drawing any comparisons with tropical, sub-tropical or other temperate mangrove systems. The role played by mangroves in New Zealand estuarine foodwebs is, however, probably significant.

There does not appear to be any evidence for mangrove-dependency in any New Zealand species of fish, marine invertebrates or birds. The terrestrial invertebrate fauna is poorly known and the degree of dependency on mangroves is therefore impossible to determine. Of the terrestrial invertebrates known from New Zealand mangroves, very few are known to feed exclusively on mangroves. However, two species are endemic to and fully dependent upon these habitats: a tortricid moth, the mangrove leafroller, (*Planotortrix avicenniae*) and an eriophyid mite *Aceria avicenniae*.

Benthic fauna of mangroves

Relatively few studies have been undertaken on the benthic assemblages and species of mangrove forests in New Zealand. The benthic invertebrate fauna of New Zealand’s mangroves forests appear to be modest in both abundances and species diversity compared to other estuarine habitats. A study in South Australia concluded there was no evidence for a benthic assemblage that was uniquely characteristic of mangroves in South Australia. Even the species that occurred most commonly in mangroves were rare or absent at some sites, and none was found exclusively in mangroves. Data from New Zealand mangroves suggests that the same is true. Differences between assemblages from mangroves and adjacent unvegetated sediments are generally identifiable in ordination plots, for example, but are based on differences in relative abundance of a largely common suite of species rather than differences in species composition.

Fish fauna of mangroves

Recent studies have shown that the temperate mangrove forests of northern New Zealand support high abundances of small fishes, but that species diversity is low compared to other estuarine habitats, with most of the small fish assemblage dominated by juveniles of the ubiquitous yellow-eyed mullet (*Aldrichetta forsteri*), as well as juvenile grey mullet (*Mugil cephalus*) in the west coast estuaries. This general pattern of relatively low species diversity, and a numerical dominance by only a few species, agrees with the findings discussed previously from temperate *Avicennia marina* forests in Australia. The majority of the species associated with New Zealand mangroves were semi-pelagic and/or relatively mobile, given the daily migrations needed to transit over the tidal flats from the low-tide channels to the half-tide level mangroves. Short-finned eels (*Anguilla australis*) were caught throughout all the mangrove forests sampled, and were positively associated with the presence of three-dimensional bottom structure (seedlings, saplings, tree trunks), the only fish species to show such associations. This species is rarely caught in estuarine beach seine samples, and may remain in mangrove habitats during low tide periods through the use of shallow pools, rivulets, and burrows.

With the exception of grey mullet and short-finned eels, no commercial species were common in the mangrove habitats. Sand and yellow-belly flounder (*Rhombosolea plebeia* and *R. leporina*) were caught at most sites, but in low numbers relative to their high and widespread abundance over bare mud and sand habitats in the wider estuarine environment. The most conspicuously absent commercial species was the sparid *Pagrus auratus* (snapper), which utilises northern New Zealand estuaries and sheltered coastal embayments as nursery grounds.

It seems unlikely that New Zealand mangroves are important as spawning grounds for coastal fish or as habitat for their larvae. Based on the consistent and widespread numbers of short-finned eels and parore (*Girella tricuspidata*) in mangroves, and their low abundance in many alternative habitats, we suggest that mangroves can probably be viewed as "effective juvenile" habitat for these two species. Mangroves on the west coast can probably be classified as nursery habitats for grey mullet. Overall, this would result in New Zealand's temperate mangroves being considered nursery or "effective juvenile" habitat for three fish species, two of which are of commercial value.

Terrestrial invertebrate fauna of mangroves

The terrestrial invertebrate fauna of New Zealand mangroves are poorly known but likely to be less diverse than those of tropical mangroves. Three species of moths, the tortricids *Ctenopseustis obliquana* and *Planotortrix avicenniae* and the pyralid *Ptyomaxia* sp., and an eriophyid mite, *Aceria avicenniae*, have been described from mangroves in New Zealand. *A. avicenniae* and the larvae of *P. avicenniae* are restricted to *Avicennia marina*, whereas *C. obliquana* is distributed throughout New Zealand and its larvae are polyphagous. The larvae of the lemon-tree borer, *Oemona hirta*, often excavate long tunnels throughout the woody tissue of mangroves, with side tunnels leading to holes to the outside, through which frass (droppings) are ejected. Ant colonies may establish within the tunnels.

Reptiles of mangroves

Various geckos have been reported from mangroves There are anecdotal reports of seasnakes in mangroves as far south as Tauranga Harbour, but these are likely to be rare and chance occurrences.

Birds of mangroves

A study of the use of mangroves by birds at a location in the Kaipara Harbour in the 1970s recorded 22 species, of which 12 occurred regularly within the mangroves and 6 or 7 bred there. The regulars included several native species, namely white-faced heron, harriers, grey warblers, kingfishers, welcome swallows, pukeko and silvereyes. The native breeding species were grey warblers, silvereyes, fantails and shining cuckoos. Species recorded in mangroves at other locations include roosting colonies of pied and little black shags, bitterns, royal spoonbills and banded rails. With the possible exception of the banded rail, which is commonly associated with them, mangroves seem to be a fairly marginal habitat for birds, in that none is totally dependent on them, but many species make extensive use for roosting, feeding and breeding.

The role of mangroves in trapping sediment and reducing erosion

Mangroves enhance sediment accretion by damping currents, attenuating waves and altering patterns of water flow. Their vertical roots (pneumatophores and prop roots), low branches and trunks encourage the settling of fine silts, clays and organic-rich sediments, which are either transported into the system or produced in-situ from the mangrove plants. Within a mangrove stand, highest sedimentation rates usually occur at the seaward fringe or along the banks of tidal channels, resulting in a deeper accumulation of sediment often with higher mud content.

Once established, mangrove stands gradually influence estuarine sedimentary processes, raising the height of the surrounding mudflat and altering the sediment characteristics. This, in turn, can lead to further increases in mangrove growth and abundance. Whether mangroves are responsible for "land building", and whether they are steady-state systems or are eventually replaced by different habitats as they modify the environment (for example, saltmarsh or terrestrial vegetation), is still widely discussed and the question has not yet been fully addressed in relation to New Zealand mangroves.

By reducing the velocity of currents and attenuating waves, mangroves are considered to play an important role in erosion control and shoreline protection. The horizontal subterranean roots of mangroves also have a role in stabilizing sediments.

Changes in the distribution of mangroves over time

Changes in the distribution of mangroves have been documented in several studies, generally using sequences of historical aerial photographs. In the first part of the 20th century there was probably a significant net reduction in the area of mangroves in New Zealand as coastal areas were filled in to create farmland or for urban and industrial development. Grazing of livestock in mangroves also seems to have been common practice. Infilling to create farmland was prevented by legislation in 1977, and destruction of mangroves, where permitted, became a much more controlled activity after that.

Expansion of mangroves has been occurring at least since aerial photographic records began (the late 1930s) but seems to have been most active since the late 1970s. In some places there has been little change in distribution, often because the mangroves occupy a small estuary where their spread is restricted by the presence of a low-tide channel along their seaward edge (where propagules cannot gain purchase) and by their elevation limit on their landward side. In these cases the canopy may become denser over time as more trees take root and existing trees mature, but the area occupied stays roughly the same. There are also cases where little change has occurred even when apparently suitable habitat is present.

In many cases, however, the area occupied by mangroves increases over time. This may involve the colonisation of small harbours or embayments, such as Whangape Harbour, Puhoi Estuary and parts of the Kaipara, Manukau, Waitemata and Tauranga Harbours, where mangrove areas have expanded rapidly (over a decade or so) to occupy large areas. On more open coasts, such as the southern Firth of Thames, mangroves form a broad front that advances seaward as the mudflats on which they live extend (during the period 1944-1993 the seaward edge of the mangroves in the southern Firth advanced 200-250 m).

In New Zealand, mangrove expansion invariably seems to occur seawards. Interestingly, this contrasts with the situation in southeastern Australia where expansion of areas of mangroves (the same species as in New Zealand) is also occurring. Here expansion is usually in a landward direction, and seaward expansion is much less common. In spreading up the shore, Australian mangroves seem to be extending beyond their normal range of elevation relative to tidal levels. The reason for this difference in patterns of spread is unknown but may involve responses to local geomorphology (the shape and patterns of water movement of the coast), histories of sedimentation, or differences in the nature of plant communities higher up the shore (their susceptibility to mangrove invasion).

Because our best source of information on changes in mangrove distribution over time comes from aerial photographs, changes occurring before the late 1930s are relatively poorly known. In addition, documenting changes from aerial photographs is a time-consuming process and has only been done for selected locations. Consequently, we do not have much idea of the total area lost through human activities or gained through recent spread and cannot, therefore, estimate the net change since, say, European colonisation of New Zealand.

Causes of mangrove spread

Evidence suggests that increased rates of sedimentation in estuaries and harbours have resulted in spread of mangroves through increases in the elevation of intertidal areas and creation of suitable habitat. Sedimentation rates in many New Zealand estuaries and harbours appear to have increased following human, and particularly European, settlement, in response to clearance of native vegetation associated with logging, mining, farming and, more recently, urban development. However, the rate of spread of mangroves is also dependent upon hydrodynamic parameters, such as the influence of wind-waves that remobilise sediments and reduce net sedimentation rates, leading to a gradient of sedimentation down the length of an estuary. Elevated nutrient loadings (particularly nitrogen), by contributing to enhanced growth rates of plants, are also thought to be a determining factor in the acceleration of mangrove spread in some New Zealand estuaries. As yet, however, there is no conclusive evidence that nutrients are the main cause of the observed expansion.

Effects of climate change on mangroves

Several aspects of current and potential future climate change may affect the growth and distribution of mangroves. Increased concentrations of carbon dioxide in the atmosphere and increased average temperatures may lead to increased rates of photosynthesis and growth of many plants, including mangroves. The effects of climate change likely to affect mangroves most strongly, however, are sea-level rise and changes in rainfall, through their impact on sediment budgets. At sites where mangroves currently occur, their distribution up and down the shore may change as a result of several interacting factors. Rising sea level may reduce their down-shore range as lower parts of the shore are flooded by the tide more frequently or permanently submerged. This may be exacerbated by erosion of lower parts of the shore at more exposed sites, due to increased frequencies of storms associated with climate change. In areas where rates of sediment accumulation are high, however, the resulting rise in the level of the shore may keep pace with, or even exceed, the rate of sea-level rise.

Where sediment accumulation does not keep pace, rising sea level may either reduce the width of the mangrove zone on the shore or cause them to migrate upshore, as higher levels on the shore become flooded more frequently. This migration may occur at the expense of saltmarshes behind the mangroves, unless they too are able to migrate upshore. There is evidence for such upward migration of mangroves during periods of sea-level rise from studies of shoreline changes of glacial/interglacial cycles. However, there may be much larger shorter-term variation in sea level, so that even if sedimentation rates or mangrove migration rates are able to keep pace with the average rate of sea-level rise, there may be net loss of mangroves or saltmarsh during these periods of more rapid change. Increased rainfall may allow mangroves to migrate and out-compete saltmarsh vegetation at locations where their distribution up the shore is currently limited by high soil salinity. Migration of both mangroves and saltmarshes will be restricted where coastal defences are present – a process referred to as "coastal squeeze".

Migration of mangroves to higher latitudes has also been predicted as a result of climate change as increasing average temperatures allow them to survive at higher latitudes. Expansion of the geographical range of mangroves in New Zealand will depend on whether mangrove propagules can actually reach suitable habitats further south, and may also be limited by periodic extremes of temperature.

Mangroves can only colonise new areas through a supply of propagules and the subsequent establishment of seedlings. There are a number of factors affecting supply and establishment of propagules and the successful recruitment to sampling and maturity stages, that subsequently influences how much (if any) newly-available habitat is colonized by mangroves, and also the likely maximum extent of their growth. Dispersal of *A. marina* propagules is dependent on water movement and is therefore influenced by tides and currents. Observations in southern Australia indicate that dispersal and gene flow among populations may be limited. Should any stage of the reproductive process be halted due to the effects of an unfavourable environment, disease, or herbivory, then propagule supply and potential for mangrove presence in any given area may be reduced. Reproductive success may be reduced by low air temperatures, although the presence of propagules on plants at and beyond their current natural range in New Zealand indicates that these populations are potentially self-maintaining. Propagules are also vulnerable to effects of frost during their early development.

Effects of mangrove spread on other habitats and their biota

The landward migration of mangroves in southeastern Australia has resulted in consequent loss of saltmarshes as mangroves invade and eventually shade out other plants. In New Zealand there is little evidence of this happening, partly because most expansion occurs towards the sea (saltmarshes generally occur higher on the shore than mangroves). There is evidence of limited invasion of the lower edge of saltmarshes in Tauranga Harbour, but it seems that healthy saltmarsh (rush) communities are resistant to invasion. Areas of sparse or disturbed saltmarsh (such as vehicle tracks), or where channels through the marsh allow mangrove propagules to be transported, seem to be most vulnerable.

Different types of habitat (mangrove stands, pneumatophore zones, seagrass beds, low-tide channels, channel banks, and sandflats) in Matapouri Estuary, Northland had distinctive faunal assemblages, although some taxa, such as cockles (*Austrovenus stutchburyi*) and pipis (*Paphies australis*) occurred across all habitats. Diversity and total abundance were highest in sandflats and lowest in mangroves. Pneumatophore zones, however, had relatively high abundance and diversity and appear to act as important transition environments between seagrass and mangroves. Abundances of cockles were lowest, but the individual animals were largest, in the mangrove habitats. Seagrass beds contained large numbers of juveniles, suggesting that they recruit to this habitat but that mangroves and pneumatophore zones may still represent important habitats for this species in some estuaries.

Where seagrass beds occur adjacent to mangroves, as in Matapouri Estuary, any downshore progradation would be expected to invade seagrass beds and eventually exclude them through a combination of shading and effects of increased sedimentation. It is, however, likely that seagrass beds will already have been adversely affected by high concentrations of suspended sediment and sediment deposition in those estuaries and harbours where mangroves are spreading rapidly.

As mangroves colonise mudflats and the stands mature, there may be a coincident decrease in the abundance and diversity of the animals living in the sediments. In these mature stands, however, the focus of faunal diversity may change from the sediment to the terrestrial vertebrate and invertebrate fauna of the trees themselves.

Expansion of mangroves may benefit those birds that commonly use them to feed, roost or breed. Where expansion of mangroves converts more open habitats, such as intertidal flats, into areas suitable for high-tide roosts or provides more concealment, there may be a local net increase in the area of suitable habitat for these birds. This does not necessarily imply a consequent increase in the total number of birds, however, because birds may simply redistribute themselves to include the new areas of mangroves.

Conversely, colonisation of intertidal flats may deprive wading birds of feeding and roosting areas. Loss of roosting areas has been documented in the Firth of Thames, where dense stands of mangroves have colonised parts of the inner Firth. Use of these roosting sites by shorebirds has steadily decreased and there has been no substantial use of the area since 1990. This change in distribution has been particularly noticeable for wrybills (*Anarhynchus frontalis*), golden plovers (*Pluvialis fulva*), red knots (*Calidris canutus*) and whimbrels (*Numenius phaeopus*). There is a long-standing debate about the significance of gain or loss of feeding habitat to wading birds at the population level. Effects probably depend on the relative quality of the affected area and whether other suitable habitat within the range of local populations is at carrying capacity, among other factors. There is not sufficient information available at present to assess population-level effects of mangrove expansion on wading birds in New Zealand.

Does mangrove expansion reduce biodiversity?

Mangrove expansion may result in reduced diversity for some components of estuarine biots. For example, infaunal diversity appears to be generally higher in seagrass beds, sandflats or mudflats than in nearby mangroves, and diversity of birds that feed on intertidal flats also decreases when mangroves colonise their habitat. The diversity of other components, such as insects, spiders and birds living on the mangrove trees themselves may, however, increase but our knowledge of these relative changes is very incomplete. Consequently, it is difficult to assess changes in diversity when a particular area of mudflat or seagrass bed changes to a stand of mangroves. At an estuarine scale, however, it is likely that loss of habitat diversity as a result of mangrove expansion will lead to overall loss of biological diversity. It is also important to bear in mind that loss of habitat diversity, and the diversity of species associated with habitats that are lost, may be caused by the factors that led to mangrove spread, such as increased rates of sediment deposition or reduced water quality, rather than the mangroves themselves.

Does the value of mangrove to the ecosystem vary with their location?

The previous discussions of variation in plant size, architecture and productivity and the diversity and abundance of associated species among different locations suggests that the answer to this question is "yes". There are a number of different gradients present within mangrove habitats, each of which may influence the characteristics of the mangroves living there, and many of which interact. These are discussed in the report.

Mangrove management initiatives in New Zealand

The Resource Management Act (1991) allows governing bodies to uphold protection of mangroves against indiscriminate destruction and/or reclamation. However, concerns over recent expansion of mangrove areas, coupled with a push to preserve the ecology of adjacent habitats (e.g., saltmarsh, seagrass beds and open mudflats), has 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 polarized, 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 iwi working closely to find a balance between mangrove and other estuarine habitats.

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 style of management may be more suited to relatively stable mangrove areas where little change has occurred in the populations over several decades. A similar approach may also be applied in preserving mangrove areas**.** In New Zealand this 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.

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 Waikato and Bay of Plenty Regional Councils to allow such activities in Whangamata and Tauranga Harbours.

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 pre-determined baseline. The main aims of this approach are to preserve the ecology of habitats threatened by mangrove encroachment (for example; saltmarsh, eelgrass beds, open mudflat); to restore aesthetic values in an estuary (for instance; 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. The environmental effects of removal, including its effectiveness in achieving the management objectives, such as dispersal of accumulated fine sediments, are poorly known at present.

Management focus has now moved towards catchments since there is a general acceptance that mangrove expansion is a response to increased sediment input into harbours and estuaries. River and Catchment Programmes of the Regional Councils are focused to provide 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.

Rregardless of which approach is decided upon, sustainable management may only be achieved if evaluation of mangrove areas is undertaken on a site-by-site basis. Research has established that 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.

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 proved inadequate not only for communities seeking guidance or action on mangrove management, but also for the governing agencies responsible for providing those services. The present review is intended to provide a baseline of information on mangroves in New Zealand to inform the debate on their management.

2 Introduction

The Auckland Regional Council (ARC) is proposing to amend the Auckland Regional Plan: Coastal to introduce objectives and policies relating to mangrove management. To support this proposed change, ARC has commissioned NIWA to:

"Produce a balanced, "impartial, but technically robust and reputable report that provides a one-point reference to the scientific literature, technical reports, and discussion papers on mangrove related matters relevant to the proposed plan change. The report is to provide a review of the current state of knowledge, and where possible to include an update on the latest research being undertaken."

This review will be used as a resource to support the proposed change and as an up-to-date references source on the current state of knowledge of mangrove-related matters.

Three recent opinion pieces have discussed the role of mangroves in New Zealand estuaries and harbours. LaBonte et al. (2003) and McShane (2005) argued that, because of a lack of local information, perceptions of the ecological importance of mangroves in New Zealand are heavily and unjustifiably based on comparisons with tropical mangroves. They suggested that this has resulted in inappropriate management of mangroves focussed on their conservation when, in fact, mangroves are currently in a "logarithmic growth phase", at the expense of other marine habitats (LaBonte et al. 2003). Burns (2003) refuted LaBonte et al.'s claim that lack of information on New Zealand mangroves had led to uncritical and inappropriate acceptance that their ecological value was equivalent to that of their tropical counterparts, citing quantitative evidence from referenced sources. In contrast to Burns' letter, however, much of the debate about management of mangroves in New Zealand has been based on opinion, unsupported by peer-reviewed or even documented evidence. The present review is therefore intended to provide a baseline of information on mangroves in New Zealand to inform the debate on their management.

The results of the review, emphasising information needs for management issues, are presented in this report. The review has drawn on a range of types of information. These include discussions with researchers involved in mangrove studies regarding current work, scientific journals, "grey" literature (consultancy reports, reports produced by regional councils and other statutory bodies, and MSc and PhD theses), popular books, opinion pieces such as open letters, and articles in the press. There are important differences among these types of source. Publications in scientific journals have in general been subjected to independent peer-review (exceptions are explicitly-identified opinion pieces or editorials). The information they contain comes either from the study itself or from referenced sources. Grey literature has generally been reviewed within the organisation that produced it or, in the case of theses, by the student's supervisors and possibly examiners, but not usually by an independent reviewer outside the organisation. Again, information presented comes either from the study itself or from referenced sources. Popular books, opinion pieces and press articles have not usually been subject to any scientific review and often do not contain detailed references for the information they contain. The reliability and verifiability of information is consequently usually highest in peer-reviewed scientific papers.

Our knowledge of the ecology of mangroves in New Zealand is very incomplete. Some aspects have been better studied than others and consequently some sections of the report contain more information than others. There are a number of studies of mangrove ecology currently in progress, the results of which are not yet published. Where the unpublished data were available to us, we have incorporated them into the present report. These sections (for example, use of New Zealand mangroves by fish) include more background information, such as methods, than sections based on published data, because this information is not currently available elsewhere.

3 Mangrove ecology and coastal processes

3.1 The status of the mangrove *(Avicennia marina)* as an indigenous species

3.1.1 Classification and Taxonomy

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 (Duke 1991, Tomlinson 1986). They normally occupy the zone between mean sea level and high tide, growing on a variety of substrates 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 breathing roots, support structures (buttresses or above-ground roots), the ability to excrete or exclude salts, salt tolerance, and vivipary (seeds that germinate while still on the adult tree) enable mangroves to successfully adapt to and thrive within their environments (Tomlinson 1986).

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 (Chapman 1977, McNae 1966). 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, whilst those at the southern limits are species-poor; supporting between one and three species (Miyawaki 1980). New Zealand has only one mangrove species.

The New Zealand mangrove, or Manawa, is one of several taxa within 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 which 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 indicates that it may have closer affinities to the Acanthaceae s.l. (Schwarzbach & McDade 2002).

Manawa is presently ranked as a sub-species within *Avicennia marina* (grey mangrove), a species occurring in both northern and southern hemispheres of the globe. Historically, Manawa has been known by several combinations, including *A. officinalis* auct. non L. (Sp. Pl. 1753), *A. resinifera* G. Forst. (Allan 1961), *A. marina* var. *resinifera* (Forst.f.) Bakh. (in Bull. Jard. Bot. Buitenz 1921), and *A. marina* (Forsk.) var. *australasica*. However, the currently accepted name for this taxon is *Avicennia marina* (Forsk.) Vierh subsp. *australasica* (Walp.) J. Everett. The change in ranking from variety to subspecies of *A. marina* was based on work by Duke (1991), which showed that interbreeding between varieties (i.e., the three varieties of *A. marina* that are recognised in the region of Australasia) occurs where distributions overlap and so the distinctions between them are not maintained. In addition, the varietal name was never validly published, so the subspecific ranking was formalised (Everett 1994, Herbarium, 2000).

3.1.2 Indigenous status of *Avicennia* and history of its presence in New Zealand

An indigenous species may be defined as one that has not been introduced (either intentionally or unintentionally) to an area by humans (Allaby 1998). By definition then, the mangrove *A. marina* subsp. *australasica* qualifies as an indigenous member of the New Zealand flora, given that its existence here can be dated some thousands of years before humans inhabited, or even visited, these islands.

Mangroves have inhabited New Zealand coastlines for approximately 19 million years, as indicated by the presence of *Avicennia*-type silicified woods associated with lower Miocene rocks from the Kaipara Harbour (Sutherland 2003). Although these wood fossils share many features of present-day Manawa, the samples studied were sufficient in number only that the genus *Avicennia* could be verified, rather than the identity of the actual species. However, pollen preserved in sediments from the Firth of Thames (North Island) confirms the presence of *A. marina* in New Zealand from around 11 000 years BP (Pocknall 1989). *Avicennia* pollen has also been reported from middle Holocene sediments (between 9000 and 7000 years BP) in Te Puroa Lagoon, northern Hawke Bay on the east coast (Mildenhall 2001), and from Sponge Bay, and Awapuni; both locations in Poverty Bay on the east coast of the North Island (Mildenhall & Brown 1987, Mildenhall 1994).

The origin of New Zealand's mangroves remains in question. It has been suggested that some populations may have arisen from sporadic introductions of propagules (the young plantlets) rafting across the Tasman Sea (McNae 1968).

3.2 The geographic distribution and habitat requirements within New Zealand of mangroves, and key drivers of this distribution

3.2.1 Global connections

A. 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* (Manawa) 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°54′ S) (Crisp et al. 1990, Duke 1991).

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. 1998a, Maguire et al. 2002).

3.2.2 Latitudinal distribution of *Avicennia marina* in New Zealand

Mangroves in New Zealand are confined to the northern coastlines of the North Island, forming often dense stands along the sheltered littoral margins of most major estuaries, shallow harbours, lagoons, tidal creeks and rivers north of about latitude 38°S (Figure 1). Their southern natural limit occurs at almost identical latitudes on both east (Kutarere, Ohiwa Harbour, latitude 38°03′S) and west (Kawhia Harbour, latitude 38°05′S) coasts of the North Island (de Lange & de Lange 1994). Mangrove populations on the west coast, near the southern limits of their range at Aotea and Kawhia Harbours, are small and fragmented with fewer than 25 individuals present (Graeme, 2005a,b).

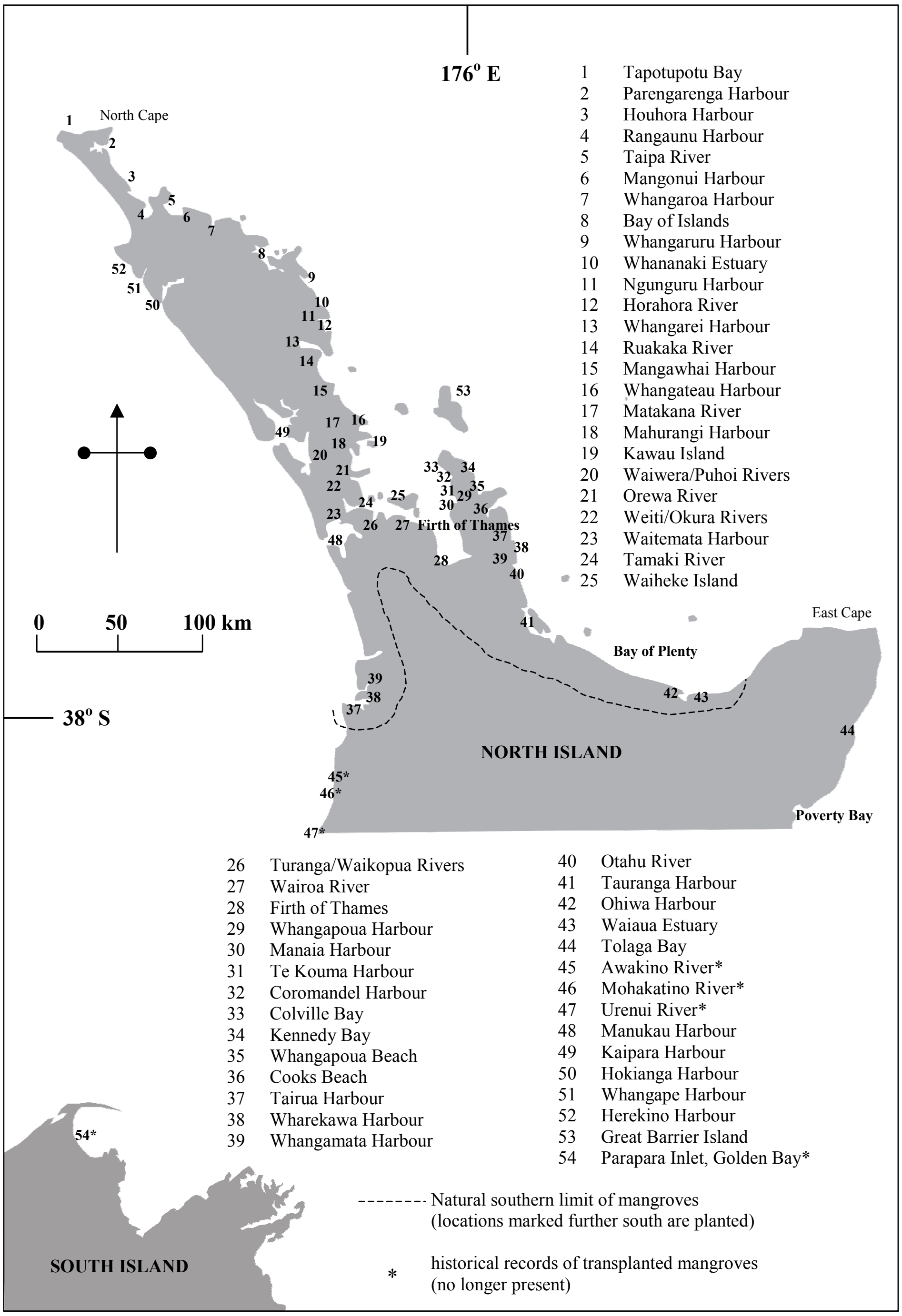
When transplanted, mangroves are known to grow south of their natural range. At the present time, New Zealand's southernmost surviving mangrove plants are located in the Uawa estuary, Tolaga Bay, at latitude 38°23′ S on the east coast of the North Island. Here, a number of plants sourced from Ohiwa Harbour were planted in 1980, and the population has since become naturalised (Crisp et al. 1990, Daniel 1986).

Transplanted mangroves were also previously documented from, but are no longer present, further south on the west coast of the North Island at the Awakino, Mohakatino and Urenui river mouths (Crisp et al. 1990, de Lange & de Lange 1994) and alongside the Hutt River at latitude 41°13′ S (de Lange & de Lange 1994). Isolated plants also survived at Parapara Inlet, Golden Bay, at latitude 40°43′ S in the South Island of New Zealand (Walsby 1992) for a number of years, one being removed from that location by the Department of Conservation as recently as March 2005 (C. Jones pers. comm.).

Historically, the range of *Avicennia* extended much further south than it does today. Pollen in sediment cores from Sponge Bay and Awapuni (Poverty Bay) puts the range of mangrove approximately 140 km south of its present southernmost natural limit in New Zealand. Radiocarbon dates indicate that *Avicennia* became locally extinct in this region approximately 6000-6500 years ago, at the time when post-glacial sea levels receded or when tectonics lifted the coastlines (Mildenhall 2001).

Figure 1

Distribution of mangrove in New Zealand (after Crisp et al. 1990).



3.2.3 Key drivers of mangrove distribution: latitudinal effects

Mangroves are generally 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 1976a, 1977). The actual geographic limits of mangrove growth are coincident with ground frost occurrence and, in addition, their global distribution appears 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. (1998b) suggested that these outlying distributions either coincide with extensions of irregular warm oceanic currents or that they are refugia for relict populations established during periods of warmer climate and greater poleward distributions.

Until fairly recently, two main theories had been proposed to account for the southern latitudinal boundaries of mangrove in New Zealand; either that distribution is constrained solely by the lethal effects of extreme, low winter temperatures (i.e., frosts) (Chapman & Ronaldson 1958, Sakai & Wardle 1978, Sakai et al. 1981), or that limits are set by poor dispersal potential and lack of suitable habitat (de Lange & de Lange 1994). More recent hypotheses suggest that *Avicennia* distribution may be constrained by its physiological limitations under chilling (non-freezing) conditions (Beard 2006, Walbert 2002), or that latitudinal limits are set by constraints on internal water transport as a result of vessel size, and embolism in the xylem vessels following freezing (Stuart et al. 2007).

Frosts play an important, additional and episodic role in defining the range of mangrove in New Zealand, but the main driver enforcing their latitudinal limit appears to be physiological stress. Physiological performance in *Avicennia* becomes increasingly depressed near its geographic limits. Importantly, when exposed to low overnight temperatures, *Avicennia* responses are found to be more consistent with those of subtropical plant species. Major decreases in photosynthetic production following exposure to overnight temperatures of 4°C and lower indicate that critical stress limits are reached well above freezing. These effects are compounded by exposure to freezing temperatures, and in frost-prone areas, lead to additional reductions in productivity by way of physical damage to leaves, branches and reproductive tissue. Freeze-injury of this form also reduces the likelihood of successful seedling production, establishment and long-term survival of saplings. It appears, therefore, that the destructive affects of frost, in combination with chronic reduction in photosynthetic rate from chilling, explain the inability of *Avicennia* to grow further south in New Zealand except where suitable microclimates exist (Beard 2006, Walbert 2002). It is also possible that establishment of plants in suitable microclimates further south of the present limits may be prevented by dispersal barriers (unsuitable coastline) and unfavourable ocean currents (de Lange & de Lange 1994).

3.2.4 Key drivers of mangrove distribution: habitat requirements

3.2.4.1 Tidal elevation

Colonisation by *A. marina* can only occur where active sediment accretion has raised the level of the substratum sufficiently to expose seedlings to the air for part of the tidal cycle, because very young seedlings are intolerant of continuous submersion (Clarke & Hannon 1970). In open estuaries in southeastern Australia, the upper and lower limits of *A. marina* distribution lie between mean high water and mean sea level (Clarke & Myerscough 1993). The seaward limits of mangrove growth in New Zealand have not been examined in detail in many areas, but in locations where they are known (e.g., Tauranga Harbour), undisturbed populations occupy habitat out to the level of approximately 0.23 m above mean sea level (Park 2004). In the southern Firth of Thames, the lower elevation limit of mangroves was ≥0.5 m above mean sea level. Restriction of these distributions to above the mean sea level limit reported by Clarke & Myerscough (1993) may be due to inhibitory effects of waves on propagule establishment and/or a lag between elevation change and mangrove colonisation.

3.2.4.2 Exposure

Shallow, low-energy and gently-shelving shorelines are required not only for mangrove seedlings to anchor, but to allow these plants to persist in an area. Mangroves have significant value in the coastal zone as a buffer against erosion and storm surges. However, it is important to note that mangroves themselves require some protection from high-energy waves and currents. They are often subject to erosion pressures along channel edges within and at the seaward margins of mangrove stands (Semeniuk 1980).

3.2.4.3 Sediment/Substrate

The preferred habitat for mangroves in general is soft, muddy, waterlogged sediment, but some, such as *Avicennia*, will also grow successfully on a wide variety of other substrates including volcanic rock, sand and soil (Crisp et al. 1990, Kathiresan & Bingham 2001).

Situations where sediments gradually accrete promote growth of mangroves by providing habitat of suitable elevation for them to colonise. However, seedlings are susceptible to burial as a result of sudden sedimentation and water turbulence (Ellison 1998). Experimental work has shown that *Avicennia* seedlings are unable to survive if they are suddenly covered by sediment to a depth of 32 cm (Thampanya 2006). Early growth of newly-established seedlings may also be arrested by the combination of excess silt and microalgal growth on their first true leaves. This can result in photosynthetic shutdown and gas-exchange stresses, and may end with the death of the plant.

3.2.4.4 Light and photosynthesis

Once anchored in the substrate, seedlings lose their cotyledons after 1-2 months of growth. New individuals are most likely to persist beyond this stage in light gaps or on open sites, rather than under a canopy. Seedlings are only shade-tolerant up to the end of their cotyledon stage and high light intensity is crucial for their ongoing development and survival (Burns 1982, Osunkoya & Creese 1997). Further development from this stage may be arrested if conditions are not suitable, with plants remaining in a 'seedling bank' for several years before progressing to the next size class (Burns & Ogden 1985, Clarke & Allaway 1993).

3.2.4.5 Salinity

Seedling development is affected by salinity of the substrate in which they grow. A study by (Downton 1982) of development of *A. marina* seedlings at different salinities revealed that early seedling development was most rapid in the absence of salt but declined soon after, with optimum growth occurring between 10 and 50% seawater. Plants growing in higher salinities were comparatively slow to develop and had lower biomass.

Photosynthetic performance of adult plants is also affected by salinity. Both low salinity (<12 psu) and hypersaline conditions (60 psu) have an adverse affect on photosynthetic performance (Sobrado 1999, Tuffers et al. 2001). However, despite these limitations, *A. marina* exhibits a wide range of salt-tolerance and an ability to grow in waterlogged soils of salinities ranging from 0 to 90 psu.

3.2.4.6 Nutrients

Several processes in mangrove ecosystems, including above- and below-ground productivity and decomposition, are affected when the supply or availability of one or more essential nutrients becomes limiting (Feller et al. 2003). Overseas research has shown that patterns of nutrient limitation in mangrove systems are complex, with essential nutrients not uniformly distributed and limits imposed by one or more nutrients (usually nitrogen or phosphorus). In addition, not all ecological and physiological processes are limited by the same nutrient (Boto & Wellington 1983, Feller et al. 2003).

Mangroves, as nutrient-limited systems, are particularly susceptible to nutrient pollution. Nutrients are produced either within the mangrove forest itself (autochthonous) or derived externally (allochthonous) from both terrestrial (via freshwater rivers and streams) and marine sources. Freshwater inputs may affect mangroves by modifying salinity gradients and by increasing sediment and nutrient loadings. Incoming sediments may be a direct source of particulate nutrients, and incoming water may contain high concentrations of dissolved nutrients. However, additional nutrient supply will only result in growth increases if some other factor is not already limiting growth, and if the rate at which nutrients become available to the plant is increased (Schwarz 2002).

Elevated nutrient loadings (particularly nitrogen) have been thought to play a part in the acceleration of mangrove spread in some New Zealand estuaries, by contributing to enhanced growth rates and biomass (Yates et al. 2004), and increasing their potential to produce more propagules. As yet, however, there is no conclusive evidence that nutrients are the main causal factor of the observed expansion (Schwarz 2002).

3.2.4.7 Natural catastrophes

Occasionally 'natural' disturbances have severe impacts on mangrove stands, resulting either in severe dieback or death of mangrove. Pegg et al. (1980) (cited in Maxwell 1993) reported extensive mortality in *A marina* on the Queensland coast due to the pathogenic fungus *Phytophthora*, and Maxwell (1993) identified a similar, but rather smaller scale, dieback at Pipiora on the Piako River (Hauraki Plains). However, dieback is not always disease-related. In some New Zealand estuaries extensive areas of mangroves are occasionally decimated by severe winter frosts (Beard 2006).

Effects of herbivorous insects on mangroves are discussed in section 2.3.4.

3.2.5 The productivity of mangroves and their carbon/nutrient contribution to the marine environment

3.2.5.1 Productivity of New Zealand mangroves

A review of trends in biomass and litterfall (incorporating 91 measures of litterfall across species and locations, including New Zealand) identified trends of decreasing biomass and rates of litterfall with increasing latitude (Saenger & Snedaker 1993). From this it would be expected that values from New Zealand would fall at the lower end of the reported range, but this is not always the case.

There have been several studies of the productivity of mangroves in New Zealand (Woodroffe 1985a; May 1999, Oñate-Pacalioga 2005, Burns et al. submitted: Table 1). Productivity has been reported as rates of production of litter (leaves, twigs and other woody material, flowers and fruit). Although this does not represent net primary production completely (since it does not include net increase in plant biomass), it represents an important component of it. It also reflects changing events in the lifecycle 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. The rates of litter production reported for adult trees (i.e., not saplings) vary from 0.61-8.1 t ha^{-1} yr^{-1}, with the smaller value from stunted (0.8 m tall) plants in Puhinui Creek, Auckland (Burns et al. submitted) and the larger from 4 m-high trees in Tuff Crater, Auckland (Woodroffe 1985a). The average value for full-size, mature trees was 3.6 (SD 2.05) t ha^{-1} yr^{-1}. Similar methods of sampling were used in all of these studies.

Recorded rates of litterfall for *Avicennia marina* from New Zealand are below the maximum values reported from other parts of its distribution (for example, those from tropical Australia) but are comparable with values from subtropical and temperate Australia (Table 1). 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 1.10-15.98 t ha^{-1} yr^{-1}, indicative of considerable variation within and among locations.

Table 1

Summary of published information on litterfall and above-ground biomass for *Avicennia marina*. Data for Australia and South Africa are ordered by increasing latitude. Data for various mangrove species in various tropical and subtropical countries are also shown for comparison.

Country	Location	Estuary	Latitude	Height of trees (m)	Litter production t ha^{-1} yr^{-1} dw	Above-ground biomass t ha^{-1}	Notes	Source
Australia	Northern WA, Gulf of Carpentaria	Various	10°50' - 17°57'S		2.34-4.30 (SD 2.11)		Hot, dry winter	Bunt 95
Australia	Darwin, NT	Darwin Harbour	12°26'S	13	12.51 (SD 1.793)			Woodroffe et al. 1988
Australia	Darwin, NT	Darwin Harbour	12°26'S	10.8	0.68 (SD 0.43)			Woodroffe et al. 1988
Australia	Northern Qld	Various	15°28' - 18°21'S		10.49 (SD 4.57)		Hot, generally short dry season	Bunt 1995
Australia	Central WA coast	Various	20°18' - 24°53'S		8.79 (SD 1.68)		Hot, arid	Bunt 1995
Australia	Qld	Mary River	25°26'S			200-250	Ratio of below:above ground biomass varied with distance from seaward edge of mangroves - lowest upstream, and reached 1 at the frequently inundated seaward edges of intertidal flats in channel mouth	Saintilan 1997b
Australia	Qld	Mary River	25°26'S			120		Saintilan 1997b
Australia	Qld	Mary River	25°26'S			10		Saintilan 1997b
Australia	Brisbane		27°25'S			110-340		Mackey 1993
Australia	Subtropical eastern Australia	Brisbane, Various	27°33' - 33°59'S		3.07 (SD 1.83)		Hot summer, uniform rain	Bunt 1995
South Africa	Durban	Mgeni River	29°48'S	4.9-8.2		94.5		Steinke et al. 1995
Australia	NSW	Kooragang Is, Newcastle	32°51'S	3		7.1		Burchett & Pulkownik 1983 in Saenger & Snedaker 1993
Australia	NSW	Kooragang Is, Newcastle	32°51'S	7.5		86		Burchett & Pulkownik 1983 in Saenger & Snedaker 1993
Australia	NSW	Kooragang Is, Newcastle	32°51'S	10		104		Burchett & Pulkownik 1983 in Saenger & Snedaker 1993
Australia	NSW	Kooragang Is, Newcastle	32°51'S	4.3	5.14	21.7		Murray 1985
Australia	NSW	Kooragang Is, Newcastle	32°51'S	4.4	5.62	21.8		Murray 1985
Australia	Temperate NSW, WA, Vic	Merimbula, Westernport, Bunbury	33°20' - 38°25'S		4.36 (SD 1.48)		Long, mild summer, cool winter	Bunt 1995
Australia	NSW	Hawkesbury River	33°30'S	<3		52.1		Saintilan 1997a
Australia	NSW	Hawkesbury River	33°30'S	<3		60.1		Saintilan 1997a
Australia	NSW	Hawkesbury River	33°30'S	>3		400		Saintilan 1997a
Australia	Sydney	Middle Hbr	33°46'S	8-9	5.8	220	Ave 79%=leaf	Goulter & Allaway 1979
Australia	Jervis Bay, NSW	Carama Inlet & Moona Moona Ck	35°00'S	5-8	3.67		Average of 9.2% of litter=fruit and flowers.	Clarke 1994
Australia	Sydney, NSW	Lane Cove River	35°50'S	<0.8		0.2-3.4		Briggs 1977

Table 1 (Cont.)

Country	Location	Estuary	Latitude	Height of trees (m)	Litter production t ha^{-1} yr^{-1} dw	Above-ground biomass t ha^{-1}	Notes	Source
Australia	Sydney, NSW	Lane Cove River	35°50'S	6.5-8.2		112.3-144.5	Means of 2 sites (total above-ground biomass)	Briggs 1977
Australia	Victoria	Westernport Bay	38°46'S		2			Attiwill & Clough 1974 in Goulter & Allaway 1979
New Zealand	Auckland	Puhinui Creek	37°01'S	0.5-1.6 (sapling)	0.11-0.38		Young stands (4-13yo)	Burns et al submitted
New Zealand	Auckland	Puhinui Creek	37°01'S	0.8 (stunted)	0.61		Medium-age (13-31yo)	Burns et al submitted
New Zealand	Auckland	Puhinui Creek	37°01'S	2.3-2.6	2.89		Medium-age (13-31yo)	Burns et al submitted
New Zealand	Auckland	Puhinui Creek	37°01'S	3.4-4	1.55-4.05		Old stands (31+yo)	Burns et al submitted
New Zealand	Northland	Rangaunu Harbour	34°57'S	6.23	6.24		Leaves=73%	May 1999
New Zealand	Northland	Rangaunu Harbour	34°57'S	3.06	3.89			May 1999
New Zealand	Northland	Rangaunu Harbour	34°57'S	5.12	4.83			May 1999
New Zealand	Northland	Rangaunu Harbour	34°57'S	1.68	1.77			May 1999
New Zealand	Auckland	Whangateau Estuary	36°19'S	<0.5-1.5 (sapling)	1.68			Oñate-Pacalioga 2005
New Zealand	Auckland	Whangateau Estuary	36°19'S	2-4	1.56			Oñate-Pacalioga 2005
New Zealand	Auckland	Tramcar Bay	36°19'S	2-4	1.3			Oñate-Pacalioga 2005
New Zealand	Auckland	Tuff Crater	36°48'S	4	7.12-8.09	130	Leaves=69%, fruits and flrs 12.3%	Woodroffe 1985a
New Zealand	Auckland	Tuff Crater	36°48'S	0.95 (stunted)	2.90-3.65	10	Leaves=74%, fruits and flrs=2.6%	Woodroffe 1985a
Various tropical	Various locations and species		23N-23S		0.01-7.71		Min. value for *Ceriops tagal* in Andaman Islands, max. for *Avicennia germinans* in Guyana.	Kathiresan & Bingham 2001
Various tropical	Various locations and species		23N-23S	3.9-35	3.74-18.7	57-436	Average 193 t/ha biomass, 3.74-14.02 t/ha/yr litter. Min value for *Avicennia* sp. in Sri Lanka, max for *Bruguiera* in China. Max value recorded for *Avicennia* sp. 14.0 in Australia and Malaysia.	Saenger & Snedaker 1993
Various subtropical	Various locations and species		23-30S and N	1-12.5	1.3-16.31	7.9-164.0	Min and max both for *Rhizophora* in USA. Max value for *Avicennia* sp. 7.15 in South Africa.	Saenger & Snedaker 1993

Table 2

Comparison of primary production and biomass in selected terrestrial and marine plants and plant assemblages. ^{a} indicates value for g C m^{-2} yr^{-1} was converted from value for t ha^{-1} yr^{-1} using a conversion factor of 37.6 derived from Larkum 1981 and ^{b} indicates that the reverse conversion was done.

		Primary production		**Biomass**	
Primary producer	**Comments**	**g C m^{-2} yr^{-1}**	**t dw ha^{-1} yr^{-1}**	**t ha^{-1}**	**Reference**
Terrestrial					
Napier Grass	Above-ground	3322	88		ILarkum 1981
Sugar cane	Above-ground	2482	66		Larkum 1981
Tropical reed swamp	Above-ground	2227	59		ILarkum 1981
Annual crops	Above-ground	840	22		ILarkum 1981
Evergreen crops	Above-ground	803	21		ILarkum 1981
Desert	Above-ground	37	1		ILarkum 1981
Mangroves					
Avicennia marina New Zealand	Litter fall	23-305^{a}	0.61-8.1	10-130	Review in this study
Avicennia marina worldwide	Litter fall	26-470^{a}	0.68-12.51	7-400	Review in this study
Saltmarshes					
Spartina marsh (subtropical)	Above-ground	752	20		Larkum 1981
Juncus kraussii saltmarsh (temperate Australia)	Above-ground	305^{a}	8.1	0.96-44 (mean 11.16)	Clarke & Jacoby 1994
Sarcocornia saltmarsh (temperate Australia)	Above-ground			9.8	Clarke 1985
Sarcocornia saltmarsh (temperate Australia)	Above-ground			0.52-11.84 (mean 3.17)	Clarke & Jacoby 1994
Sporobolus saltmarsh (temperate Australia)	Above-ground			9.8	Clarke 1985
Sporobolus saltmarsh (temperate Australia)	Above-ground			1.48-8.52 (mean 3.49)	Clarke & Jacoby 1994
Juncus kraussii saltmarsh (temperate Australia)	Above-ground	113-489^{a}	3-13	14.24	Congdon & McComb 1980
Juncus roemerianus saltmarsh (eastern USA)		301^{a}	8		Christian et al. 1990
Average for temperate areas (SD)		**302 (2.3)**	**8 (0.1)**		
Seagrasses					
Thalassia testudinum (tropical seagrass)	Above-ground	292-694	9-18		Larkum 1981
Zostera capricorni (Brisbane, Australia)	Above-ground, inshore			0.4 (SE 1.8)	Conacher et al. 1994
Zostera capricorni (Brisbane, Australia)	Above-ground, midshore			0.38 (SE 2.3)	Conacher et al. 1994
Zostera capricorni (Brisbane, Australia)	Above-ground, offshore			0.68 (SE 4.5	Conacher et al. 1994
Zostera marina (temperate seagrass)	Above-ground	329	8.6		Larkum 1981
*Zostera marina (*Massachusetts, USA)	Shoots	155-345	4-9^{b}		Roman & Able 1988
*Zostera marina (*Netherlands)	Shoots	160-412	4-11^{b}		van Lent & Verschuure 1994
Zostera marina (Virginia, USA)	Shoots	252	7^{b}		Buzzelli et al. 1999
Posidonia sinuosa (temperate Western Australia)	Above-ground	226-338^{a}	6-9^{b}		Cambridge & Hocking 1997
Posidonia australis (temperate Western Australia)	Above-ground	338-414^{a}	9-11^{b}		Cambridge & Hocking 1997
Halodule wrightii, *Ruppia maritima* (Dzilam Lagoon, Mexico)		82	2^{b}		Medina-Gómez & Herrera-Silveira 2006
Various (Celestun Lagoon, Mexico)		783	21^{b}		Medina-Gómez & Herrera-Silveira 2006

Table 2 (Cont.)

		Primary production		**Biomass**	
Primary producer	**Comments**	**g C m^{-2} yr^{-1}**	**t ha^{-1} yr^{-1}**	**t ha^{-1}**	**Reference**
Seagrasses (continued)					
Various (Terminos Lagoon, Mexico)		444	12^b		Medina-Gómez & Herrera-Silveira 2006
Average (SD)		**358 (168)**	**10 (5.0)**		
Macroalgae					Cambridge & Hocking 1997
Laminaria longicruris	Minimum estimate	602	16		Larkum 1981
Laminaria hyperborea	Minimum estimate	391	11		Larkum 1981
Phytoplankton					
Phytoplankton (coastal waters)		99	2.6		Larkum 1981
Chesapeake Bay, USA		185	5^b		Smith & Kemp 1995
Narragansett Bay, USA		102	3^b		Keller 1989
Narragansett Bay, USA		36-109	$1\text{-}3^b$		Keller 1989
North Carolina, USA		373	10^b		Boyer et al. 1993
North Carolina estuaries, USA		52-500	$1\text{-}13^b$		Mallin 1994
Virginia, USA		52	1^b		Buzzelli et al 1999
Marennes-Oléron Bay, France		185	5^b		Struski & Bacher 2006
Dzilam Lagoon, Mexico		37	1^b		Medina-Gómez & Herrera-Silveira 2006
Celestun Lagoon, Mexico		150	4^b		Medina-Gómez & Herrera-Silveira 2006
Terminos Lagoon, Mexico		219	6^b		Stevenson et al. 1988
Average (SD)		**159 (103)**	**4 (3.0)**		
Benthic microalgae					
Mudflat (England)		143	4^b		Joint 1978
Marsh (Mississippi, USA)		57	2^b		Sullivan & Moncreiff 1988
Mudflat (Massachusetts, USA)		250	7^b		Gould & Gallagher 1990
Marsh (South Carolina, USA)		55-234	$1\text{-}6^b$		Pinckney & Zingmark 1993
Virginia, USA		99-239	$3\text{-}6^b$		Buzzelli et al. 1999
Average (SD		**153 (69)**	**4 (1.8)**		

There is also considerable variation in reported rates of litterfall among studies within New Zealand. Osunkyoya & Creese (1997) described a cline of decreasing tree height and propagules size with increasing latitude with New Zealand, and this 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 following studies.

Burns et al. (submitted) measured litter production in each of 6 stands in Puhinui Creek. Stands were divided into 3 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 2 locations along the creek (young stands were generally nearer the creek and old stands highest up the shore). Litterfall in the 2 young stands was 0.11 and 0.38 tonnes 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% consisted of leaves. One of the medium-age sites contained stunted adult trees (average canopy height 0.8 m) where litterfall was 0.61 tonnes ha^{-1} yr^{-1} (43% wood, 33% leaves). Stunting may have been due to nitrogen-limitation of growth, as discussed in section 2.2.4. The other stand of this age (average canopy height 2.3 m) produced 2.89 tonnes ha^{-1} yr^{-1} (67% leaves). The 2 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 tonnes 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 2 locations, separated by 250 m, on opposite sides of the mouth of the Awanui River in Rangaunu Harbour, Northland. 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 tonnes ha^{-1} yr^{-1} (75% leaf material) and 6.24 tonnes ha^{-1} yr^{-1} (76% leaf material), respectively. Equivalent values for the high-shore sites were 1.77 tonnes ha^{-1} yr^{-1} (86% leaf material) and 4.83 tonnes 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 tonnes ha^{-1} yr^{-1} (average values for 2 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 tonnes 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 were recorded at the Tuff Crater site on the northern side of Waitemata Harbour, rather than at the most northerly site (Rangaunu Harbour), 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 1.5m 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 tonnes 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 abundance at the study location of the citrus borer (*Oemona hirta*) and other insects that feed on mangroves. Insect populations may be very variable in space and time and the amount of insect damage may influence the amount of litter shed by the trees. The small number of studies in New Zealand, and the large within-location variation recorded by those studies, makes 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 mangroves in New Zealand.

3.2.6 Mangrove productivity compared to other New Zealand coastal habitats

The variability in reported rates of litter production and the general lack of information makes it difficult to compare values of biomass or productivity for mangroves in New Zealand with those of other intertidal habitats. We are not aware of any estimates of primary productivity for saltmarshes, seagrass beds or benthic microalgae in New Zealand with which to compare the values for mangroves in Table 1. Consequently we have resorted to comparisons with equivalent habitats in other parts of the world, including temperate Australia (Table 2). Note that in some cases (indicated in Table 2) we had to convert published values expressed as the amount of carbon produced per m^2 per year to the amount of plant material (litter) produced per ha per year in order to make comparisons. This was done using a conversion factor (0.027) modified from that given by Larkum (1981). Larkum's factor assumes that ash content is 20% of the dry weight of litter and that 1 g of organic matter is equivalent to 0.47 g C. Use of this conversion factor, although unavoidable, introduces an additional level of uncertainty to some of the comparisons of values from different studies.

Very broad-scale comparisons of rates of primary production suggest that the range of values for New Zealand mangrove forests is within the range of values from temperate Australian and USA saltmarshes (*Juncus* spp.) and northern European and USA seagrass (*Zostera marina*) beds (Table 2). Mangrove productivity is comparable to or slightly higher than published values for coastal phytoplankton or benthic microalgae. Valiela (1984, his Table 1-14) gave ranges of published values for productivity of various marine primary producers (g C m^{-2} yr^{-1}): rocky shore macroalgae 300-2500; saltmarsh grasses 600-1700; seagrasses 100-1500; mangroves 300-1000; benthic microalgae 100-2100 and; coastal phytoplankton 100-500. These values are at the upper ends of the ranges reported from the present review (Table 2) but, again, indicate that mangroves in New Zealand (range of productivity 23-305g C m^{-2} yr^{-1}) may be of comparable productivity to other coastal habitats such as seagrasses and intertidal flats in New Zealand.

Unfortunately, these broad comparisons conceal large variation among and within locations, making them of little use in assessing the value of individual forests or other habitats. Nevertheless, they do indicate that it is not justified to assume that New Zealand mangroves are relatively unproductive because they are at the limit of the species' range, and therefore of lesser ecological importance than other estuarine habitats.

3.2.7 Mangrove productivity compared to terrestrial primary producers

Valiela (1984) also gave a range of productivity values for temperate forests (location not stated, but presumably north American or European) of 200-500 g C m^{-2} yr^{-1}. Values for *Avicennia marina* in New Zealand (and elsewhere) are comparable to this range. They are, however, generally less productive than some agricultural crops (Table 2).

Woodroffe (1982, his Table 3) compiled data on litter production from a range of forest-types in New Zealand and compared them to production by mangroves in Tuff Crater. These data indicated that the taller mangroves in Tuff Crater were more productive than most forest types and were only exceeded by hard beech *Nothofagus truncata*, *Pinus radiata* and *Pinus nigra* in very productive years. Wardle (1991, his Table 14.5) also presented data from various sources on litter production from native vegetation. Although Woodroffe's values for mangrove litterfall are at the top end of the range recorded in New Zealand, the average value for mature mangroves (3.6 tonnes ha^{-1} yr^{-1}, derived from data in Table 1) is within the range reported for native beech forests (3.51-8.85 tonnes ha^{-1} yr^{-1} for *N. truncata*, 3.10-5.70 tonnes ha^{-1} yr^{-1} for *N. solandri* var. *solandri*, 3.5-4.7 tonnes ha^{-1} yr^{-1} for *N. menziesii* in Southland) and plantations of larch (*Larix decidua*: 3.29-4.12 tonnes ha^{-1} yr^{-1}), *Pinus radiata* (2.91-10.30 tonnes ha^{-1} yr^{-1}) and douglas fir (*Pseudotsuga menziesii*: 2.49-3.32 tonnes ha^{-1} yr^{-1}). The average value for mangroves is also slightly less than those for a mixed stand of red beech (*N. fusca*) and silver beech (*N. menziesii*) in the central North Island (4.9 tonnes ha^{-1} yr^{-1}: Sweetapple & Eraser 1992), manuka (*Leptospermum scoparium*) in the Marlborough Sounds (7.8 tonnes ha^{-1} yr^{-1}: Wardle 1991) and hinau (*Elaeocarpus dentatus*) near Wellington (5.0 tonnes ha^{-1} yr^{-1}: Cowan & Waddington 1991).

3.2.8 The importance of mangrove productivity within estuaries and harbours

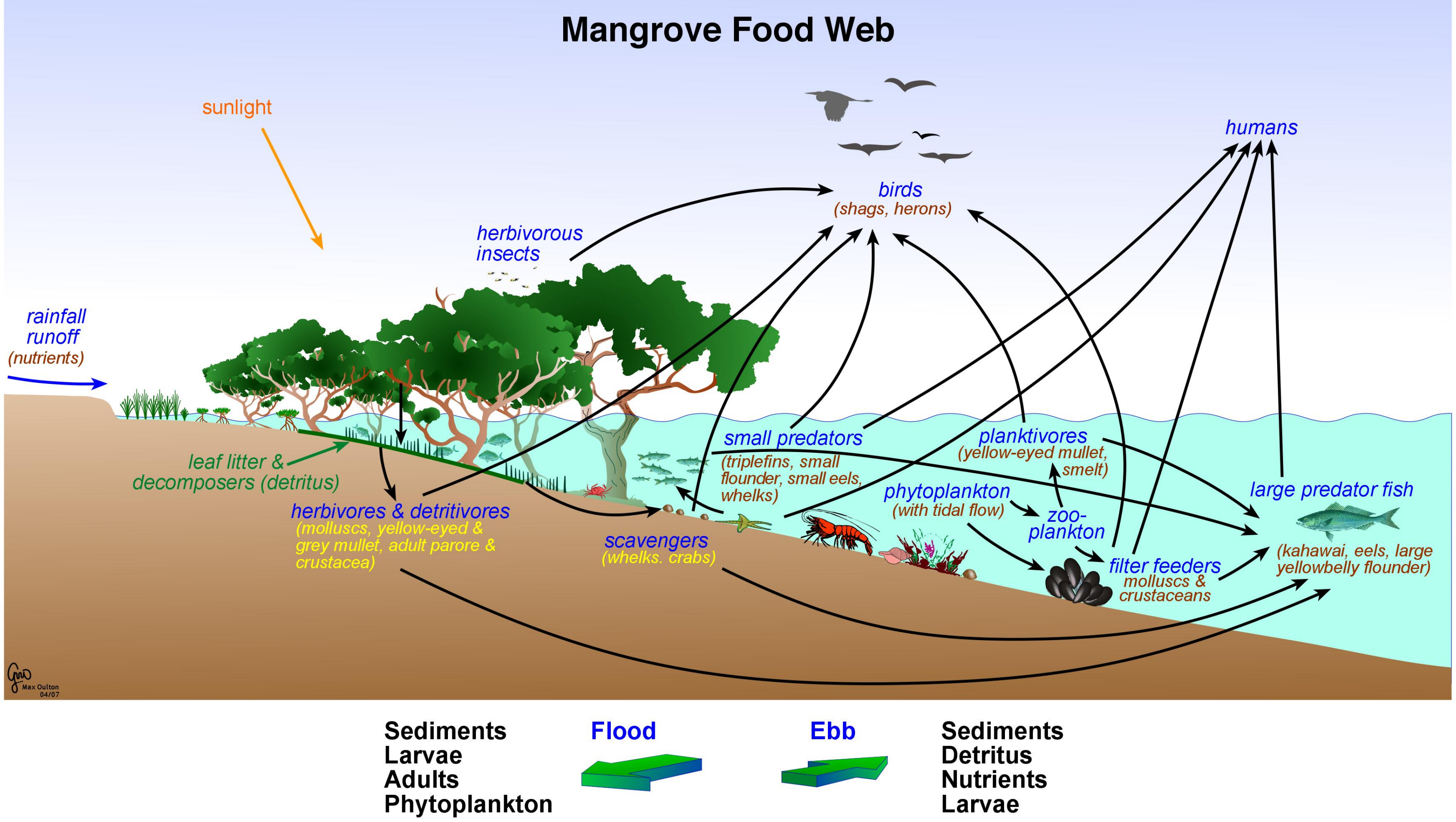
The ecological relevance of mangrove productivity to estuaries and harbours depends not just on how much organic material mangroves produce but also how and where this is broken down to become available to other organisms. Biomass lost as litter decomposes to release nutrients that may be recycled within the mangrove system (as in a terrestrial forest) or potentially exported to adjacent habitats by tidal flushing. Woodroffe (1985a) estimated that 35% of the total above-ground mangrove biomass in the Tuff Crater, Auckland falls as litter each year. The Tuff Crater contains a large area of stunted and sparse mangroves and leaf turnover appeared to be higher among the smaller trees, so this rate of turnover may be faster than in stands of taller trees.

3.2.8.1 Direct consumption of mangrove material

Primary production by mangroves may enter the surrounding and adjacent food webs by direct grazing or as detritus (dead plant material). A generalized (and probably simplified) food web for New Zealand mangroves is shown in Figure 2. Fresh mangrove leaves can contain large amounts of tannins, cellulose and lignin, making them indigestible or unpalatable to many herbivores (Lee 1995). Some animals are, however, capable of feeding on fresh material. Crabs (*Sesarma* spp.) are responsible for consuming up to 30% of annual mangrove leaf fall in tropical northern Queensland (Robertson 1986) and 44% of *Avicennia marina* leaf fall in subtropical South Africa (Emmerson & McGwynne 1992). The mudcrab *Helice crassa* is often abundant among mangroves in New Zealand (see section 2.5.1) and belongs to the same family (Grapsidae) as the crabs studied by Robertson (1986) and Emmerson & McGwynne (1992), but it is not known whether they consume fresh mangrove material. The feeding behaviour of *H. crassa* is currently being studied in Matapouri Estuary, Northland (Andrea Alfaro, Auckland University of Technology, pers. comm.).

Figure 2

Generalised example of a temperate mangrove foodweb. Arrows point in the direction of flow of energy and nutrients.



Insects are another group of direct grazers on fresh mangrove tissue (Farnsworth & Ellison 1997), including *Avicennia marina* in temperate Australia (mainly by beetles and the larvae of fruit flies and moths: Clarke 1992, Minchinton & Dalby-Ball 2001), Hong Kong (complete defoliation by moth larvae: Anderson & Lee 1995) and South Africa (by moths on up to 50% of propagules examined: Farnsworth & Ellison 1997). The ecology of insect assemblages in New Zealand mangroves is not well known and their trophic role in relation to mangroves is unknown. Farnsworth & Ellison (1997) concluded that predation on propagules before dispersion is a "ubiquitous feature of mangrove forests world-wide" so this form of attack seems likely in New Zealand mangroves. Woodroffe (1985a) reported low levels of consumption of mangrove leaves in Tuff Crater and Johnstone (1981) made similar observations among mangroves around Auckland. Larvae of the moth *Planotortrix avicenniae*, endemic to New Zealand mangroves (Dugdale 1990), consume mangrove leaves, as do those of the leaf-roller moth *Ctenopseustis obliquara* (Cox 1977) and the pyralid moth *Ptyomaxia* sp. (John Dugdale, pers. comm.). Mature mangroves in Auckland are often attacked by stem-boring insects (Kronen 2001), though this does not seem to be so common in Matapouri Estuary (Andrea Alfaro, pers. comm.). The insect likely to be responsible, the lemon-tree borer (*Oemona hirta*) is, however, distributed throughout New Zealand, and this apparent regional difference may simply reflect temporal variation in abundances and effects of the insects.

3.2.8.2 The importance of mangrove detritus

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 (Woodroffe 1985a). The nutritional value of this 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) and decreases in carbon content and net weight (Robertson 1988). Concentrations of tannins also decrease rapidly during early stages of decomposition (Robertson 1988). Leaves of *Avicennia marina* are inherently rapidly decomposed relative to other mangrove species because of their relatively high nitrogen content, low C:N ratio and low tannin content (Robertson 1988). Concentrations of nitrogen in the leaves of young (0.6-1.6 m tall, 2.72% dw) and mature (1.88% dw) *A. marina* in Auckland (Morrisey et al. 2003) are slightly higher than the concentration reported by Robertson (1988) in Queensland (ca 0.9% dw from his Figure 2).

Rates of decay vary with climate and latitude (Mackey & Smail 1996). However, effects of latitude can apparently be obscured by local differences in position within the intertidal area and associated period of immersion, and by seasonal effects, as illustrated by comparison of studies from different latitudes in eastern Australia. Robertson (1988) recorded a time of 11 d 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') and 90 d for leaves in the mid-intertidal area (leaves of *A. marina* decomposed considerably faster than those of other mangrove species at the same locations). Further south, near Brisbane (latitude 27° 24'), Mackey & Smail (1996) recorded times for 50% loss of AFDW of 44 d low on the shore (inundated by 100% of high tides) and 59 d higher on the shore (inundated by 20% of high tides) in summer. Equivalent times for winter were 78 d (low shore) and 98 d (high shore). In Westernport Bay, Victoria (latitude 38° 20') times for 50% loss of dry weight in summer were ca 80 d for leaves placed on the sediment surface in mesh bags and ca 40 d for unbagged leaves (van der Valk & Attiwill 1984). Unbagged leaves decayed faster because of loss of small fragments that were retained by the bags.

In New Zealand, 50% loss of leaf weight occurred after ca 53d in early summer (October-December) for leaves placed on the mud surface in Whangateau Harbour, north of Auckland (latitude 36° 19': 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 weeks (time to 50% reduction in AFDW), 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 (although there was no measure of variation in rates of decay at each sampling time because only one sample was measured each time). The lack of difference between summer and winter 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. She found that 50% loss of AFDW occurred after 8 weeks in mature stands in autumn but took more than 12 weeks in winter and spring. Equivalent times for newly-establishing stands were 12 weeks in autumn and >12 weeks in winter and spring.

Comparison of the decomposition rates reported by Robertson (1988) and Mackey & Smail (1996) with those for New Zealand suggests that rates are not necessarily slower at the higher latitudes at which New Zealand mangroves occur. Variation among sites at a given latitude seems to be as large as variation among latitudes. There is a need for studies that specifically address this question of variation in rates of decomposition at different spatial and temporal scales.

The rate of decomposition of litter is increased by the activities of animals that break the litter 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). Lee (in press) has suggested that gastropods may provide a similar service in parts of the world where crabs are a less dominant part of the macrofauna, and this may be the case in New Zealand but as yet there is little information available.

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). It is not know 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 recent study in subtropical Japanese mangroves (Mchenga et al. 2007) suggests that the related species *Helice 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). The trophic roles of the snail *Turbo smaragdus* and the crab *Helice crassa* are currently being investigated in Matapouri Estuary (Andrea Alfaro, pers. com.). 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 also exclude larger macrofauna and, by preventing them from breaking up the litter, underestimate rates of decomposition, as most studies have acknowledged.

3.2.8.3 Export of nutrients from mangrove areas

Nutrients derived from mangrove material, either though 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. Woodroffe (1985a) noted that the organic content of sediments in mangrove areas in the Tuff Crater was high and, while 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). Conversely, concentrations of particulate organic matter were also high in the water in the tidal creeks of Tuff Crater, indicating that some of this material is exported (Woodroffe 1985a).

3.2.8.4 The importance of mangroves to other estuarine habitats

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 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 assumed (Lee 1995, Loneragan et al. 1997, Kathiresan & Bingham 2001). Marguiller et al. (1997) used carbon and nitrogen stable isotope signatures of mangroves, seagrasses and benthic macrofauna to identify trophic relationships in a Kenyan estuary. Seagrasses nearer to the mangroves had signatures indicating that they utilised dissolved inorganic carbon derived from decomposition of mangrove litter. Some macrofaunal species collected within the mangroves had signatures similar to the mangroves themselves, while others had signatures that suggested they might also have used organic matter derived from nearby seagrass beds or phytoplankton. Macrofauna collected along a 3-km transect from mangroves to seagrasses showed a gradient in isotope signature indicating decreasing dependence on mangrove material with distance from the forest. Export is strongly dependent on patterns of water movement above and within the sediment, and the amount and type of material exported from a particular mangrove stand will depend on local hydrodynamic conditions, particularly tidal flow.

Crisp et al. (1990) illustrate the assumption of the importance of mangrove productivity to adjacent habitats in the New Zealand context. They state that "The dense numbers of plants and animals of the intertidal zone owe their existence to the remarkable ability of the mangle to sustain them…The nutrients released through the breakdown of Manawa litter are available for the growth of new plants and, having been carried by the tides to the marine environment, for phytoplankton, the basic building block in marine food chains". In fact, the lack of information on the fate of organic material produced by mangroves, and its importance to other coastal habitats, is even more acute in New Zealand than overseas. There has, however, been one notable recent study that has investigated the issue.

Guest & Connolly (2004, 2006) found that the ^{13}C signatures of crabs (*Parasesarma erythrodactyla* and *Australoplax tridentata*) and slugs (the pulmonate *Onchidina australis*) in saltmarshes in southeast Australia reflected that of the dominant saltmarsh plant (*Sporobolus virginica*). The signatures of the same animals living in mangroves reflected those of *A. marina*. The sharply-defined zone of transitional ^{13}C values between the 2 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 saltmarsh had signatures matching those of *S. virginica*, while the signatures of those in smaller patches indicated that they had assimilated carbon from both *S. virginica* and mangroves.

Alfaro et al. (2006) used lipid biomarkers and stable isotopes to identify the trophic dynamics of an estuarine food web in Matapouri Estuary, Northland. Mangroves are the dominant habitat in the estuary but seagrass beds, sandflats and saltmarshes 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 (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 3 filter-feeding species sampled (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. *T. smaragdus* occur in association with mangrove pneumatophores, in addition to brown algae and seagrass, while *N. atramentosa* occurs on mangrove trunks, hence the present 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 *T. 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 it consumes 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 diversity was reflected by the diversity of biomarkers found in these crabs. 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 the Upper Waitemata Harbour Study (though 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). *H. banksii* is present all year and is very abundant among mangrove pneumatophores, presumably because they trap the alga and also 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 provided material to the detrital food chain. May (1999) noted that in Rangaunu Harbour, a large estuarine system with high water clarity, extensive seagrass beds and mangrove forests, prevalent southeasterly winds often imported drift seagrass into mangrove forests on the fetch 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. The seagrass meadows present extended from the low tide channel up and into the pneumatophore zone (Morrison pers. obs.).

Work on the trophic role mangroves play in supporting fish production has also shown then 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 ciliate*; and winter whiting, *Sillago maculate*) 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, particulate organic matter (POM), and microphytobenthos. For yellow-fin bream, seagrass, saltmarsh and POM were important trophic sources at the whole estuary scale, while 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). Similarly, for sand whiting, only POM appeared to be important at the whole estuary scale, while at more localised scales, mangroves and microphytobenthos were also important, with up to 25% (upper 95% C.I.) 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 the above study, Melville & Connolly (2005) examined ^{13}C-isotope markers in twenty-two species of estuarine fish collected from bare mudflats in the same estuary. They pooled the similar isotopic signatures of three mangrove species (*A. marina*, *Aegiceras corniculatum*, and *Rhizophora stylosa*), and also those of three seagrass species (*Zostera capricorni*, *Halophila ovalis*, and *Halophila spinulosa*). Other primary producers identifiable by their isotopic signatures included epiphytes on seagrass, saltmarsh plants, and microphytobenthos. The majority of the carbon in the fish 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 (including parore *Girella tricuspidata*), however, the contribution from mangroves may be up to 50%, and possibly even higher for yellow perchet (*Ambassis jacksonienis*).

In summary, evidence worldwide for the suggested importance of mangrove productivity to estuarine and coastal food webs is equivocal (Lee 1995). Information on nutrient and energy flows between mangroves and other habitats in New Zealand estuaries is very limited but the recent study in Matapouri Estuary, Northland (Alfaro et al. 2006) suggests 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. The macroalga *Hormosira banksii* seems to be an important source of organic material to estuarine foodwebs and is abundant year round among mangrove pneumatophores and seagrass beds, indicating an additional, indirect role for these habitats.

The amount of plant material and nutrients exported is presumably related to the size of trees (and the amount of material produced ha^{-1}) and the duration of tidal inundation. Consequently, high-shore mangroves may be less important as sources than stands of large trees growing along the edges of creeks.

3.3 The intrinsic and unique values of mangroves to the marine environment

Historically, many of the ecological values, physical processes and biological properties commonly associated with tropical and subtropical mangrove forests have been uncritically attributed to New Zealand mangrove stands (e.g., Chapman, 1976b). These include the assumption that mangroves support a high diversity of species, and are critically important to fish and other estuarine or marine organisms for food and habitat. However, given that many aspects of New Zealand mangrove systems have not yet been sufficiently studied, their importance in relation to marine and estuarine species in New Zealand, and their role in terms of ecosystem structure and function, should be carefully questioned before drawing any comparisons with tropical, sub-tropical or other temperate mangrove systems. The role played by mangroves in New Zealand estuarine foodwebs is, however, probably significant and is discussed in detail in section 2.3. Provision of habitat is another important service provided by mangroves, including a sheltered habitat in which larval and post-larval organisms can settle, and protection from predators (Manson et al. 2005). This role discussed in section 2.5.

Mangroves, however, usually represent only one of several types of habitat present in any estuary (though they may often be the dominant one), and the services they provide and the functions they perform are in many cases the same as those provided by other estuarine habitats (Manson et al. 2005).

Manson et al. (2005) have pointed out that mangroves share with estuaries in general the properties of shallow water, reduced wave action, organically-rich sediments, high productivity and protection from predators (because of the shallow depth of water and the presence of structural habitat complexity). It remains to be determined whether mangroves provide these services in a different way to other estuarine habitats, such as saltmarshes, sandflats or seagrasses. Furthermore, the relative importance of mangroves is likely to vary among species using them.

For estuarine management purposes it is important to separate the roles of mangrove from those of other habitats, although this is generally difficult to do. It is also important to note that some species, such as larger fish, only use mangrove areas when they are flooded by the tide. These species cannot, therefore, be completely dependent on mangroves and must use other habitats at least some of the time.

Manson et al. (2005) identified 3 groups of fishes and invertebrates using estuarine habitats, including mangroves. Some are found only occasionally in estuaries and have no dependence on either estuaries or mangroves. Others use estuaries for significant portions of their lives, often as juveniles. They include species whose juveniles are only found in mangroves, and migratory species that use mangroves in passage between freshwater and the sea (for example, barramundi, *Lates calcarifer*, in northern Australia). The degree of dependency on mangroves, as opposed to estuarine habitats in general, varies among species. The third group consists of species that complete their entire life cycle within estuaries and, in the case of fish and invertebrates, these tend to be small, short-lived and make limited or no contribution to fisheries (the focus of Manson et al.'s study). Among the mangrove-associated species, juveniles of some commercially important prawns in Australia are only found in mangroves. Evidence for strong mangrove dependency is weaker for other species, such as barramundi.

There does not appear to be any evidence for mangrove-dependency in any New Zealand species of fish, marine invertebrates or birds (see section 2.5). The terrestrial invertebrate fauna is poorly known and the degree of dependency on mangroves is therefore impossible to determine. Of the terrestrial invertebrates known from New Zealand mangroves, very few are known to feed exclusively on mangroves. However, two species are endemic to and fully dependent upon these habitats: a tortricid moth, the mangrove leafroller, (*Planotortrix avicenniae*: Dugdale 1990) and an eriophyid mite *Aceria avicenniae*, which form galls on the leaves of mangroves (Lamb 1952).

3.4 The role of mangroves as a food source or habitat for other species

3.4.1 Benthic macrofauna

Relatively few studies have been undertaken on the benthic assemblages and species of mangrove forests in New Zealand.

Taylor (1983) visually described the mangrove forests and faunal/floral associations of Whangateau Harbour. This harbour can probably be placed at the more pristine end of harbours in the greater Auckland region. Taylor (1983) found the pneumatophores and trunks to "bear wefts of red and-blue-green algae", and noted that the blue-green algae present were active nitrogen fixers. Living amongst these were isopods and amphipods. The main grazer was a gastropod, the cats-eye *Turbo smaragdus*, consisting of only large individuals in the mangrove forest. These animals were up to 45 mm long, with 90% of individuals over 30 mm. Taylor estimated these animals to be around 25 years 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 ca 12 hr so that it would be possible for periodic recruitment to occur (Ken Grange, NIWA, pers. comm.). Rock oysters (*Crassostrea glomerata*) were found attached to trunks and pneumatophores, and on *Turbo* shells, while barnacles (*Elminius modestus*) were also characteristic of pneumatophores, trunks and leaves. Burrowing animals were rare, apart from the crab *Helice crassa*. The 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*, whose main food items were stated to be crabs and *Amphibola*, and polychaetes.

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). 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 from sedimentation, rather than to the presence/absence of the mangroves themselves.

The benthic community composition at the upper mangrove sites was dominated by corophiid and paracalliopiid amphipod, oligochaetes, the crabs *Halicarcinus whitei* and *Helice crassa*. Sites closest to the intertidal sandflats were differentiated by the limpet *Notoacmea helmsi*, several bivalve species, including the pipi *Paphies australis*, the wedge shell *Macomona liliana*, the cockle *Austrovenus stutchburyi*, and the nutshell *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 adjacent mudflats were dominated by amphipods, *H. crassa* and polychaetes, with 53% of the total abundance consisting of the amphipod *Paracorophium excavatum* (a surface deposit feeder). Intertidal sandflats were dominated by a higher percentage of bivalves, including *M liliana*, *A. stutchburyi* and *N. hartvigiana*. The average number of species per sample was 8.13 in mangroves, 9.1 in tidal mudflats, and 18.1 in intertidal sandflats. This pattern is in agreement with work by Alongi & Christofferson (1992), who documented the influence of out-welled mangrove detritus on macro- and meiofaunal densities in tropical Australia, finding a negative relationship between the percentage of clay and mangrove leaf litter content, and total infaunal density, and a predominance of small, surface-dwelling polychaetes and amphipods. Work by Thrush et al. (2003), along gradients from sand to mud on un-vegetated tidal-flats across a range of northern New Zealand estuaries, found decreases in both benthic species diversity and abundances of individuals with increasing mud content.

Morrisey et al. (2003) investigated the effect of mangrove stand age (young 3–12 years, and old > 60 years) on associated benthic assemblages, at two locations within the Manukau Harbour (West Coast). 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 mangrove stand 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 *H. crassa*, *Hemicyclops* sp, *P. antipodarum*, bivalve spat, *Nicon aesturinus*, *Scolecolepides benhami*, oligochaetes, and *Capitella capitata*. All taxa varied in their abundance at smaller spatial scales (among sites and plots) apart from bivalve spat and *H. 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, fauna on the mangrove plants themselves were not sampled.

Alfaro (2006) sampled six distinct habitats in Matapouri Estuary, east 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 work of Ellis et al. (2004) and Morrisey et al. (2003), no mud-snails (*Amphibola crenata*) or gastropods (*Potamopyrgus antipodarum*) were sampled, being found only in saltmarsh areas of the estuary (outside the study area). *H crassa* was present in very low densities in mangroves, but were 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*.

Information on the benthic invertebrate (prey) fauna in mangrove forests was also collected in the 'fish in mangrove habitats' project (section 2.5.2 and as yet unpublished). This work is part of a larger project quantifying the relationships between small fish assemblages and their prey, across multiple habitats and estuaries. At each of 3 mangrove sites sampled for small fish in each of the Kaipara, Manukau, Rangaunu, and Mahurangi Harbours, 3 sediment cores (13 cm diameter, 15 cm depth) were also collected. Cores were sieved in the field through a 1-mm mesh. The choice of a 1-mm sieve was a pragmatic one, enabling a wider range of locations to be sampled than if a smaller (e.g., 0.5-mm) size had been chosen. This sieve size will have resulted in some under-representation of some smaller fauna, in particular small polychaetes and juveniles of some macrofauna.

For all of the twelve sites, species abundances and diversity were relatively low (Table 3), and fell within the range recorded by Morrisey et al. (2003) and Ellis et al. (2004). The assemblages were largely comprised of the same species as the earlier studies. Small polychaete worms tended to dominate the benthic assemblages, with a few species occurring at higher, albeit quite patchy, abundances (*Heteromastus filiformis*, and *Scoloplos cylindrifer*). With the exception of high abundances of *Potamopyrgus antipodarum* (a small surface-dwelling gastropod) at one site in each of the Kaipara and Manukau Harbours, molluscs and crustaceans were rare. The crab *Helice crassa* occurred at densities ranging from 0.7-5.7 per core at most sites, but was rare in Rangaunu Harbour. Rangaunu Harbour in general is considered to be at the more pristine end of harbour quality in northern New Zealand, with exceptionally clear waters and very extensive seagrass meadows. Despite this, its mangrove invertebrate fauna appeared little different from that of the other three harbours sampled, with species diversity and abundance falling across the same variability range. Mangrove extent in Rangaunu Harbour is estimated to have increased by 33% between 1944 and 1981 (Shaw et al. 1990).

Table 3

Mean numbers of benthic macrofauna per core (by site and harbour: ±SE, n=3) from the 'fish-in-mangroves' project (see section 2.5.2). Mean total abundances and numbers of taxa per core are also shown.

	Kaipara			**Manukau**			**Rangaunu**			**Mahurangi**		
	Site 3	**Site 4**	**Site 5**	**Site 1**	**Site 3**	**Site 5**	**Site 6**	**Site 7**	**Site 10**	**Site 2**	**Site 5**	**Site 6**
Nemertea	–	–	–	–	–	–	–	–	–	0.3 (0.3)	–	–
Sipuncula												
Dendrostomum aeneum	0.3 (0.3)	–	–	–	–	–	–	0.3 (0.3)	–	–	–	–
Polychaeta												
Aglaophamus macroura	–	–	–	–	–	0.3 (0.3)	–	–	0.3 (0.3)	0.3 (0.3)	–	–
Aquilaspio aucklandica	–	–	–	–	–	–	–	0.7 (0.3)	–	3.0 (2.1)	0.7 (0.7)	–
Aricidea sp.	0.3 (0.3)	–	2.3 (2.3)	–	2.0 1.0)	–	–	0.7 (0.3)	0.3 (0.3)	–	–	–
Capitella capitata	–	–	–	1.0 (1.0)	7.7 (6.2)	–	–	–	–	–	–	–
Cirratulid sp.	–	–	–	–	–	–	–	0.7 (0.3)	–	–	–	–
Cossura consimilis	–	–	–	–	–	–	–	0.7 (0.3)	–	–	–	–
Heteromastus filiformis	3.3(1.8)	14.0(7.2)	0.3(0.3)	5.0 (2.3)	7.7 (6.2)	1.0 (0.6)	–	1.0 (1.0)	10.7 (7.3)	37.3 (28.8)	3.3 (0.3)	–
Lumbrinerid sp.	–	–	–	–	–	–	–	1.0 (1.0)	–	–	–	–
Nereid sp.	2.0 (0.6)	0.7 (0.7)	6.3 (4.3)	1.7 (0.9)	2.7(0.9)	2.7 (0.9)	–	10.3 (1.5)	1.3 (0.7)	0.7 (0.7)	0.7 (0.7)	0.3 (0.3)
Notomastus tenuis	–	–	4.3 (4.3)	–	–	–	–	–	3.7 (1.9)	–	–	–
Polychaete sp. 1	–	–	–	0.3 (0.3)	–	–	–	0.7 (0.7)	–	0.3 (0.3)	–	–
Scolecolepides sp.	–	0.3 (0.3)	–	–	–	1.7 (0.3)	–	–	0.7 (0.7)	0.3 (0.3)	–	–
Scoloplos cylindrifer	–	–	–	5.7 (4.2)	1.0 (1.0)	0.7 (0.7)	0.7 (0.7)	1.7 (1.2)	7.3 (3.2)	0.3 (0.3)	7.3 (2.2)	
Spionid sp.	–	–	0.3 (0.3)	–	–	–	–	–	–	–	–	–
Syllid sp.	0.7 (0.3)	–	–	–	–	–	–	–	–	–	–	–
Timarete anchylochaeta	0.3 (0.3)	–	–	–	–	–	–	–	0.3 (0.3)	–	–	–

Table 3 (Cont.)

	Kaipara			**Manukau**			**Rangaunu**			**Mahurangi**		
	Site 3	**Site 4**	**Site 5**	**Site 1**	**Site 3**	**Site 5**	**Site 6**	**Site 7**	**Site 10**	**Site 2**	**Site 5**	**Site 6**
Oligochaeta				–	–	–	–	–	–			
Oligochaete sp.	1.3 (1.3)	1.7 (1.2)	–	3.7 (0.5)	1.2 (0.6)	–	–	5.3 (2.7)	–	–	0.7 (0.7)	–
Mollusca												
Amphibola crenata	–	–	1.3 (0.7)	0.7 (0.7)	0.3 (0.3)	1.0 (1.0)	–	–	–	–	0.7 (0.3)	1.3 (0.7)
Arthritica bifurca	–	0.7 (0.7)	–	–	–	–	–	–	–	–	–	–
Bivalve sp.	–	–	0.3 (0.3)	–	–	–	–	–	–	–	–	–
Eatoniella flamulata	–	–	–	–	–	–	0.3 (0.3)	–	–	–	–	–
Nucula hartvigiana	–	–	–	0.3(0.3)	–	–	–	–	–	–	–	–
Potamopyrgus antipodarum	–	1.3 (0.3)	45 (1.0)	–	–	113.3 (26.8)	–	–	–	–	–	–
Theora lubrica	–	–	0.3 (0.3)	–	–	–	–	–	–	–	–	–
Trochidae sp.	–	–	–	–	1.3 (0.7)	–	–	–	–	–	–	–
Zeacumantus lutulentus	–	–	–	–	–	1.0 (0.6)	–	–	–	–	0.3 (0.3)	–
Nodilittorina antipodum	–	–	–	–	–	–	0.3 (0.3)	–	–	–	–	–
	Kaipara			Manukau			Rangaunu			Mahurangi		
	Site 3	Site 4	Site 5	Site 1	Site 3	Site 5	Site 6	Site 7	Site 10	Site 2	Site 5	Site 6
Crustacea												
Corophium sp.	–	–	0.3 (0.3)	–	–	–	–	–	–	–	1.3 (1.3)	1.0 (1.0)
Gammarid amphipod	–	–	1.7 (1.2)	–	0.3 (0.3)	–	–	–	0.3 (0.3)	–	1.7 (0.3)	–
Paracalliope novaezelandiae	–	–	–	–	–	–	0.3 (0.3)	1.0 (0.6)	–	–	1.3 (0.7)	–
Peramphithoe aorangi	–	–	–	–	–	–	–	–	–	–	–	0.3 (0.3)
Phoxocephalid	–	–	–	0.3 (0.3)	–	–	–	0.7 (0.3)	–	–	–	–
Table 3 (Cont.)	–	–	–	–	–	–	–	2.3 (1.2)	–	–	–	–
.	–	–	–	–	–	–	–	–	–	–	–	0.3 (0.3)
Chamaesipho columna	–	–	–	1.3 (1.3)	–	–	–	–	–	–	–	–

Cirolana woodjonesi	–	0.3 (0.3)	–	0.3 (0.3)	–	–	–	–	–	–	–	–
Juvenile crab sp.	–	0.3 (0.3)	–	–	–	–	–	–	–	–	–	–
Crab megalopa	0.7 (0.3)	–	–	–	–	–	–	–	–	–	–	–
Halicarcinus whitei	–	–	–	–	–	–	0.3 (0.3)	–	–	–	–	–
Helice crassa	2.3 (1.9)	5.7 (1.5)	1.0 (0.6)	2.3 (0.9)	3.7 (0.7)	1.0 (0.0)	0.7 (0.3)	–	–	1.0 (1.0)	1.0 (1.0)	0.7 (0.7)
Insecta												
Chironomid larvae	–	–	–	–	–	–	0.3 (0.3)	–	–	–	–	–
Chironomidae sp.	–	–	–	–	–	–	–	–	–	0.3 (0.3)	–	–
Mean abundance (SE)	16.0 (2.1)	26.3 (9.2)	64.0 (5.0)	27.3 (10.9)	29.0 (11.6)	121.7 (27.2)	8.3 (3.3)	37.0 (3.8)	29.7 (5.7)	44.3 (27.8)	19.0 (4.2)	3.7 (1.7)
Mean no. taxa (SE)	5.7 (0.9)	5.7 (0.3)	7.0 (0.6)	8.0 (2.1)	7.3 (0.9)	5.7 (0.9)	3.7(0.9)	9.3 (0.3)	6.0 (0.6)	4.7 (0.7)	6.3 (0.9)	2.09 (0.6)

Work on temperate *Avicennia* forests in Australia is also relevant. Chapman & Tolhurst (2004), working on an urbanised mangrove forest in Sydney Harbour, New South Wales, attempted to relate bio-dependent properties of the sediments, to the invertebrate assemblages that were present. Taxa that were found in at least 33% of cores included amphipods, insect larvae, oligochaetes, crabs, capitellid, nereid, sabellid and spionid polychaetes, and gastropods. Across three habitats (mangrove patches with and without leaf litter; and mudflats adjacent to or between mangrove patches) the benthos showed relatively little difference among habitats, with higher levels of variation within and among sites in each habitat type. In contrast, bio-dependent properties of sediment (water content, water-soluble fraction of carbohydrates, total carbohydrate, chlorophylls *a* and *b*) showed less variation at small scales, and larger among-habitat variation. For all taxa examined, and the assemblage as a whole, most (50-100%) of the variation among the benthos was at the scale of metres within the different sites in 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 bio-dependent properties at any of the spatial scales. The individual variable most strongly correlated with patterns in the benthos was chlorophyll *a* concentration, but the relationship was not very strong (Spearman rank correlation coefficient= -0.10).

Chapman & Tolhurst (2007) expanded the approach taken in 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, varied across 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.

Gwyther & Fairweather (2002) described the algal and meiofaunal communities found on *Avicennia marina* pneumatophores in the Barwon River, Victoria. Pneumatophores at this site extend up to 20 m from the trunk, with a single tree of 2–3 m height having up to 10,000 pneumatophores (Hogarth 1999). They found 3 categories of assemblage: the barnacle *Elminius modestus*; algae assemblages dominated by the rhodophytes (red algae) *Caloglossa* spp and *Catenella* spp. and the chorophytes (green algae) *Ulva* spp. and *Enteromorpha* spp; or bare pneumatophores (frequent under the mangrove canopy). Each of these assemblages in turn supported a distinctive meiofaunal assemblage. Halacarid mites dominated barnacle–encrusted roots; algal epiphytes supported a more even biota of harpacticoid copepods, nematodes, and halacarid mites; while bare roots were largely devoid of animals except a few mites. The surrounding soft sediments had significantly different invertebrate assemblages, dominated by nematodes.

In summary, the benthic invertebrate fauna of New Zealand's mangroves forests appear to be modest in both abundances and species diversity compared to other estuarine habitats. There is some limited spatial variability in taxonomic composition. For example, Alfaro (2006) working in a small, presumably less-impacted estuarine system (Matapouri Estuary, Northland) did not record mud-snails (*Amphibola crenata*) or gastropods (*Potamopyrgus antipodarum*) from her mangrove sites, and only very low abundances of the crab *H. crassa*, in contrast to most other New Zealand mangrove forests sampled to date. She also recorded an assemblage of the grazing gastropod snails *Turbo smaragdus, Diloma subrostrata*, and *Melagraphia aethiops*, associated with large volumes of drift brown alga (Neptune's necklace, *Hormosira banksii*) trapped in the pneumatophore zone. Taylor (1983), working in Whangateau Harbour (another less impacted system), also found some of these gastropods (*T. smaragdus, D. subrostrata*), along with *Zeacumantus lutulentus*, *Z. subcarinatus*, and the whelk *Cominella glandiformis.* These species were rare or absent from most of the other mangrove systems that have been sampled.

In Australia, a similar finding of lower densities and biodiversity of macro-fauna within these habitats has been attributed to the high proportion of tannins from mangrove detritus and mud associated with mangrove habitats (Alongi & Christofferson 1992, Lee 1999, Alongi et al. 2000). Butler et al. (1977) concluded there was no evidence for a benthic assemblage that was uniquely characteristic of mangroves in South Australia. Even the species that occurred most commonly in mangroves were rare or absent at some sites, and none was found exclusively in mangroves. Data from New Zealand mangroves suggests that the same is true. Differences between assemblages from mangroves and adjacent unvegetated sediments are generally identifiable in ordination plots, for example, but are based on differences in relative abundance of a largely common suite of species rather than differences in species composition (Morrisey et al. 2003, Alfaro 2006).

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 to tropical and sub-tropical 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 systems is *Helice crassa*, which grows to a maximum of around 4 cm carapace length, which is relatively small when compared to tropical species (Alfaro 2006).

3.4.2 Fish

3.4.2.1 Relevant studies from temperate Australia

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/critical juvenile nurseries has also been well established, although debate continues as to exactly how much of total production they contribute relative to other, 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. 1990). Until recently, these findings from sub-tropical and tropical mangroves (high fish abundance and diversity; important nursery role) have been uncritically applied to temperate mangroves, without any associated quantitative investigations or data. However, temperate mangroves systems are often different from tropical systems in many ways, including lower mangrove species diversity (e.g., one species only in New Zealand and 2 in southern Australia), less structural complexity, and smaller species pools of potentially associated organisms. Only a few studies have quantitatively sampled temperate mangrove forest fish assemblages, but those that have reported relatively low species diversity (although fish abundances can be high, dominated by a few species), with few (if any) species heavily dependent on them as nursery habitats. The overseas work most relevant to New Zealand's mangrove systems has been that done on *A. marina* systems in temperate Australia, which have a number of fish species in common with New Zealand (although their estuarine systems are much richer in fish species than those of New Zealand).

Hindell & Jenkins (2004) sampled fish assemblages on the seaward side of mangrove forests and on the adjacent mudflats in Western Port and Corner Inlet, Victoria, using a combination of fyke nets and multi-panel gill nets. They collected 41 fish species, of which 5 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*). A further 6 species were found exclusively in the mudflat habitats – hairy pipefish (*Urocampus carinirostris*) garfish (*Hyporhamphus regularis*), goby (*Mugilogobius paludis*), sand mullet (*Myxus elongates*), yank flat-head/stargazer (*Platycephalus laevigatus*), and ornate cowfish (*Aracana ornate*). However, many of these 'unique' habitat species were represented by only 1 to 3 individuals each. The general fish assemblage was numerically dominated (74% of all individuals) by silver fish (*Leptatherina presbyteroides*), smooth toadfish (*Tetracternos glaber*) and yellow-eyed mullet (*Aldrichetta forsteri*).

Overall fish abundance was always greater in mangroves than mudflats for juveniles, but there was no apparent difference for larger sub-adult and adult fish. Most of the variability was driven by atherinids, mugulids (mullets), gobiids (gobies), tetraodontids (pufferfish), pleuronectids (flatfish) and clupeids (small pelagics). However, there were also strong interactions with respect to where and when mangroves were sampled (they sampled three bays), with mangroves importance being spatially and temporally variable. They suggested that more understanding was needed of how such variability affected the ultimate value of mangrove habitats to fish.

Smith & Hindell (2005) sampled on the seaward side of mangroves, in the pneumatophore zone, and in adjacent subtidal channels during the day and at night sampling in the Barwon River, Victoria. Overall fish abundance, biomass and species richness were generally lower in the forest than the other two habitats, but this varied with time, time of day, and water depth. The general fish assemblage was dominated by only a few species – West Australian salmon (*Arripis truttacea*) and the yellow-eyed mullet *Aldrichetta forsteri*). The channel habitats held the highest fish abundances, biomass and species richness (total species pool of 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) used pop nets (5 x 5 m^2) in and adjacent to mangroves in Port Phillip Bay, Victoria, and collected 15 fish species. Catches in the 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 (half-bridled goby, *Arenigobius frenatus,* and long-fin goby *Favonigobius lateralis*). Fish densities were highest in the forest (1.98 ± 0.36 m^{-2}), 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 fish using pop-nets (3 x 3 m^2) in seagrass, mangrove (*A. marina*), saltmarsh and non-vegetated habitats in the Barker Inlet–Port River estuary, South Australia. Pop-nets were deployed during 2 three-month blocks (winter, summer), with 6 replicates in each time x habitat combination (36 total). Mangrove forests and non-vegetated habitats had more fish (257, 377) and species (7, 14) than saltmarsh (1 fish only sampled), but less than seagrass (15 species, 590 individuals). Mangrove catches were dominated by unidentified atherinid larvae (97 individuals), the atherinid *Atherinosoma microstoma* (114) and yellow-eyed mullet *Aldrichetta forsteri* (34), with four other species also being caught in low numbers – King George whiting *Sillaginodes punctata* (6), the long-fin goby *Favonigobius lateralis* (1), the bluespot goby *Pseudogobius olorum* (3), a clingfish *Heteroclinus* sp. (1), and an unidentified tetraodontid larvae (1). In contrast, the seagrass samples were dominated by the two goby species and King George whiting (71% of individuals).

Mazumber et al. (2005) also used pop-nets (5.5 x 5.5 m^2) to sample small fish in saltmarsh and mangrove habitats, further north in Botany Bay, New South Wales. Forty-eight samples were collected from each of the two habitats, with 16 species collected from saltmarsh at an average total fish density of 0.56 m^{-2}, and 23 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, the dominant species were glass gobies (*Gobiopterus semivestitus*), mangrove gobies (*Mugilogobius paludis*) and glassfish (A*mbassis jacksoniensis*).

Finally, Clynick & Chapman (2002) sampled small mangrove stands around Sydney Harbour (New South Wales) using fyke nets and beach seines. They 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 dominated by this species (>90% of all individuals sampled), with general species diversity being low (17 species sampled).

The general conclusion from these temperate Australian mangrove studies is that, while mangrove habitats do provide habitat for fish, many of the species involved were small-bodied and of little or no commercial value, and were also found in other, alternative habitats. No temperate species appears to be dependent on mangrove habitat. The fish assemblages are numerically dominated by only a few species, and overall species diversity is relatively low.

3.4.2.2 Fish assemblages of New Zealand mangrove forests

Many of the species and families of fish sampled in the Australian studies do not occur in New Zealand. Exceptions are yellow-eyed mullet, usually one of the dominant species sampled in Australian *A. marina* forests, and grey mullet (*Mugil cephalus*), parore/luderick (*Girella tricuspidata*), short-finned eels (*Anguilla australis*) and kahawai/Australian salmon (*Arripis trutta*), which are found in mangroves in low abundances (with the exception of kahawai in the Barwon River – Smith & Hindell 2005). Bell et al. (1984) also recorded relatively high numbers of juvenile parore in a temperate mangrove-lined tidal creek in Botany Bay, New South Wales.

In contrast to temperate Australia, fish assemblages in New Zealand's mangrove forests have had little (or no) directed quantitative research undertaken on them until recently. Despite this knowledge gap, it is a widely and frequently quoted paradigm that New Zealand's mangrove forests provide an important nursery role for fish, and that such habitat may be critical for sustaining coastal fisheries production for many species. This paradigm was uncritically transferred from mangrove research in tropical systems but recent research in Australian temperate mangroves has shown that it does not appear to apply to more temperate zones. In New Zealand, it is often stated/quoted that more than 30 fish species utilise mangrove forests at some point in their life-cycle. This value can probably be attributed to Mason & Ritchie (1979), who sampled assemblage of larger-sized fish in Whangarei Harbour, Northland using gillnets. They concluded that mangrove/mudflat habitats, in comparison with other habitats in the harbour, were characterised by higher overall utilisation by fish, had the highest abundance of commercially important fish (especially snapper, mullet, kahawai, yellow-belly flounder and jack mackerel), and that these habitats were used by more species than all other habitats. Their overall conclusion was that many of the northern inshore fisheries had either a complete, or very high, dependence on the mangrove/mudflat habitat. Following on from this, Crisp et al. (1990) generated a summary table which listed more than 30 fish species, both those found in mangroves, and those thought to use the mangroves as part of the larger mosaic of estuarine habitats available.

Since Crisp et al.'s (1990) table was published, the value of more than 30 species has often been quoted uncritically as the number of New Zealand fish species *dependent* on mangrove forests during some stage in their life-cycle. Perhaps this is not surprising, as the table's caption heading is "Table 2: Fish of New Zealand Mangals". However, in the actual table, the column headings are "Species" "Utilisation of estuarine habitats, *including mangals*" and "Commercial Importance" (our emphasis). This table actually lists fish species found in estuaries in general, rather than specifically in mangroves. In addition, while individuals of a given fish species may be seen/caught in a mangrove forest this does not necessarily mean that mangrove habitats are important to that species. Such observations need to be placed in the broader context of what other habitats the species also utilises, and whether such individuals are part of a larger mangrove–associated population, or simply occasional 'stragglers' from other habitats where their numbers are much higher. In the 17 years since Crisp et al.'s table was published, a large amount of new information has been generated on use of habitats by fish in estuarine and coastal ecosystems. That information is discussed in the following sections, and used to update Crisp et al.'s table.

The most relevant recent work is a study that quantified the small fish assemblages of eight estuarine mangrove systems, collectively encompassing different coasts and gradients of latitude and system 'pristineness' (Morrison et al, in prep). Eight estuaries were selected, two on the west coast (Kaipara and Manukau Harbours), and six on the east coast (Rangaunu, Mangawhai, Mahurangi, Waitemata, Whangapoua, and Tauranga), and sampled during February–March 2005. This time of year is when abundances and species diversity of small fish are highest in the intertidal estuarine habitats of northern New Zealand. Within each system, 6 sites were selected along environmental gradients running from the lowest seaward extent of the forest, up to the highest reaches navigable by a small boat. Two separate mangrove channel gradients were sampled in Rangaunu Harbour (i.e., 12 sites), because this estuarine system is thought to be one of the most pristine remaining in Northland. Fine-mesh fyke nets (9 mm, coarse braid) were used to sample the small fish leaving the mangrove forests as the tide fell, with these nets set flush with the forest edge just before daylight high tides. Once the fyke was exposed, the fish catch was removed through a draw-string at the end, and the net left to fish overnight through another tidal cycle. These two catches (high-to-low day, and high-to-low night) were combined, to give an overall sample of the number of fish leaving per 14.5 m of forest edge tidally over a 24-hour period. The daytime fish were also preserved in 10% formalin for subsequent gut-content analysis. The night-time fish were not used for gut analysis because these fish remained in the nets for ~10–12 hours overnight, without preservation.

Once the mangrove forest area adjacent to the fyke net drained of water, a 10 x 10 m block was measured out, and within this measures were made of forest architecture (seedling/sapling/tree densities; tree height and diameter at first branching, and height; and the width of the pneumatophore zone). The physical environment was also assessed, including the distance to the nearest subtidal channel, total organic carbon of the sediment, sediment grain size, total suspended sediments, water clarity, and water depth (measured at high tide). The spatial coordinates of the site were read from a hand-held GPS, and used in conjunction with Land Information New Zealand (LINZ) digital coastline data and mangrove forest cover to generate a distance variable representing the site's position along a estuarine gradient, from the lowest seaward local limit of the mangrove forest (0), though to the uppermost limit (~100). During analysis, various multivariate methods were employed to relate the fish assemblage and species catches to the associated environmental measures.

The eight estuaries were found to vary widely in the characteristics of their mangrove zones, with a strong division between the west and east coasts. The west coast sites were generally characterised by larger, more complex mangrove trees (in terms of height, diameter, and height of first branching), within an environment of high suspended-sediment loads, correspondingly lower water clarities, high organic carbon in the sediments, and smaller mean sediment grain sizes. East coast sites that also displayed these characteristics were found in the upper reaches of the Waitemata, Mahurangi and Rangaunu Harbours. However, most of the east coast stations had smaller, less complex mangrove trees, with higher water clarities and larger mean sediment grain sizes. Within a given estuary, there was also some site separation related to where sites fell relative to their position along the lower to upper mangrove forest axis. Sites further up the axis were usually characterised by higher tree densities, with smaller tree heights and trunk diameters, reduced water depths, and shorter distances to the adjacent subtidal channels.

Fifty-three stations were sampled for their small fish assemblages across the eight estuaries, with one station (Tauranga Harbour) lost due to human interference with the net. Six sites could not be retrieved during the first day due to access difficulties, and so catches are an aggregate of the day and night period. Overall, 17,327 fish representing 19 species were sampled (Table 4). Eighty-eight percent of all individuals were small semi-pelagic schooling species (mullets, pilchards, and smelt), and 98% of all individuals were juveniles (Figure 3). Four species dominated the catch; yellow-eyed mullet (*Aldrichetta forsteri*), grey mullet (*Mugil cephalus*), estuarine triplefin (*Grahamina nigripenne*), and the pilchard (*Sardinops neopilchardus*) comprised 92% of all fish sampled. Most of the remaining species were demersals, including short-finned eel (*Anguilla australis*), parore (*Girella tricuspidata*), sand flounder (*Rhombosolea plebeia*), and yellowbelly flounder (*Rhombosolea leporina*). Only occasional individuals of the remaining nine species were caught, including 2 commercial species (snapper, *Pagrus auratus*, and kahawai, *Arripis trutta*), and the introduced bridled goby (*Arenigobius bifrenatus* – Mahurangi Harbour only) (Table 4). Comparison of the day and night components of the catches (available for 47 stations) showed variable catches but most grey mullet and all but one of the short-finned eels were caught overnight.

The average number of fish caught per site varied across the eight estuaries from 121 (± 25 SE) to 751 (± 305) individuals (day and night combined). The highest numbers occurred in the Manukau Harbour (dominated by grey mullet), followed by the Mahurangi, Waitemata, Whangapoua, and Tauranga Harbours (dominated by yellow-eyed mullet) (Figure 3). While there was a significant overall estuary effect on fish abundances (shown by ANOVA analyses), there was high variability within individual estuaries, and only Kaipara and Rangaunu (second gradient) had significantly different total fish abundances from each other (Figure 4). Mean species richness per estuary ranged from 4.7 (± 0.33) to 8.3 (± 0.8) (Figure 4), and was significantly different among estuaries, with the Mahurangi estuary having higher mean species richness than the Kaipara, Mangawhai, Whangapoua and Tauranga harbours (Figure 4). At the individual species level, there was large-scale patchiness for several species; e.g., 99% of all pilchard individuals came from just one site in each of Mangawhai and Mahurangi Harbours, and 73% of anchovies (*Engraulis engraulis*) from one site in the Manukau. Abundance comparisons across individual species found significant differences among some estuaries for yellow-eyed and grey mullet, estuarine triplefin, sand flounder, parore and yellow-belly flounder (Figure 4), but there was no consistent pattern across estuaries among the different species.

Table 4

Average fyke net catch summaries by harbour and species. Abundances are expressed as average numbers of individuals (SE) per 14.5 m net set (day and night catch combined). Group; P, semi-pelagic; D, demersal.

Common name	Scientific name	Code	Group	Kaipara		Manukau		Rangaunu		Mangawhai		Mahurangi		Waitemata		Whangapoua		Tauranga	
Yellow-eyed mullet	**Aldrichetta forsteri**	YEM	P	84.8	(28.8)	234.5	(104.8)	55.1	(17.4)	112.5	(47.4)	340.6	(100.0)	482.7	(193.2)	342.1	(92.3)	183.4	(53.2)
Grey mullet	**Mugil cephalus**	GMU	P	24.2	(18.0)	473.1	(298.7)	1.6	(1.3)	–	–	0.3	(0.2)	0.2	(0.1)	0.5	(0.5)	0.6	(0.4)
Estuarine triplefin	**Grahamina nigripenne**	GNI	B	0.3	(0.2)	2.5	(2.1)	40.9	(11.2)	2.3	(1.2)	92.5	(50.4)	4.8	(2.2)	1.8	(1.0)	0.2	(0.2)
Pilchard	**Sardinops neopilchardus**	PIL	P	–	(0.0)	1.5	(1.3)	–	–	58.5	(58.5)	47.0	(47.0)	–	–	–	–	–	–
Smelt	**Retropinna retropinna**	SME	P	0.3	(0.3)	17.7	(6.5)	10.9	(7.0)	–	–	12.0	(3.9)	2.3	(1.6)	–	(0.0)	12.2	(9.2)
Short-finned eel	**Anguilla australis**	SFE	B	10.5	(2.5)	2.8	(1.0)	5.0	(3.3)	5.3	(3.9)	7.2	(2.2)	3.5	(1.5)	4.5	(1.4)	6.8	(2.7)
Anchovy	**Engraulis australis**	ANC	P	24.8	(24.0)	0.3	(0.3)	1.5	(1.2)	0.5	(0.5)	2.0	(0.9)	0.5	(0.5)	1.0	(1.0)	–	–
Sand flounder	**Rhombosolea plebeia**	SFL	B	1.2	(0.8)	4.7	(3.2)	1.7	(0.5)	0.3	(0.2)	14.7	(9.0)	1.0	(0.6)	0.7	(0.4)	0.4	(0.4)
Parore	**Girella tricuspidata**	PAR	B	–	–	0.7	(0.6)	1.3	(0.5)	2.3	(0.9)	1.8	(0.9)	0.2	(0.1)	11.7	(8.7)	0.4	(0.2)
Yellow-belly flounder	**Rhombosolea leporina**	YBF	B	1.5	(0.5)	9.0	(5.0)	–	–	0.2	(0.1)	3.2	(1.5)	3.2	(1.3)	0.8	(0.4)	0.2	(0.2)
Exquisite goby	**Favonigobius exquisitus**	FAE	B	1.2	(0.8)	0.7	(0.4)	2.8	(0.7)	1.0	(0.5)	1.7	(1.0)	0.8	(0.4)	0.2	(0.1)	–	–
Mottled triplefin	**Grahamina capito**	GCA	B	–	–	3.2	(3.1)	–	–	0.2	(0.1)	1.0	(0.8)	–	–	0.3	(0.3)	0.2	(0.2)
Bridled goby	**Arenigobius bifrenatus**	ARB	B	–	–	–	–	–	–	–	–	1.3	(0.9)	–	–	–	–	–	–
Garfish	**Hyporhamphus ihi**	GAR	P	0.5	(0.5)	–	–	0.2	(0.1)	–	–	0.2	(0.2)	–	–	–	–	–	–
Sprat	**Sprattus sprattus**	SPR	P	–	–	–	–	0.2	(0.2)	–	–	–	–	–	–	–	–	0.4	(0.4)

Table 4 (Cont.)

Common name	**Scientific name**	**Code**	**Group**	**Kaipara**		**Manukau**		**Rangaunu**		**Mangawhai**		**Mahurangi**		**Waitemata**		**Whangapoua**		**Tauranga**	
Jack mackerel	**Trachurus novaezelandiae**	JMN	P	–	–	–	–	0.2	(0.1)	–	–	–	–	–	–	0.2	(0.1)	–	–
Snapper	**Pagrus auratus**	SNA	B	–	–	–	–	0.2	(0.1)	–	–	0.2	(0.1)	–	–	–	–	–	–
Spotty	**Notolabrus celidotus**	STY	B	–	–	–	–	0.2	(0.1)	–	–	–	–	–	–	–	–	–	–
Kahawai	**Arripis trutta**	KAH	P	–	–	–	–	–	–	–	–	–	–	–	–	0.2	(0.1)	–	–
Total species				9		11		13		9		14		9		11		9	

Figure 3
Length frequencies of the 10 most abundant species sampled. Dotted vertical lines denote length at maturity where known (taken from a range of primary sources cited in Hurst et al. 2000). Black shading denotes night-caught fish; white, day-caught fish, grey, samples could not be retrieved during the first day of sampling.

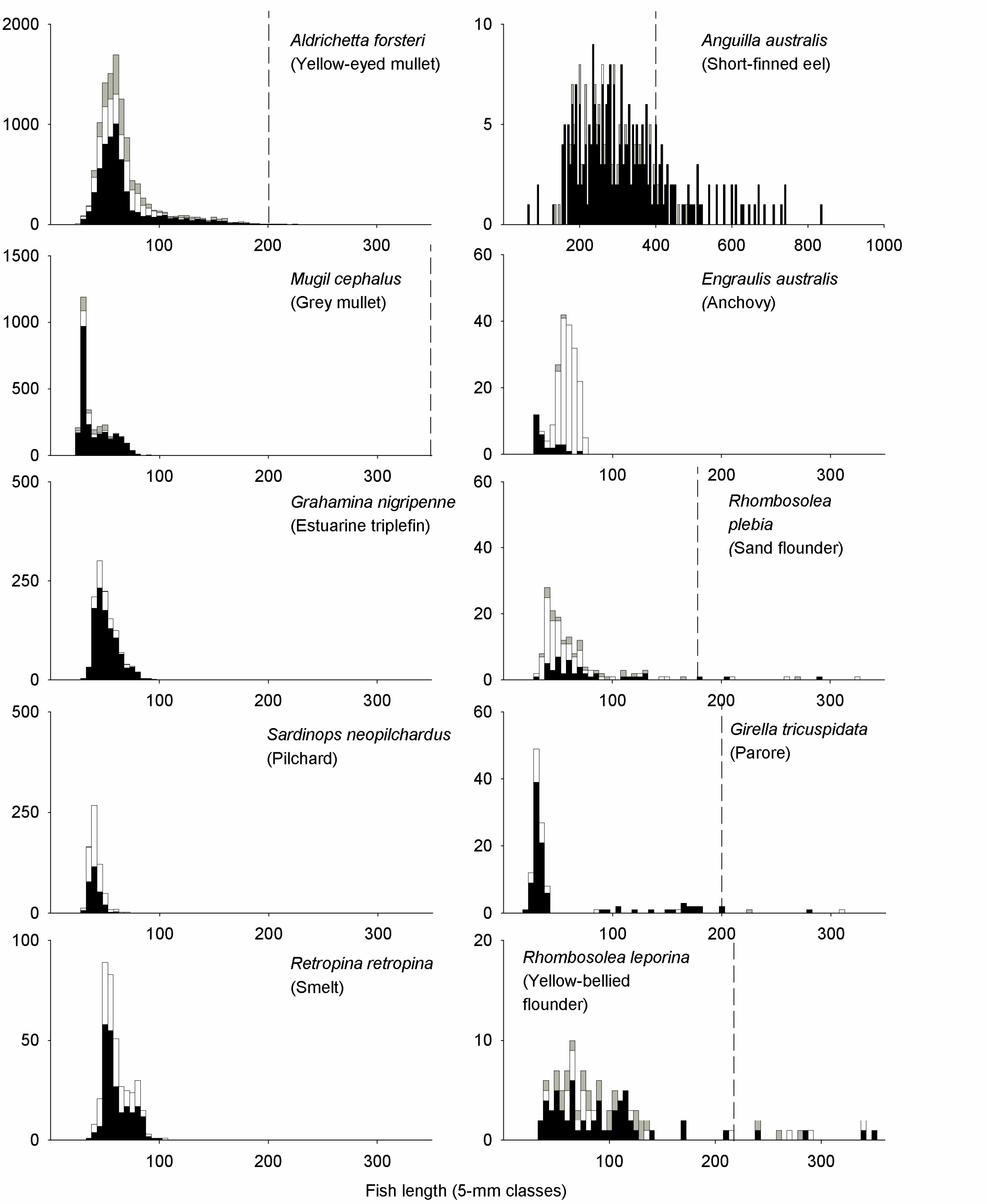
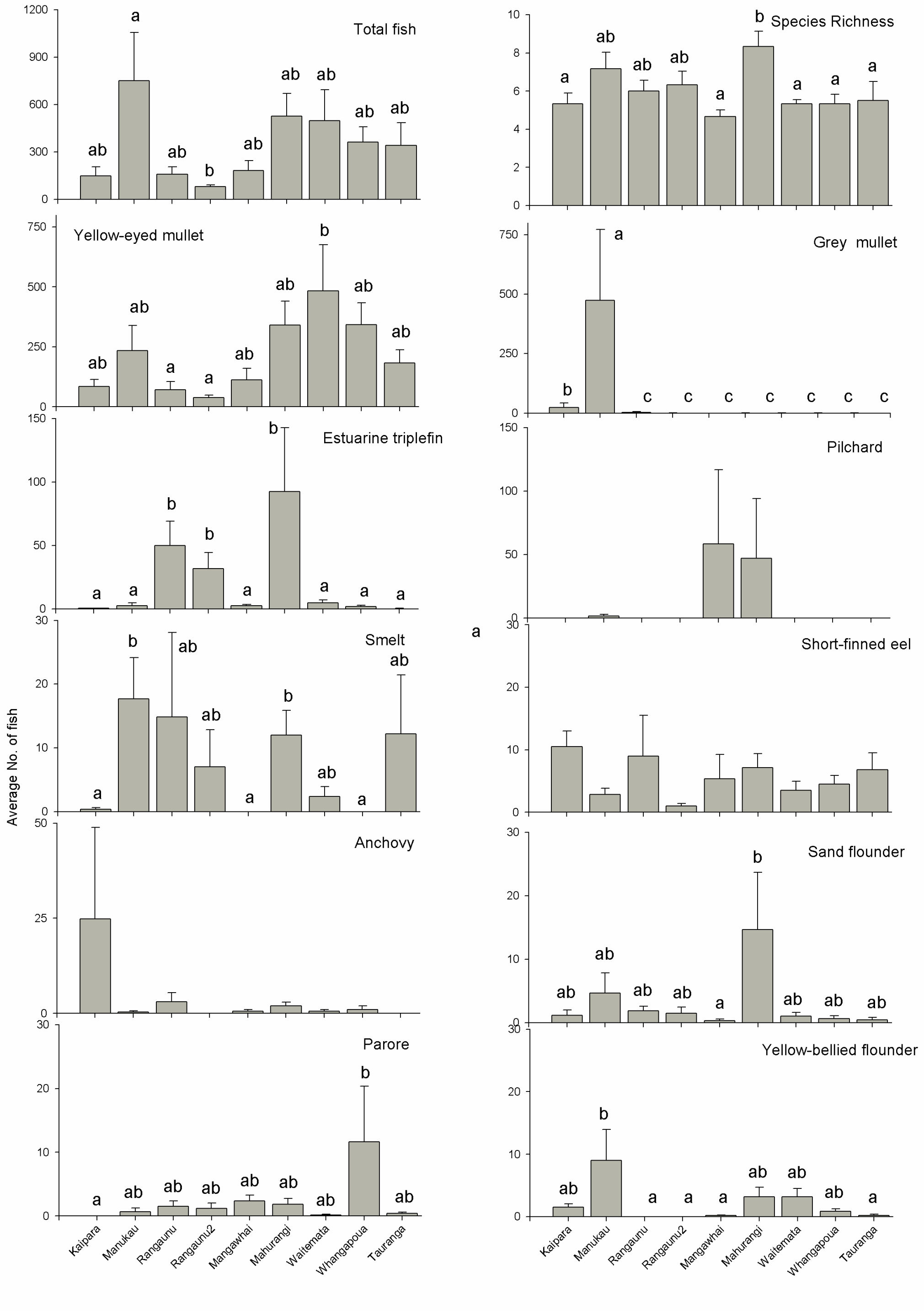


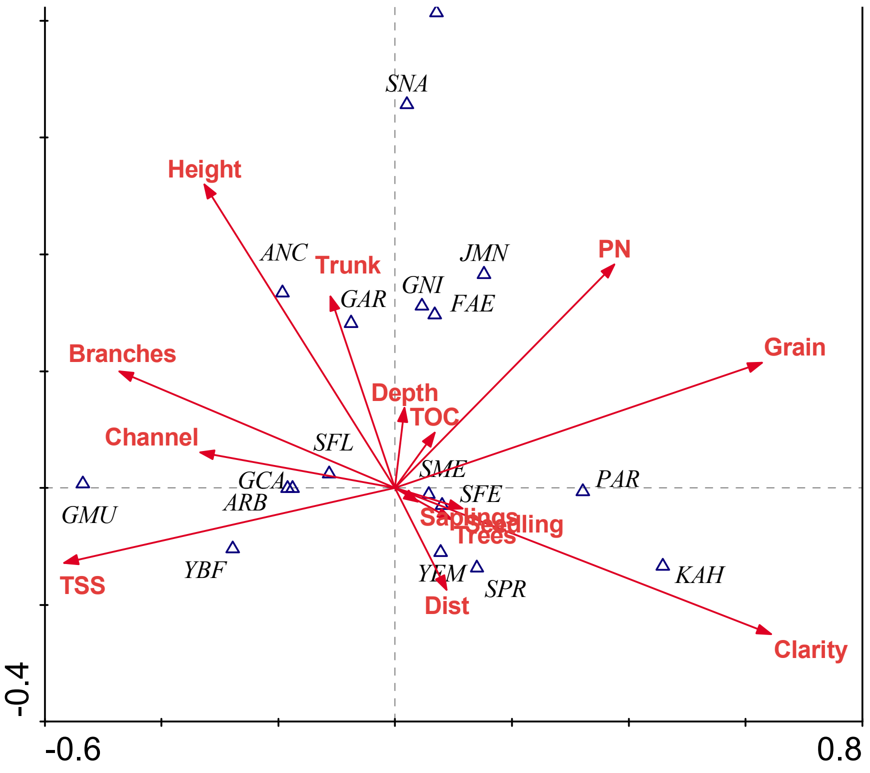
Figure 4
Mean abundance, species richness, and individual species abundances for the eight estuaries sampled. Bars with the same letter are not statistically significantly different.



A multivariate comparison (ANOSIM: Clarke 1993) found a significant difference in fish assemblages at the spatial level scale of west versus east coast estuaries, and also among individual estuaries, with the exception of Whangapoua vs Waitemata, and Whangapoua vs Mangawhai estuaries. At the coast scale, most of the dissimilarity was generated by differences in the three numerically-dominant species; grey mullet, estuarine triplefin, and yellow-eyed mullet. These species also contributed much of the dissimilarity among individual estuaries. Overall, mangrove fish assemblage differences between coasts and among estuaries were driven more by large variations in the relative abundance of a few species, than by differences in the species pool present. There was no evidence of estuaries perceived to be more pristine (Rangaunu, Whangapoua) having markedly different fish assemblages to those of more impacted estuaries.

Individual species varied in their response to the forest and physical environmental parameters measured (Figure 5). Grey mullet and yellow-belly flounder were strongly positively associated with higher total suspended sediments (TSS in Figure 5), while yellow-eyed mullet were positively associated with increasing distance from the sea. Short-finned eels were positively associated with increasing mangrove habitat complexity (seedlings, saplings, and number of trees), while parore were associated with higher water clarities and intermediate sediment grain sizes. Estuarine triplefin showed no obvious responses to any of the variables measured. Of the remaining species, too few individuals were sampled to infer associations with environmental conditions. In general, plant architecture in the vicinity of the nets did not appear to play a significant role in structuring fish assemblages, although it is important to note that these characteristics were quantified along and immediately inside the forest edge, while the fish sampled by the fyke nets came from the full extent of the mangrove forest.

Figure 5
Canonical correspondence analysis (CCA) of the fish assemblage composition across the 8 estuaries sampled in relation to changing mangrove and environmental conditions. The plot represents the relationships between measured environmental variables and the distribution of individual fish species. Fish species identifiers as per Table 4. Habitat variables are total suspended sediments (TSS), distance to channel (channel), height of first branch (branches), tree height (height), trunk girth (trunk), water depth at mangrove edge (depth), total organic carbon (TOC), width of pneumatophore zone (PN), sediment grain size (grain), sapling, seedling, and tree density (sapling, seedling, trees), water clarity (clarity), and distance along the mangrove gradient (dist).



These findings show that the temperate mangrove forests of northern New Zealand support high abundances of small fishes, but that species diversity is low compared to other estuarine habitats (*sensu* Morrison et al. 2002, Francis et al. 2005, Morrison & Carbines 2006), with most of the small fish assemblage dominated by juveniles of the ubiquitous yellow-eyed mullet, as well as juvenile grey mullet in the west coast estuaries. This general pattern of relatively low species diversity, and a numerical dominance by only a few species, agrees with the findings discussed previously from temperate *Avicennia marina* forests in Australia (Clynick & Chapman 2002, Hindell & Jenkins 2005, Smith & Hindell 2005). The majority of the species associated with New Zealand mangroves were semi-pelagic and/or relatively mobile, given the daily migrations needed to transit over the tidal flats from the low-tide channels to the half-tide level mangroves. The only real exception to this was the estuarine triplefin, found in large numbers in Rangaunu and Mahurangi Harbour, which is capable of moving up to several hundred metres across intertidal flats (Morrison et al. 2002). Short-finned eels were caught throughout all the mangrove forests sampled, and were positively associated with the presence of three-dimensional bottom structure (seedlings, saplings, tree trunks), the only fish species to show such associations. This species is rarely caught in estuarine beach seine samples (Francis et al. 2005), and may remain in mangrove habitats during low tide periods through the use of shallow pools, rivulets, and burrows. One medium-sized individual was observed in an intertidal burrow in the Waitemata Harbour 100 m from the subtidal. Very small grey mullet (<50 mm) may also adopt similar behaviours, having been observed sheltering in small cascade-pools (with associated plant detritus), draining relatively steep mangrove mud-banks. However, most fish species and individuals are probably forced by the tides to leave the mangrove forests and move distances of 10s to 100s of metres to adjacent low tide channels.

A number of dominant northern New Zealand species of small estuarine fish (Morrison et al. 2002, Francis et al. 2005) were seldom or never sampled from mangrove habitats, including speckled sole (*Peltorhamphus latus*), exquisite goby (*Favinogobius exquistitus*), and sand goby *Favinogobius lentigosus* (a species restricted to the east coast). Speckled sole move only partially up tidal flats when the tide is high, regardless of the presence/absence of mangroves or other fringing vegetation (Morrison et al. 2002). The other species range up to the high tide mark on sand and/or mudflats, and it is likely that these species actively chose not to utilise mangrove habitats in any substantial way. While pilchards and anchovies were sampled in the mangrove forests, they were found in high abundances at only a few sampling stations. These species are known to occur as large, abundant schools in open-water estuarine habitats (Morrison et al. 2002), and those caught in the mangroves are probably just the inner depth fringe of such populations.

With the exception of grey mullet and short-finned eels, no commercial species were common in the mangrove habitats. Sand and yellow-belly flounder were caught at most sites, but in low numbers relative to their high and widespread abundance over bare mud and sand habitats in the wider estuarine environment (Morrison et al. 2002, Francis et al. 2005). The most conspicuously absent commercial species was the sparid *Pagrus auratus* (snapper), which utilises northern New Zealand estuaries and sheltered coastal embayments as nursery grounds. Estimated densities of 0+ snapper in subtidal habitats range from 2,700–8,400 fish per km^2, often associated with the presence of horse mussels (Morrison & Carbines 2006, authors unpublished data), while in the extreme low intertidal/upper subtidal, there are also strong associations with seagrass meadows, with densities in the thousands, with extremes of 5 x 10^6 per km^2 (note that such habitats usually exist only at the 100s of metres scale) (Schwarz et al. 2006, Morrison et al., unpublished data). In the current study, only three snapper were sampled from mangroves; one adult in the Mahurangi Harbour, and two juveniles in Rangaunu Harbour. However, there may be temporal and other effects not encompassed by this study. Gear trials in Rangaunu Harbour in early February 2005 collected 10 juvenile snapper and a number of spotties (*Notolabrus celidotus*) from 4 trial fyke sets, at outer mangrove sites where the seagrass meadows directly abutted onto the mangrove forest edge. Such co-occurrence of seagrass and mangrove habitats only occurs in more pristine northern New Zealand estuaries. There may be important habitat landscape connectivities at work in such situations.

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 seagrass beds, relative to seagrass beds without adjacent mangroves, while Skilleter et al. (2005) demonstrated similar patterns for two prawn species. Jelbart et al. (1997), working in the temperate Pittwater Estuary, just north of Sydney, New South Wales; sampled 3 seagrass (*Zostera capricorni*) beds close to mangroves (*A. marina*) (<200 m), and three seagrass beds further away (> 500 m). They found seagrass beds closer to mangroves to have greater fish densities and diversities than beds further away, 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 *Rhabdosargus sarba* (sparid), and hairy pipefish *Urocampus carinirostris*. A negative relationship was found between the density of (high-tide) mangrove-utilising fish species found in seagrass beds (low tide), and the distance of the seagrass bed from mangroves. This showed important daily connectivity through tidal movements between mangrove and seagrass habitats. Such habitat connectivities are probably present in New Zealand estuaries, and are also likely to be highly sensitive to habitat change/loss through human-mediated disturbance. Currently we have no information on where and when they might operate, and for what species/assemblages. However, they are likely to be restricted to less degraded environments, which still maintain a wider mosaic of interconnected habitats.

3.4.2.3 Are New Zealand's mangroves important as juvenile fish nurseries?

The issue of whether New Zealand's temperate mangrove forests are important/critical nursery habitats is best addressed through the framework proposed by Beck et al. (2001), where for a habitat to be defined as a nursery habitat (NH), it must be demonstrated that the habitat's contribution per unit area is greater than the average contribution per unit area for all habitats. This definition was further refined by Dahlgren et al. (2006), who allowed for habitats where the average contribution per unit area was low but, because of their large total area they still contributed the majority of the adult population's recruitment (Effective Juvenile Habitat, EJH). To effectively apply these definitions requires either standardised sampling across a range of habitats for which the areal extent is known (NH), or a suitable natural marker (e.g., otolith microchemistry) to identify relative contributions of different habitats to adult population/s (EJH).

Our knowledge of New Zealand's estuarine and coastal fish habitats is not yet sufficiently advanced (nor, we would argue, is that of any other temperate region) to undertake such formal, quantitative meta-analysis across all habitats and systems within a species range. However, sufficient knowledge exists to assess the relative value of mangroves within the context of estuaries. Of the species we sampled from mangrove forests, only short-finned eels, parore and grey mullet occurred in sufficiently high and/or widespread abundances to distinguish mangroves from other estuarine habitats (c.f. Morrison et al. 2002, Francis et al. 2005, Schwarz et al. 2006).

Short-finned eels (*Anguilla australis*) have not been found in abundance in other estuarine or coastal habitats, being a rare component in beach seine samples (Francis et al. 2005), and occasionally observed at low densities over estuarine and coastal seagrass meadows at night (Schwarz et al. 2006). This species primarily occurs in streams, rivers, and lakes (Glova et al. 1998, 2001), where stocks are over-fished (some fishing also occurs around mangroves). The relatively high and consistent catch rates of eels per 14.5 m fyke-net set in this study (5.6 ± 1.0 SE) suggests that mangroves may support a significant number of juveniles given the large extent of northern mangrove forests. Similarly, parore (*Girella tricuspidata*) densities, while lower than those of short-finned eels, and effectively confined to east coast mangroves, were consistent across most estuaries. Juveniles of this species are associated with three-dimensional estuarine habitats, notably beds of seagrass (*Zostera* sp.) and Neptune's necklace (*Hormosira banksii*), brown kelp (*Carpophyllum maschalocarpum*) forests, and man-made structures such as pontoons (Bell et al. 1984, Morrison 1990, Francis et al. 2005, Morrison et al. unpublished data). Individuals use different habitats as they grow, eventually joining adult populations on open coasts (Morrison 1990). However, use of these habitats is spatially patchy and inconsistent, and not all such habitats consistently support high juvenile abundances. Adults are associated with coastal reefs (Anderson & Miller 2004), but also occur in estuaries and over coastal soft-sediments (Morrison & Carbines 2006). Adults are uncommon on the west coast. Based on the consistent and widespread numbers of short-finned eels and parore in mangroves, and their low abundance in many alternative habitats, we suggest that mangroves can probably be viewed as effective juvenile habitat (EJH) for these two species.

Juvenile grey mullet (*Mugil cephalus*), in contrast to parore, were sampled in relatively high numbers from Manukau Harbour, and to a lesser extent, Kaipara Harbour mangroves, but not from east coast estuaries. This species supports important commercial fisheries in west coast estuaries (Ministry of Fisheries 2006, Paulin & Paul 2006). Abundances of juvenile grey mullet in mangrove forests were substantially higher than for any other estuarine habitats surveyed, including intertidal/subtidal seagrass meadows, sand and mudflats, and subtidal channels (Morrison et al. 2002, Francis et al. 2005, Morrison & Carbines 2006, authors unpublished data). Additionally, most fish sampled outside mangroves were larger, older juveniles (50–150 mm length, 1–2 years old), suggesting a possible ontogenetic habitat shift from higher- to lower-complexity estuarine habitats. We suggest that mangroves on the west coast can probably be classified as nursery habitats (NH) for this species. Overall, this would result in New Zealand's temperate mangroves being considered NH or EJH for three fish species, two of which are of commercial value.

Based on this new knowledge, we have modified and updated Crisp et al's (1990) Table 2 ("Fish of New Zealand Mangals") (Table 5). We have expanded its scope slightly to include estuarine fish in general, because Crisp et al's (1990) table was really a listing of species found in estuarine systems, rather than just those of mangroves habitats. Also included is some new information on diet for some species. Based on this summary, 19 species are 'confirmed' from mangroves, of which three species are probably partially reliant on them as juvenile nurseries. Although the other species listed in the table are also likely to be seen in and around mangrove habitats occasionally, mangroves are very unlikely to be more than a marginal habitat for them relative to other estuarine (and coastal) habitats.

Table 5

Summary of fish usage of New Zealand mangroves and other estuarine habitats (broadly adapted from Crisp et al. (1990). Note that many of these species also utilise more coastal habitats, both as juveniles and/or adults. The table shows whether each species has been sampled in mangrove forests and its relative abundance (abundant, common, present, rare), whether mangroves are considered to be differentially important as a juvenile nursery habitat (bold type denotes a nursery role), how it uses mangroves and general estuarine habitats, and dietary patterns where known (based on a number of collections of estuarine fish, including those from the mangrove study detailed in this report).

Species	Present in mangroves? Mangroves differentially important?	Differential mangrove habitat use? General estuarine habitat usage	Commercially valuable?	Dietary patterns
Species sampled from mangroves				
Yellow-eyed mullet (Aldrichetta forsteri)	Abundant / No	Juveniles (<250 mm) found across most estuarine habitats including mangroves, except clear, deeper water areas close to estuary entrances. Thought to recruit into estuaries from coastal spawning as nekton (surface-associated post-larval fish). Juveniles and sub-adult extremely abundant in estuaries, but adults less so – thought to migrate to sea and spawn outside estuaries.	Limited	Juvenile (30–90mm) diet is mainly zooplankton, especially the harpacticoid copepod *Euterpina acutifrons* and calanoid copepod *Corycaeus aucklandicus,* plus barnacle cyprids, mysids, plant material and detritus. Larger individuals (90–130mm) feed predominantly on detritus and algae.
Grey mullet (Mugil cephalus)	Abundant / Yes (West Coast)	High juvenile (20–40 mm length) association with west-coast mangroves. Lower abundances of same size class also found in association with intertidal seagrass meadows – west coast only. Larger juveniles (50–150 mm) commonly sampled in shallow subtidal areas away from mangroves. Most of commercial fishery is on west coast. Juvenile abundances largely coincide with estuarine mangrove distribution. Adults are wide ranging, but commonly caught around mangroves, and have been observed inside mangrove forests. Strong use of estuarine systems, also found in coastal surf zones. Known to move between west coast estuaries as adults (tagging studies).	High, fully exploited stocks	Mainly detrital feeders. There appears to be some inter-harbour diet variability, with juveniles (25–30mm) in the Kaipara Harbour consuming high numbers of the copepod *Euterpina acutifrons*.

Table 5 (Cont.)

Estuarine triplefin (Grahamina nigripenne)	Patchily abundant / No	Patchily abundant in some mangrove forests, and associated shallow channels. Widespread in estuarine systems, usually associated with seafloor habitat structure. Also often found in high abundances in subtidal seagrass areas.	None	Feeds mainly on small amphipods *(e.g., Paracalliope novaezelandiae*) and crabs (*Helice crassa, Halicarcinus whitei)*. In mangrove forests diet also includes isopods and midge larvae (Chironomidae sp.).
Pilchard (Sardinops neopilchardus)	Patchily abundant / No	One large catch in recent mangrove study. Probably only extends into mangroves on the fringes of its main distribution in more open estuarine waters Often encountered in open water habitats of west coast harbours.	Limited, adults targeted as bait fishery in coastal waters	
Smelt (Retropinna retropinna)	Common / No	Consistently found in mangrove habitats at small abundances. Common in freshwater systems, and in very high numbers in upper estuarine habitats (and estuaries) dominated by high freshwater inputs. Includes more southern estuaries without mangroves.	No Traditionally important species	Planktivorous. Predominantly consumes the harpacticoid copepod *Euterpina acutifrons.* Also feeds on midges.
Short-finned eel (Anguilla australis)	Common / Yes (West and East coasts)	Juveniles and sub-adults common in more structurally complex mangrove habitats. Only encountered during night sampling. Rarely sampled in other estuarine habitats, and usually in highly turbid, muddy areas. Also seen at night foraging for crabs over shallow seagrass meadows	Yes, fully exploited fisheries. Some fishing of mangrove habitats	Feeds mainly on crustaceans such as the crab *Helice crassa*, and shrimp *Palaemon affinis,* along with some amphipod species. Larger eels (>350mm) also feed on small fish e.g., the exquisite goby *Favonigobius exquisitus*.
Anchovy (Engraulis australis)	Patchily abundant / No	One large catch in recent mangrove study. Probably extends into mangroves on the fringes of its main distribution in more open estuarine waters. Juveniles very common on adjacent tidal mudflats and near the water surface in subtidal areas. Probably moves to coastal waters as approaches adult size.	No	Planktivorous. Feeds mostly on calanoid copepods (e.g., *Paracalanus indicus*) and the harpacticoid copepod *Euterpina acutifrons*.

Table 5 (Cont.)

Sand flounder (Rhombosolea plebeia)	Common / No	Found as both juveniles and sub-adults in mangroves, along with occasional adults, but abundances modest compared to other habitats. Very high juvenile abundances in estuarine systems, especially in shallow water mud-habitats, and sand to a lesser extent. Adults are relatively uncommon in estuarine systems, but common in shallow coastal areas. Tagging studies in the 1960s showed strong links between estuarine nursery grounds and coastal fisheries (Christchurch region – no mangroves).	Yes	Consumes bivalve species such as mussels *(Perna canaliculus)* and pipis (*Paphies* sp.) plus crabs and a variety of other small crustaceans including cumaceans and amphipods. Larger individuals (>90mm) also fed on brittle–stars (*Amphiura rosea*).
Parore (Girella tricuspidata)	Common / Yes (East) Probably important nurseries for adult parore rocky reef populations	Juveniles consistently found in east coast mangroves, probably in association with the pneumatophore zone (forest edge). Largely a northeastern New Zealand species, main adult distribution coincides with mangrove distribution in estuaries. Adults in small schools use mangrove forests. This species is rare on the west coast and its estuaries. On the east coast, high juvenile abundances are often associated with subtidal seagrass, some Neptune's Necklace (*Hormosira banksii*) beds, brown kelp (*Carpophyllum*) forests and man-made structures e.g., floating pontoons. It abundance in mangrove forests is lower, but the large extent of mangroves, relative to other habitats, make it likely to be an important juvenile parore nursery. This species uses a series of inter-connected habitats as it grows in size/age. Adult parore are common across both soft sediment and rocky reef systems.	Very limited	Predominantly a benthic feeder. Diet includes amphipod species such as *Paracalliope novaezelandiae*, and barnacle cirri in mangrove forests. Smaller individuals (20–30mm) also feed on zooplankton species such as the copepods *Paracalanus indicus,* and *Temora turbinata)*
Yellow-bellied flounder (Rhombosolea leporina)	Common / No	Found as both juveniles and sub-adults in mangroves, along with occasional adults, but abundances modest compared to other habitats. This species is strongly estuarine associated, and was also historically fished along open coast beaches. Juveniles are most abundant in upper harbour, turbid muddy habitats, and absent from sandflats. Adults are more widely distributed than juveniles, including sand habitats. Especially common in west coast systems, which support relatively large fisheries.	Yes, short-lived species (~3+ years), strong natural fluctuations in abundance.	Feeds mainly on crabs (*Helice crassa; Halicarcinus* spp.) and mysids (*Tenagomysis sp.)*. Also consumes bivalves (*Paphies australis*), bivalve siphons, and amphipods.

Table 5 (Cont.)

Exquisite goby (Favonigobius exquisitus)	Present / No	Modest abundances in mangroves. Very abundant on open intertidal and subtidal flats, down to a depth of at least 19 metres.	No	Benthic and planktonic diet. Consumes crabs (*Helice crassa*) and other crustaceans including cumaceans, amphipods and the copepod *Euterpina acutifrons*.
Mottled triplefin (Grahamina capito)	Present / No	Occasionally found in mangroves. Widespread in estuarine systems, usually associated with seafloor habitat structure.	No	
Bridled goby (Arenigobius bifrenatus)	Patchily abundant / Yes (Invasive species)	Mangrove associated – agrees with its habitat usage in Australia. An introduced species, large adults found in relatively high abundance in Mahurangi Harbour mangroves. Has been sampled from this harbour across multiple years, suggesting an established breeding population.	No	Detrital feeder. Only one specimen examined for gut contents.
Garfish / Piper / Half-beak (Hyporhamphus ihi)	Rare / No	Sampled as occasional adults in mangroves, not common in the turbid water conditions often associated with mangroves. Widespread and abundant in estuarine habitats with clearer waters, juveniles associated with seagrass meadows, adults though to adhere their eggs to seagrass blades.	Limited	Diet predominantly planktonic copepods within seagrass meadows.
Sprat (Sprattus spp.)	Rare / No	Sampled as occasional juveniles (2 closely related species). Juveniles are some-times relatively common on tidal mudflats, and near the water surface in subtidal areas. Probably migrates to coastal waters as approaches adult size.	No	Mainly planktivorous (calanoid copepods) with some mysids consumed. (only specimens from Manukau Harbour examined)
Jack mackerels (Trachurus spp.)	Rare / No	Sampled as occasional juveniles in mangroves. Found across a range of estuarine habitats in relatively low numbers – strong association with subtidal seagrass meadows in some estuaries.	Yes, large coastal trawl and purse seine fisheries	Mainly zooplankton (calanoid copepods). Feeds mainly on mysids in seagrass meadows.
Snapper (Pagrus auratus)	Rare / No	Low juvenile abundances sampled in Rangaunu Harbour mangroves, at sites with very clear water, and adjacent seagrass meadows. May use mangroves to a spatially limited extent in relatively (rare) pristine environments. Historical records of large snapper actively feeding in large numbers in mangrove forests. Very high juvenile abundances associated with estuarine subtidal seagrass meadows, horse mussels, and sponge	Yes, fully exploited fisheries	In seagrass meadows juveniles (20–60mm) are predominantly planktivorous, feeding on calanoid copepods with larger individuals (80–100mm) feeding on crustaceans such as crabs, amphipods (*Aora typica*), shrimps (*Palaemon affinis*) and bivalves. Mysids dominate the diets of all juveniles associated with seafloor structure (horse

Table 5 (Cont.)

		assemblages – strongly structure associated.		mussels/sponges) in the Manukau Harbour.
Spotties (Notolabrus celidotus)	Rare / No	Very occasional juveniles in mangrove forests, east coast only. As with juvenile snapper, some evidence from Rangaunu Harbour that juveniles of this species use mangroves to a limited extent where seagrass is adjacent (more pristine systems). Very rare on the west coast, very common in east coast estuaries in association with structure, especially subtidal seagrass meadows. Adults less common, thought to move off to other habitats.	No	Primarily benthic. Feeds on amphipods and juvenile bivalves within seagrass meadows.
Kahawai (Arripis trutta)	Rare / No	Very occasional juveniles in mangrove forests. Adults have been caught along the edges of mangrove forests over tidal mudflats, feeding on juvenile flounders. Juveniles are largely associated with exposed sloping beaches with coarser sediments, and clearer water conditions, both inside and outside estuaries. Juveniles are very rare in turbid, muddy upper harbour areas.	Yes	Benthic juveniles (30–80mm) mainly feed on small mysids (*Tenagomysis* sp.) (sampled from Manukau Harbour only).
Other species found in northern estuaries – not sampled from mangroves				
Trevally (Pseudocaranx dentex)		Juveniles especially common in west coast harbours, in association with subtidal seagrass, and along the edges of channels with strong currents and clearer waters. Also found in association with reef-associated sponge assemblages, and in the Waikato River mouth.	Yes	Feeds mainly on amphipods (Paradexamine sp.; *Paracalliope novaezelandiae*) and mysids. Consumes some zooplankton in seagrass meadows.
Goatfish (Upeneichthys lineatus)		Juveniles are sometimes found in modest abundances, in association with subtidal seagrass and horse mussel beds. Adults are rare in estuaries. Structure associated.	Limited	Benthic. Feeds on amphipods (*Methalimendon* sp.; Paracalliope) and mysids (*Tenagomysis* sp.)
Leatherjackets (Parika scaber)		Juveniles occasionally found in modest abundance in association with subtidal seagrass and horse-mussel beds, larger animals very rare. Structure associated.	Yes	Benthic feeders as juveniles (30–66 mm), feed on amphipods and isopods.
Clingfish (several species)		Common in subtidal areas that contain benthic structure, such as dead shells, and in subtidal seagrass beds. Structure associated.	No	

Table 5 (Cont.)

Pipefish (5 species) (Syngnathidae)		Generally found in association with subtidal seagrass, and around seaweed, in clearer water conditions with sandier substrates. Structure associated.	No	Predominantly planktonic. Consumes high numbers of the copepod *Paracalanus indicus.* Feeds on some benthic crustaceans such as mysids and amphipods.
Black flounder		Strongly associated with riverine estuarine systems with high fresh-water inputs. Not yet sampled from northern estuarine systems.	Limited	
Speckled sole (Peltorhamphus latus)		This species does not move more than half-way up tidal flats, so is therefore unlikely to ever access mangrove forests. A dominant species in many tidal-flat fish assemblages, especially in more muddy habitats. Adults are uncommon in estuaries.	No	Primarily benthic. Feeds mainly on small crustaceans including mysids and cumaceans. (*Colurostylis lemuran*). Also feeds on mussels, ostracods and the harpacticoid copepod, *Euterpina acutifrons.*
Inanga (white-bait) (Galaxias maculatus and other spp.)		Sampled in high abundances as small adults in freshwater dominated (river) estuaries, including southern systems without mangroves.	Yes	
Red gurnard (Chelidonichthys kumu)		Juveniles sampled in low abundances from west coast estuaries, generally over muddier bottoms. Adults are seasonally common in some estuaries such as the Manukau and Kaipara Harbours.	Yes	Juveniles (28–80mm) feed mainly on mysids and cumaceans. Larger juveniles (>80mm) also feed on crabs and small fish e.g., the exquisite goby *Favononigobius exquisitus*.
John dory (Zeus faber)		Seasonally move into estuaries and shallow water areas (colder months), important predator of small fishes, including juvenile snapper.	Yes	
School shark (Galeorhinus australis)		Uses estuaries for breeding and pupping grounds (spring and summer).	Yes	
Hammerhead sharks (Sphyrna zygaena)		Juveniles relatively common in warmer months, probably pup in harbour systems and shallow coastal embayments (e.g., Tamaki Strait, Firth of Thames).	No	
Barracouta (Thrysites atun)		Occasionally sampled as large adults in channel areas (gill-nets).		
Kingfish (Seriola lalandi)		Known to have once displayed seasonal ‘runs’ into some estuaries following kahawai (e.g., Rangirere sub-estuary, Manukau Harbour), but ‘fished out’ in past decades. Adults still caught in estuarine systems.	Yes	
Eagle ray (Myliobatis		Seasonally common in some estuaries, including large numbers	No	

Table 5 (Cont.)

tenuicaudatus)		of both juveniles and adults.		
Rig (Mustelus lenticulatus)		Uses estuaries for breeding and pupping grounds (spring and summer).	Yes	
Additional species mentioned by Crisp et al. (1990), little known from estuarine systems				
Rockfish (Acanthoclinidae spp.)		This species complex is found on intertidal coastal reef platforms, and has not been sampled inside estuarine systems. However, estuarine reefs have not been sampled.	No	
Long-finned eel (Anguilla dieffenbachii)		Not known to have been sampled from estuarine environments. Must pass through estuaries as glass eels returning from the open sea.	Yes, heavily exploited	
Koheru (Decapterus koheru)		This is an open coast species associated with rocky reefs; little else is known about this species. Has not been sampled from estuaries.	No	
Big-eye (Pempheris adspersa)		Not sampled from estuaries, night foraging species usually associated with rocky reef systems. Such habitats do occur in some estuaries, but their fish assemblages have not been quantified.	No	

3.4.2.4 Why are juvenile fish in mangroves?

A number of hypotheses have been advanced as to 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, Primavera (1997) (shrimps) and Laegdsgaard & Johnson (2001) looked at the interactions between fish predation and root densities of the mangrove species *Sonneratia griffithii* and *Avicennia marina*, respectively. They concluded that 1) habitat complexity regulates predation, 2) that not all prey species use structurally-complex habitats in the absence of predators, and that 3) the use of structurally complex habitats decreases with fish size. Further field 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, and that almost all predatory fish sampled were found to inhabit the more open, seaward sites (Vance et al. 1996, Ronnback 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) during the day, and found low rates of predation across all of these habitats (Barwon River, Victoria, Australia). 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.

Faunce & Serafy (2006) reviewed 111 studies of fish in mangrove in an assessment of the state of knowledge about such systems. They found many important information gaps, including a lack of knowledge of the influence of food supply and other processes on mangrove fish assemblages within a wider framework of variable habitat quality and availability.

This knowledge gap was addressed in context of New Zealand mangrove forests during the fish-in-mangroves study discussed above. Fish collected during daytime sampling were identified to species level and measured. Where available, a minimum of 5 individuals per size cohort was sampled from each of 3 sites per harbour (see section 2.5.1 for site selection). The fore-guts (stomach) were removed and the contents identified to the lowest possible taxonomic resolution. Each individual item was assigned a size-class based on a series of increasing sieve mesh sizes (Edgar 1994). All dietary items were grouped into one of 12 major food categories as follows (1) epifaunal crustaceans, (2) infaunal crustaceans (3) planktonic crustaceans, (4) epifaunal molluscs, (5) infaunal molluscs, (6) pelagic molluscs, (7) epifaunal polychaetes, (8) infaunal polychaetes (9) other mobile epifaunal invertebrates, (10) other infaunal invertebrates, (11) demersal fishes, (12) plant and detrital material. (Edgar & Shaw 1995: note that some misclassifications of animals to functional groups are possible in this schematic, due to a lack of natural history knowledge for some groups and functional switching of some groups depending on environment). The volume of each category in fish guts was estimated using the estimated sieve-size of each individual item, and multiplied by the ash-free-dry-weight/sieve size relationships equations of Edgar (1990, Table III). The average percentage biomass each prey category contributed to diet was calculated for each 10-mm fish size classes for each fish species in each harbour (Figures 6-9).

The diets of semi-pelagic fish (anchovies, smelt, yellow-eyed mullet) were dominated by pelagic zooplankton, in particular of copepods such as *Euterpina acutifrons* and *Temora turbinata* (Figure 6). Anchovy stomach contents (Kaipara Harbour only) were wholly composed of zooplankton. Smelt sampled from the Manukau Harbour also had diets dominated by zooplankton, with additional minor contributions from insects and epifaunal crustaceans such as amphipods and isopods. Smelt from Mahurangi Harbour had larger contributions of epifaunal crustaceans and other epifaunal species. Yellow-eyed mullet from all four harbours had diets dominated either by zooplankton (mainly copepods), with increasing contributions of epifaunal crustaceans (mysids *Tenamgomysis* sp.) and polychaetes with increasing fish size; or alternatively by a mixture of fine algal and detritus material (50% of fish individuals sampled). Grey mullet, a more demersal species, had diets almost totally composed of fine algal and detritus material, across the Kaipara, Manukau and Rangaunu Harbours, with the exception of five individuals from the Kaipara that fed on planktonic copepods (Figure 7).

Parore from Manukau Harbour (no day caught fish were collected from the east coast harbours), in contrast, had a diet almost completely composed of epifaunal crustaceans (barnacle cirri), presumably grazed from mangrove trunks and/or pneumatophores (Figure 7). Exquisite gobies also relied heavily on epifaunal crustaceans such as gammarid amphipods and crab megalopa, with smaller contributions from infaunal crustaceans (including the copepod *Hemicyclops* sp.) and several other categories. There was also variation in the diet of this species among harbours within each coast. For example, Kaipara fish consumed mainly crab megalopae and *H. crassa*, which were not present in the diet of exquisite gobies from the other three harbours (not shown in figures).

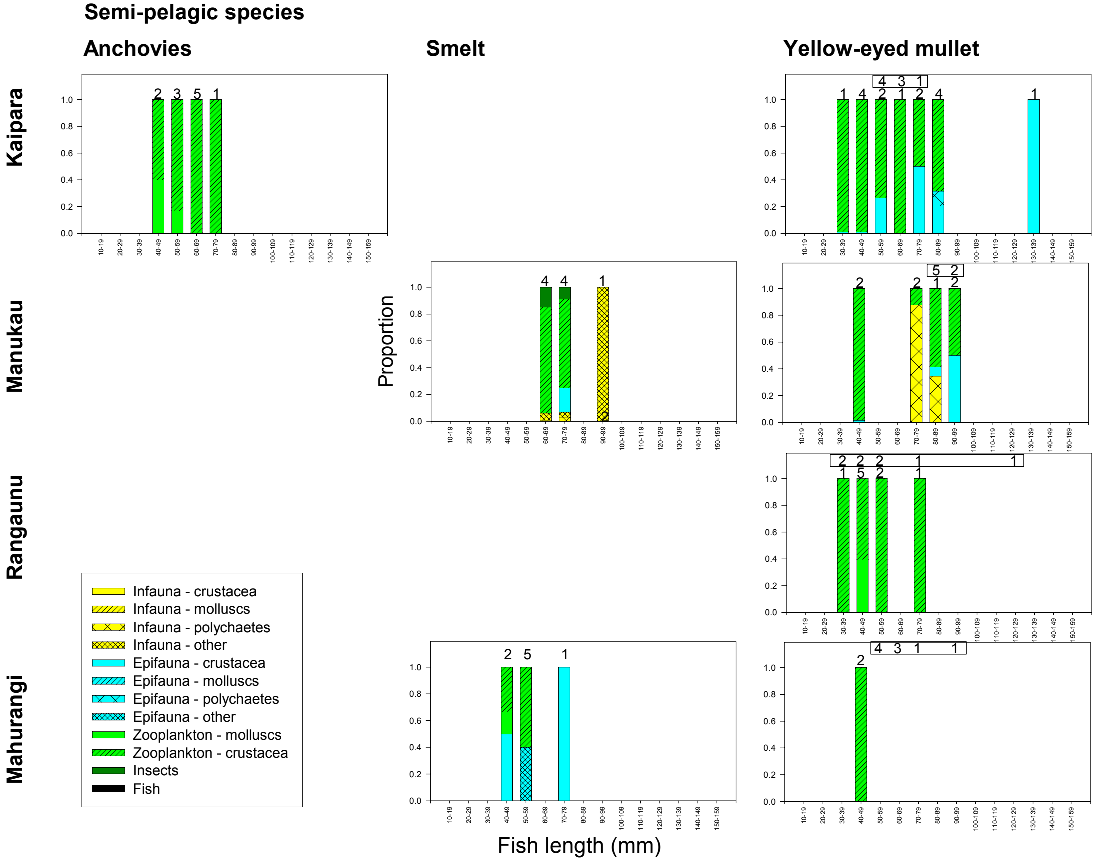
Estuarine and mottled triple-fins, with similar body shapes to exquisite gobies, also had diets dominated by epifaunal crustaceans (amphipods, isopods and crabs such as *H. crassa* and *Halicarcinus whitei*) and some infaunal crustaceans (such as the amphipod *Torridoharpinia hurleyi*), along with lesser amounts of other categories. Sand flounder, collected mainly from Mahurangi Harbour, had a diet dominated by infaunal species, including nematodes. Yellow-belly flounder, in contrast, had diets dominated by epifaunal crustaceans, largely juvenile crabs (not identifiable to species) and *H. crassa*.

The composition of the diet of short-finned eels could not be presented in the form of proportional contributions because of a lack of conversion factors for ash free dry weight of prey items larger than 5.6 mm in size (including much of the dietary size-range of this species). Eel diet was dominated by larger benthic crustaceans and, to a lesser extent, bivalves. Crabs, particularly *H. crassa*, were an important component of the diet of all the sizes of eels sampled (168–655 mm). With increasing eel size, larger numbers of shrimps, especially *Palaemon affinis,* were consumed. Larger eels at some sites also ate exquisite gobies.

Collectively, the fish assemblages of mangrove forests sampled composed several trophic groupings; semi-pelagic fish consuming predominantly zooplankton (anchovies, smelt, and half of all yellow-eyed mullet); species relying on fine algae and detritus (half of all yellow-eyed mullet, and most grey mullet); species feeding on small, benthic fauna (parore, exquisite gobies, estuarine and mottled triple-fins, and sand flounder); and species feeding on both small and larger epifauna (some of the triple-fins, yellow-belly flounder and short-finned eels). The diversity of invertebrate prey in mangrove forests was generally quite limited (see section 2.5.1) and appeared to offer only modest foraging opportunities for small fishes. Those fish species sampled in the highest abundances in mangrove forests (Table 3) appeared to rely on either food sources not directly related to the presence/absence of mangroves i.e., zooplankton, or to target specific dietary components common in mangrove forests (e.g., fine algae and detritus). Overall, mangrove forests do not appear to offer enhanced feeding opportunities for most fish species, given their relatively poor invertebrate fauna compared to other alternative habitats e.g., seagrass meadows, which support more invertebrate prey (Alfaro 2006, Schwarz et al. 2006, Morrison et al. unpublished data) and fish (Morrison et al. unpublished data). This may be a strong contributing factor to the relatively low value of mangrove forests to most fish species.

Figure 6

Relative contributions (% biomass) of different prey classes to the diets of anchovies, smelt and yellow-eyed mullet sampled from mangrove habitats by harbour and fish size (10-mm size-classes). Numbers above each bar give the number of individual fish sampled; those within the line box indicate individuals whose diet was wholly composed of fine plant material and/or detritus.


Semi-pelagic species

Anchovies **Smelt** **Yellow-eyed mullet**

Figure 7

Relative contributions (% biomass) of different prey classes to the diets of grey mullet, parore, and exquisite goby. Details as in previous figure. Grey mullet 16–19 cm in length (outside the range of the graph) all consumed plant and detritus material.

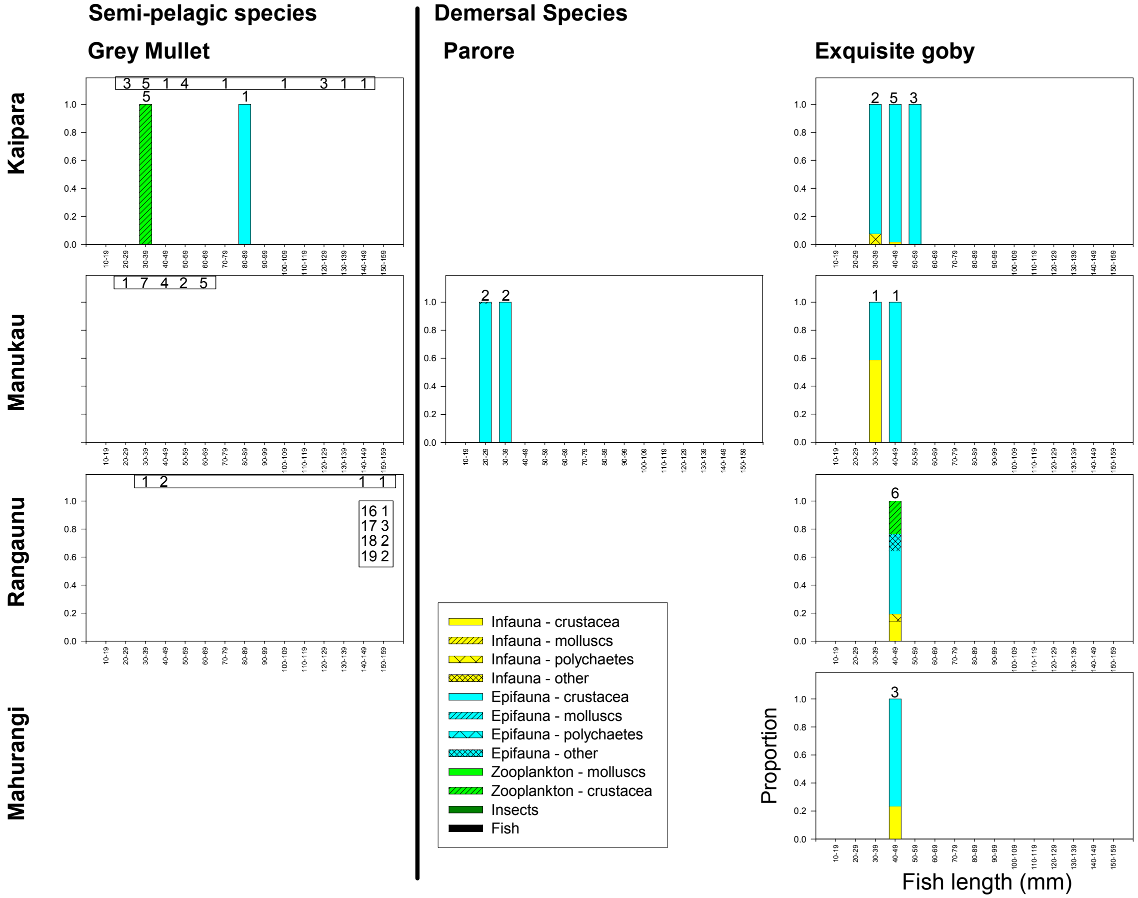


Figure 8

Relative contributions (% biomass) of different prey classes to the diets of estuarine triple-fin, mottled triple-fin, and sand flounder. Details as in previous figures.

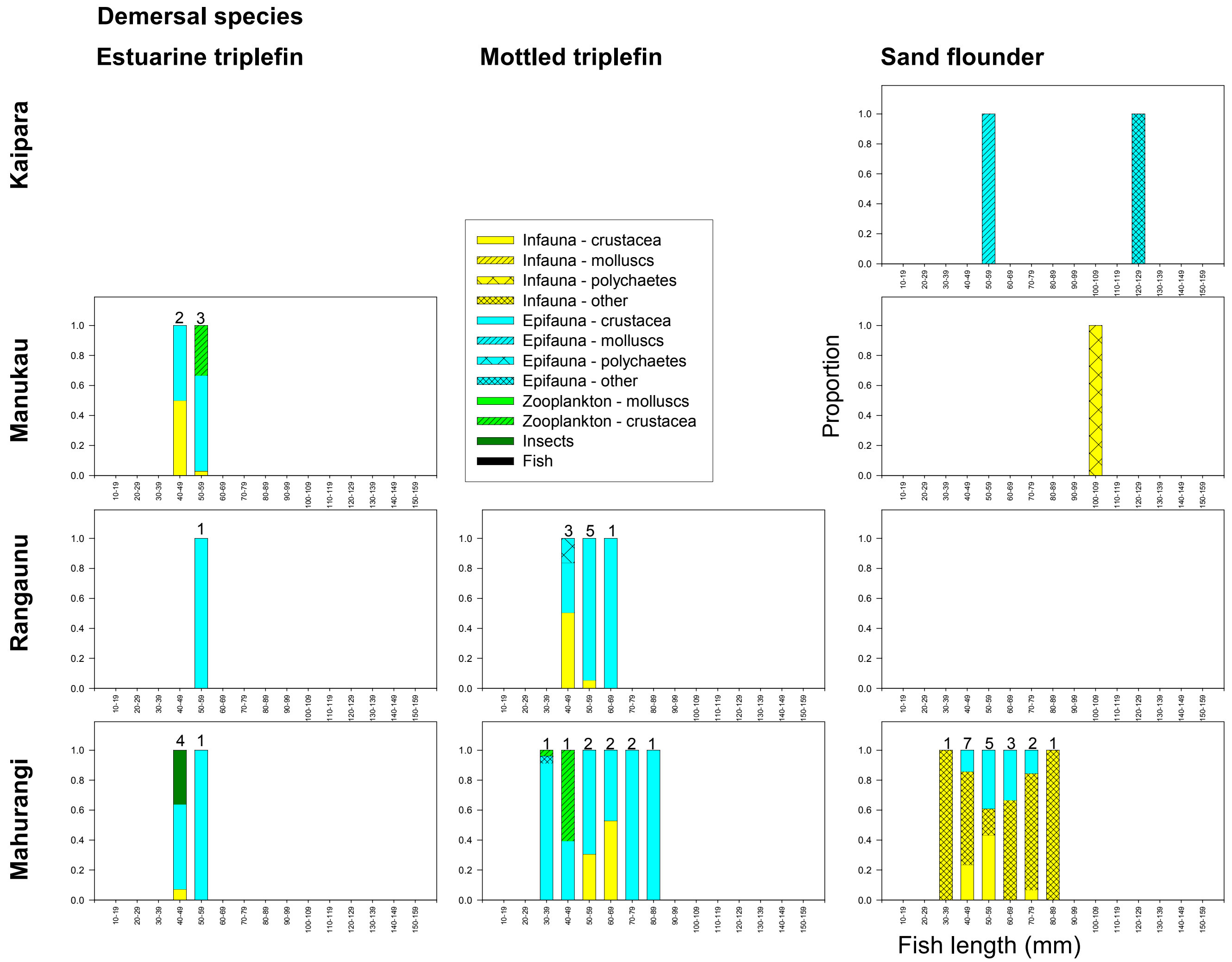
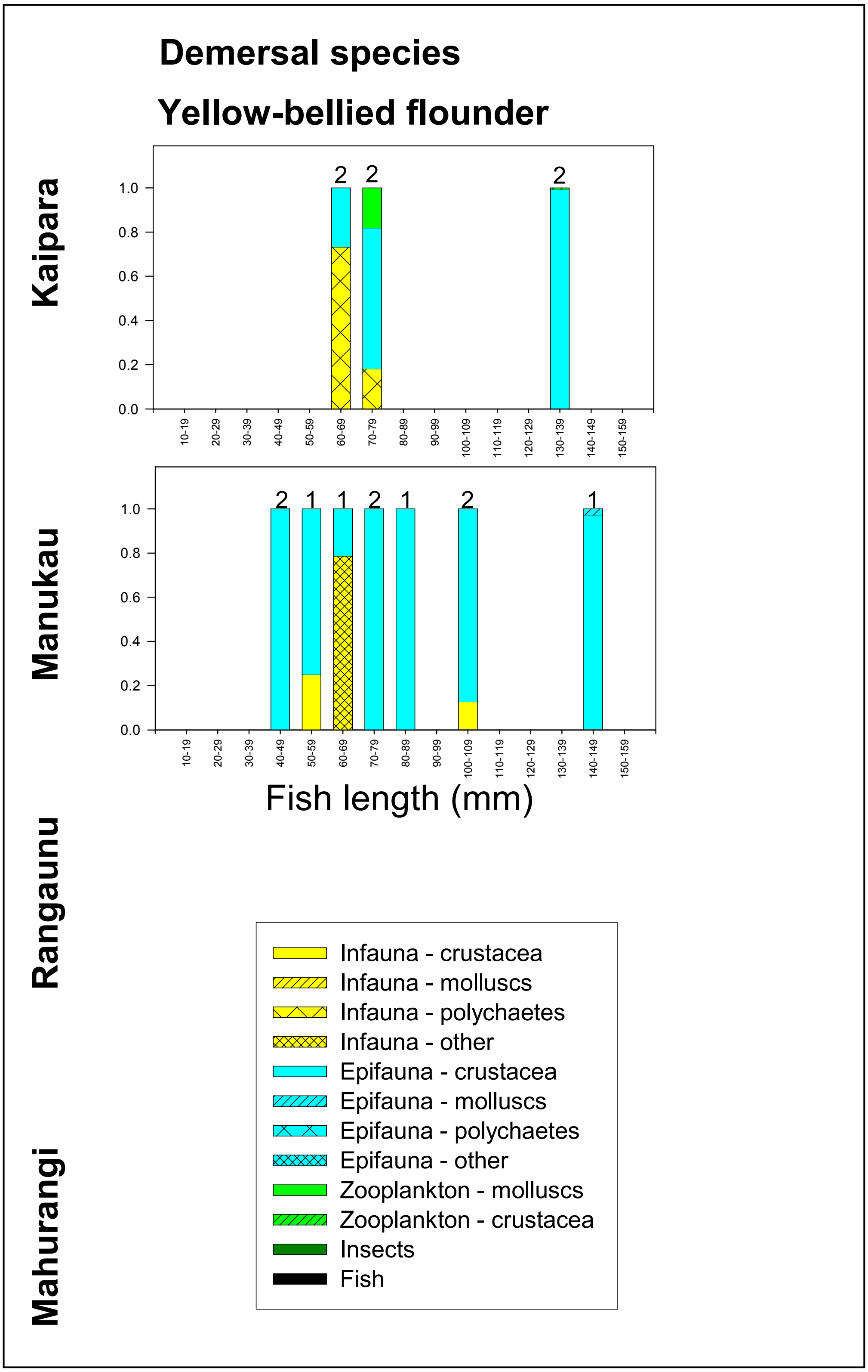


Figure 9

Relative contributions (% biomass) of different prey classes to the diets of yellow-belly flounder. Details as in previous figures.



3.4.2.5 Potential use of mangrove habitats by spawning fish and fish larvae

It has often been stated that New Zealand mangroves are important as spawning grounds for numerous fish species, but this seems highly unlikely. Little quantitative information exists apart from the work by Davenport (1979) in Whangateau Harbour, just north of Auckland. He sampled zooplankton (including fish eggs and larvae) and small fish (98% being yellow-eyed mullet, *Aldrichetta forsteri*) over a period of a year in a mangrove-lined tidal channel and non-mangrove locations. Very low total numbers of pelagic fish eggs were collected (< 100 per species), including those of snapper (*Pagrus auratus*), spotties (*Notolabrus celidotus*), leather-jackets (*Parika scaber*), flounder (*Rhombosolea* spp.), and yellow-eyed mullet.

Taylor (1983) also sampled a mangrove channel in Whangateau Harbour at monthly intervals for a year using a gill-net (mesh size not given), and found that of 948 fish caught, 95% were yellow-eyed mullet (mostly adults). It was also stated that they collected a number of "economically important fish", and that they had evidence of mangrove areas elsewhere supporting populations of "economically useful fish", but no further details were given.

Davenport (1979) concluded that this reflected the influence of general Hauraki Gulf water entering the estuary with the tides, with spawning having taken place elsewhere, and that their presence did not indicate the use of the mangrove zone as a spawning ground. In particular, it was noted that despite the high numbers of yellow-eyed mullet (largely juveniles) in the local system, the presence of few eggs suggested that this species also spawned elsewhere. Low numbers of fish larvae were also caught, but were most common at the estuary entrance, away from mangroves. He concluded that the use of mangrove zones as fish-spawning areas was likely to be minimal, given the strong restrictions imposed by the draining of the tides, including strong tidal flushing. A similar argument seems likely for the use of mangroves by most larval fish.

3.4.2.6 Mangrove contributions to commercial fish species production

The relative overall contribution of mangrove habitats to coastal fisheries productivity, relative to other estuarine and coastal habitats, remains to be quantified in New Zealand. As noted previously, two species of commercial importance (short-finned eels and grey mullet) are likely to have some partial dependence on mangrove habitats for the production of juveniles. Their relative contribution will be difficult to separate from that of other associated estuarine habitats, such as seagrass meadows, tidal banks and subtidal basins.

Saintilan (2004) examined the relationships between the weight of commercial fish landings and physical characteristics at the estuary scale, using data from 55 different estuaries along the coast of New South Wales. The fish assemblage of most commercial species show little latitudinal influence along this section of coast, thought to be a result of the influence of the east Australian current, which supplies many of the larval recruits to estuaries (Gray et al. 1996). Saintilan (2004) divided the estuaries into four different geophysical classes. Small estuaries (< 4 km^2) that were intermittently closed had comparatively low abundances and diversity of fish. In larger estuaries, the variables that best related to commercial fish catches were a combination of the areas of tidal sandbank, central mud basin, low-tide channels, saltmarsh and total water area. The extent of mangrove was not an important explanatory variable. It was, however, a significant variable in models for 'Type IV' estuaries (late, infilled estuaries that contained higher proportions of mangroves, and less seagrass and salt-marsh, than more 'immature' estuaries). These estuaries supported larger relative number of tarwine *Rhabdosargus sarba* (sparid) and king prawn *Penaeus plebujus*. At the individual species level, many were positively associated (regression analysis) with the presence of seagrass across all estuaries, including the blue swimmer crab *Portunus pelagicus* (r = 0.80), dusky flathead *Platycephalus fuscus* (0.78), garfish *Hyporhamphus* sp. (0.56), sand whiting *Sillago ciliata* (0.66), king prawn *Penaeus plebejus* (0.44), leatherjackets Monacanthidae (0.76), and tarwine *Rhabdosargus sarba* (0.51 – Type IV estuaries only). A second group of species was positively associated with the area of central mud basin – bream *Acanthopagrus* sp. (0.87), parore *Girella tricuspidata* (0.83), grey mullet *Mugil cephalus* (0.80), and silver biddy *Gerres subfasciatus* (0.74). A third group was associated with the area of tidal sand bank – mud crab *Scylla serrata*, school prawn *Metapenaeus macleayi*, estuary catfish *Cnidoglanis macrocephalus*, and the sand flathead *Platycephalus caeruleopunctatus* (r values not given). Only the long-fin river eel *Anguilla reinhartii* (0.72) and the sand mullet *Myxus elongates* (0.41) were consistently associated with the area of mangroves. Saintilan's results confirmed the suggestion of Roy et al. (2001) that the area of seagrass declines as estuaries infill and mature, as well as finding a correlation between seagrass area and the width of the estuary. This large-scale correlative study suggested that the role of mangroves in supporting commercial fisheries was modest in this temperate region. The author concluded that "*as estuaries infill and the area of seagrass and mud basin declines, so too does the catch of species dependent upon these habitats*", and that "*the results strongly suggest that seagrass is a critically important habitat for a range of commercially important species, and that declines in seagrass area resulting from natural or anthropogenic disturbance should lead directly to decreases in stocks of these species*" (Saintilan 2004).

3.4.2.7 Work in progress

Fish-benthos interactions

The fish-in-mangroves dietary work described in this report comprises part of a larger PhD project looking at the inter-relationships between juvenile fish assemblages and their benthic prey in northern estuarine systems (M. Lowe, NIWA). While the primary focus of that project is the intertidal and subtidal flats of the Papakura Channel (including Pahurehure Inlet), Manukau Harbour, information has also been collected from a range of other habitats and estuarine systems, especially seagrass meadows. The fish-in-mangroves component will be integrated into the larger estuarine fish habitat framework, allowing its relative importance (for fish feeding/foraging) to be assessed against other habitats.

Connectivity with other habitats and ecosystems (fish movement)

As more detailed knowledge is gained of which small/juvenile fish assemblages are found in different estuarine and coastal habitats, the focus is starting to shift towards how these nursery habitats are linked to adult populations, from which they are spatially discrete. The technology to physically tag small fish and track them through to sub-adult/adult forms, over several years and a large increase in body size, is not yet at sufficiently advanced to undertake such work. However, 'natural' tags (e.g., otolith microchemistry) have been successfully used in a number of overseas studies to link nursery grounds and adult fish. Current studies in New Zealand are assessing the potential of such techniques to a) link juvenile snapper and parore populations in sheltered nursery environments (e.g., estuaries; snapper – seagrass and horse mussels; parore – beds of *Hormosira banksii*, seagrass, mangroves) to more coastal rocky reef environments, and b) assessing how west-coast estuaries in northern New Zealand may act as nursery grounds for the west coast snapper fishery. Both studies are assessing otolith microchemistry as a potentially powerful tool for such applications.

Trophic "fuelling"

As part of a project on seagrass meadows, work is in progress on using stable isotopes to assess how seagrass primary production may support secondary (animal) production. While the focus of this work is on seagrass meadows some distance from mangroves, the primary 'signature' of mangroves will be collected, and used in the stable isotope source modelling. The technical approach is similar to that of Alfaro et al. (2006) and many other authors, and involves two large estuaries with extensive seagrass meadows – Rangaunu and Kaipara Harbours.

3.4.3 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 and 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 New Zealand mangroves is poorly known but likely to be less diverse than those of tropical mangroves. Three species of moths, the tortricids *Ctenopseustis obliquana* and *Planotortrix avicenniae* (Cox 1977, Dugdale 1990) and the pyralid *Ptyomaxia* sp. (John Dugdale, pers. comm.), and an eriophyid mite, *Aceria avicenniae* (Lamb 1952), have been described from mangroves in New Zealand. *A. avicenniae* and the larvae of *P. avicenniae* are restricted to *Avicennia marina*, whereas *C. obliquana* is distributed throughout New Zealand and its larvae are polyphagous (Dugdale 1990). All 3 moths have been collected in Waitemata Harbour and *P. avicenniae* and *Ptyomaxia* sp. have been collected from Matakana Island, Tauranga Harbour (John Dugdale, pers. comm.).

At Pollen Island (Waitemata Harbour), larvae of *C. obliquana* occur only on stunted mangroves away from low-tide channels, while those of *P. avicenniae* and *Ptyomaxia* sp. occur on taller, lusher mangroves further down the shore (John Dugdale, pers. comm.). The larvae of *Ptyomaxia* sp. cause distinctive distortion of the growing tips of the shoots and *A. avicenniae* cause leaf galls. The larvae of *C. obliquana* cause damage to the leaves, fruit and buds of host plants, including horticultural crops, and presumably do the same to *A. 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 (The Horticulture and Food Research Institute of New Zealand Ltd 1998a).

In some areas of mangroves, such as Puhinui Creek, Manukau Harbour (Morrisey pers. obs.) and Puhoi Estuary (Kronen 2001), damage to woody mangrove tissue by boring insects is common. The insect responsible is the lemon-tree borer *Oemona hirta* (John Dugdale, pers. comm.), 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 frass (droppings) are ejected (The Horticulture and Food Research Institute of New Zealand Ltd 1998b). Ant colonies may establish within the tunnels (John Dugdale, pers. comm.) and the ants may perhaps "farm" the introduced scale insect *Ceroplastes sinensis*, which is also common on mangroves in New Zealand (Brejaart & Brownell 2001).

Small numbers of chironomids and their larvae were collected from sediments among mangroves in Rangaunu and Mahurangi Harbours during the 'fish in mangrove habitats' project (section 2.5.1). Larvae of some tipulid flies feed on intertidal green algae and may exploit this food source growing on the trunks and pneumatophores of mangroves (John Dugdale, pers. comm.). Thase animals, in turn, provide food for fish and birds.

3.4.4 Reptiles

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

3.4.5 Birds

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).

Cox (1977) investigated use by birds of a mangrove stand in the Kaipara Harbour over 2 years, and also made one-off surveys of other locations. The Kaipara site consisted of tall (5-6 m) trees along the seaward fringe, backed by a broad flat area of stunted (1.5m) trees, bounded by a dyke at the top of the shore. He recorded 22 species at the Kaipara site, of which 12 occurred regularly within the mangroves and 6-7 bred among the mangroves. The 12 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 5 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). Cox concluded that mangroves are generally a marginal habitat for birds, and in no case was it 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, other studies have documented use of mangroves by less abundant species. Miller & Miller (1991) reported bitterns (*Botaurus poiciloptilus*) using mangroves in Patua Estuary, near Whangarei. 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 (undated) noted that mangroves are "the only northern habitat of the banded rail. .. and are a substantial breeding habitat for New Zealand kingfisher".

Crisp et al. (1990) provided a list of 48 species of native or introduced birds using mangroves in New Zealand (no references are given but parts of their commentary appear to derive from Cox's thesis). Like Cox (1977), they conceded 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. Saenger et al. (1977) listed 242 species of birds that have been recorded from mangroves in Australia, of which 13 species (5%) were exclusively found in mangroves and 60 species (25%) used mangroves as an integral part of their habitat (in much the same way that many New Zealand species do). Of the species that occur in both Australia and New Zealand (including royal spoonbills, banded rails and bitterns), all those found in mangroves in New Zealand were also found in this habitat in Australia. The Australian species found exclusively in mangroves were a heron, a rail, a kingfisher, 2 species of warblers, 2 of robins, 2 of whistlers, a silvereye (not the species that is also found in New Zealand) and 3 species of honeyeaters. 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. Mangroves can provide habitat to those birds that find it suitable when no other suitable habitat is available.

3.5 The sediment trapping role of mangroves

3.5.1 The role of mangroves in trapping sediment and contaminants

Mangroves enhance sediment accretion by damping currents, attenuating waves and altering patterns of water flow. Their vertical roots (pneumatophores and prop roots), low branches and trunks encourage the settling of fine silts, clays and organic-rich sediments, which are either transported into the system or produced in-situ from the mangrove plants (Bird 1971, Kathiresan and

Bingham 2001, Nicholls & Ellis 2002). For example, Young & Harvey (1996) found that sediment accretion correlates positively with pneumatophore density.

Once established, mangrove stands gradually influence estuarine sedimentary processes, raising the height of the surrounding mudflat, and altering the sediment characteristics (Thom et al. 1975, Furukawa et al. 1997, Swales et al. 2002) which can lead to further increases in mangrove growth and abundance (Dingwall 1984). For example, Swales et al. (2007) found that mangrove colonisation in the Firth of the Thames increased sediment accretion rates from 20 mm yr^{-1} to ≤ 100 mm yr^{-1} following mangrove colonisation, leading to rapid elevation of the vegetated mudflats.

Actual sediment accumulation rates (SAR) differ between mangrove stands, depending upon to local conditions (geomorphology, coastal oceanography and allochthonous sediment input) (Jennerjahn & Ittekott 2002).

Within a mangrove stand, highest SAR usually occur at the seaward fringe or along the banks of tidal channels, and results in a deeper accumulation of sediment often with a higher mud content (Dingwall 1984, Clarke 1993, Furukawa et al. 1997).

Whether or not mangroves are responsible for active "land building" and whether they are steady-state systems (i.e., self-maintaining and not eventually replaced by a different system) or successional systems (i.e., they modify the environment to the extent that they are replaced by another system; e.g., marine to terrestrial), has been, and still is, widely discussed in the literature (Beard 2006). This question has not yet been fully addressed in relation to New Zealand mangroves. However, previous and ongoing research, making use of long-term datasets relating to sediment deposition and sedimentation rates in conjunction with photographic records of mangrove/saltmarsh areas and changes in plant and animal communities is extending our understanding of the role of mangrove contribution to habitat change (Nicholls and Ellis 2002, Young and Harvey 1996, Hofstra et al. submitted, Swales et al. 2007).

Morrisey et al. (2000) sampled intertidal sediments at locations along Hellyers/Kaipatiki Creeks in the upper Waitemata Harbour, and Pakuranga Creek in the Tamaki Estuary, both of which consist of a low-tide channel flanked by mudflats, a pneumatophore zone and mangrove stands at the top of the shore. At each location samples were collected from each of these habitats and analysed for concentrations of copper, lead and zinc. Concentrations of all 3 metals were highest in the upper parts of the creeks but there was no consistent difference across the width of the shore from channel to mangroves. There was, thus, no evidence for enhanced trapping of contaminants among the pneumatophores or mangrove trunks, but the authors pointed out that their sampling was only done in the lower parts of the mangrove stands and could not determine whether there were gradients in metal concentrations within the mangroves.

3.5.2 Erosion protection by mangroves

By reducing the velocity of currents and attenuating waves mangroves are considered to be important for erosion control (Othman 1994, Beard 2006, UNEP-WCMC 2006) The horizontal subterranean roots of mangroves have a role in stabilizing sediments (Jennerjahn & Ittekkot 2002).

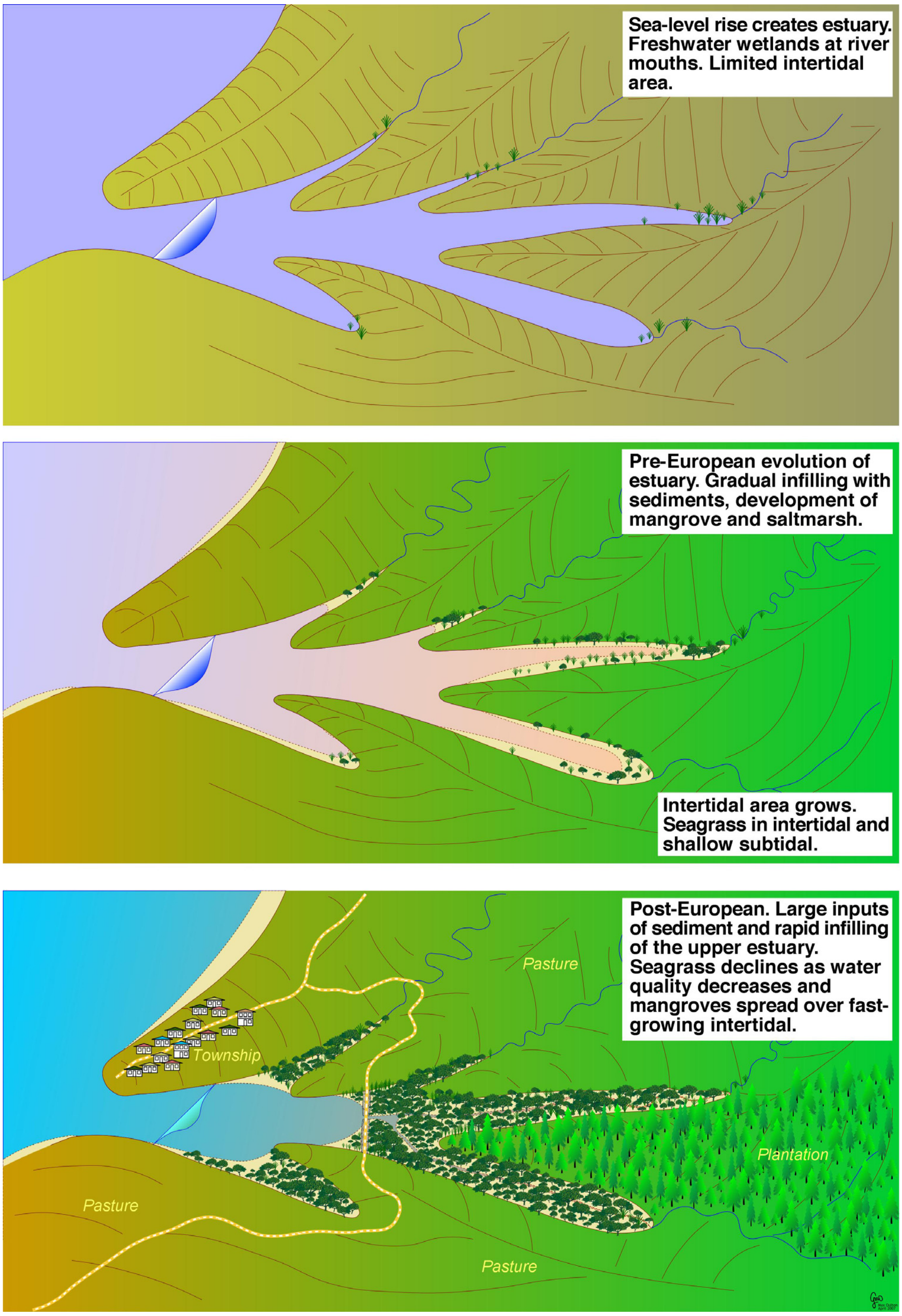
3.5.3 Sediment organic matter generated by mangroves

One of the lesser-known factors in the functioning of mangrove ecosystems is the proportion of the litter that is incorporated into the sediment as opposed to that which is flushed from the mangrove stand by tidal action. The rate of accumulation of litter detritus on and in the sediment is difficult to measure and is likely to vary in relation to substrate characteristics, the frequency of tidal inundation and the stage, and hence energy, of the tide, as well as seasonally with the pattern of production and supply of mangrove litter (Woodroffe, 1985a). Nevertheless, mangrove leaf litter that accumulates in the sediment contributes much of the organic matter content. As mangrove forests mature, increasing accumulation of leaf litter, due to larger trees and less frequent inundation by tidal waters, increases the organic matter content of the sediments ((Beard 2006). For example, the organic matter content of sediment from mature stands of mangroves in Puhinui Creek, Auckland (7.9-17.2%dw) was much higher than that of newly-establishing stands (4.4-5.8%) and correlated with leaf litter content (Morrisey et al. 2003).

3.5.4 The role of mangroves in the natural ageing of estuaries

The colonisation of intertidal areas by mangroves contributes to the natural ageing of estuaries by increasing sedimentation on the intertidal areas (Dingwall 1984), as summarised in Figure 10. This leads to accelerated infilling and creation of intertidal flats (Woodroffe 1982, 1985b, Young & Harvey 1996). However, the infilling slows down in the final stages of this process, prolonging estuarine lifespan (Hume & Swales 2003).

Figure 10
Evolution of an estuary from its formation at the end of the period of post-glacial sealevel rise (6500 years BP: top panel) to the present. The diagram shows the gradual infilling of tributary estuaries and the narrowing and shallowing of the low-tide channel in the main estuary. Concurrent changes in catchment landuse and vegetation cover are also shown.



Sea-level rise creates estuary. Freshwater wetlands at river mouths. Limited intertidal area.

Pre-European evolution of estuary. Gradual infilling with sediments, development of mangrove and saltmarsh.

Intertidal area grows. Seagrass in intertidal and shallow subtidal.

Post-European. Large inputs of sediment and rapid infilling of the upper estuary. Seagrass declines as water quality decreases and mangroves spread over fast-growing intertidal.

The effects of mangrove spread and management

4.1 Historic loss of mangrove habitat in New Zealand through human activities

Worldwide loss of mangrove habitat has been substantial and Rönnbäck (1999) estimated that whereas 75% of the world's tropical coasts were once fringed by mangroves, the current figure is 25%. Roughly 35% of the total area of mangroves has been lost in the last 20 years (Valiela et al. 2001) and the current annual rate of loss is estimated at 2.1% (exceeding that of tropical rainforests: UNEP-WCMC 2006). The greatest rate of loss is currently in the Americas (3.6% yr^{-1}: UNEP-WCMC 2006). Causes of loss include industrial, residential and tourism developments, construction of aquaculture ponds and salt production operations (UNEP-WCMC 2006).

There is much anecdotal but limited quantitative information to suggest that significant loss of mangroves has also occurred at some locations in New Zealand in the past, usually to create farmland (e.g., Glanville 1947). In the Hokianga Harbour, for example, infilling of mangroves began in the 1920s and it is estimated that 34% (1820 ha) of the "vegetated intertidal flats" were destroyed (Bellingham et al., cited in Nature Conservation Council 1984), although the true extent is difficult to determine because much of it was done illegally (estimated at 581 ha). Of this, 1132 ha were converted to pasture. It is not clear from the National Conservation Council report whether all of this 1820 ha was occupied by mangroves. Presumably it was not, because the remaining 66% (3533 ha) greatly exceeds the figure of 1899 ha of mangrove forest in the Hokianga Harbour in 1981, given in the summary table from the Atlas of Mangrove Forests in New Zealand (included in the same report).

The fact that much of the clearance took place in the first half of the twentieth century makes quantification of changes in mangrove area difficult, if not impossible, because it largely predates aerial photographic records (which began systematically in the 1940s). For example, Park (2004) measured mangrove canopy cover in 8 estuaries in Tauranga Harbour using aerial photographs dating back to 1943 and did not detect significant loss of mangroves in any of them. It is, of course, possible that loss (or gain) occurred prior to 1943 but this cannot now be determined. The Harbours Amendment Act 1977 made it illegal to infill for agricultural purposes, and rates of loss are likely to have decreased thereafter.

Hume & Roper (1986) listed changes to the estuary of Pukaki Creek, Manukau Harbour, beginning with infilling of 34 ha of Pukaki Lagoon in 1911 to create farmland. Further loss of mangroves occurred with construction of Auckland International Airport in 1960, when 26 ha was infilled. There have undoubtedly been many other such cases of mangrove destruction throughout their range.

There is also evidence of continuing and more recent, small-scale clearance of mangroves to protect access to the shore and preserve sea views. Examples include the Waiuku arm and Pahurehure Inlet in the Manukau Harbour (Kingett Mitchell 2005, Wildland Consultants 2006).

In one quantified example (Crisp et al. 1990), examination of aerial photographs showed that the total area of mangroves in the Manukau Harbour decreased from ca 580 ha to 450 ha between 1955-1960 and 1981. Areas of loss were distributed throughout the harbour (Figure 9 in Crisp et al. 1990). Nature Conservation Council (1984), however, cited information suggesting that 700 ha had already been infilled by 1978, suggesting that there was also substantial loss of mangroves prior to 1955. The source of the map of mangrove distribution in 1955-1960 in Crisp et al.'s Figure 9 is not given but, like the map for 1981, was presumably based on aerial photographs. It may be necessary to treat their figures for loss of mangroves in the Manukau with caution, for the reasons discussed below.

There is a surprising discrepancy between Crisp et al.'s maps (1955-1960 and 1981) and those in Wildland Consultants (2006) in terms of the distribution of mangroves in the part of the Waiuku arm of the Manukau covered by Wildland Consultant's study (south of approximately Glenbrook steel mill). Wildland Consultants (2006) state that "Examination of these aerial maps [presented in their Appendix 4] shows that mangrove expansion has been a relatively recent phenomenon in the upper reaches of the Waiuku estuary…Mangroves cannot be seen within the study area in aerial photographs from 1969 and 1975, although a dense stand is evident outside the study area, in an inlet on the eastern side of the estuary, approximately 2 km north of the Glenbrook steel mill. By 1980, scattered mangrove individuals and small patches can be seen in the heads of inlets on the western side of the estuary within the study area. These patches and scattered individuals had coalesced to form dense mangrove shrubland by the late 1990s…".

In contrast to the lack of mangroves in the upper Waiuku prior to 1980 reported by Wildland Consultants, Crisp et al.'s (1990) Figure 9 shows several areas of mangrove within this area in the map for 1955-1960. Some (but not all) of these are in locations that are shown as being occupied by mangroves in Wildland Consultant's 1980 map. Thus, while Crisp et al. identified a decrease in the area of mangroves in the Waiuku arm between 1955-1960 and 1981, Wildland Consultants identified the reverse trend, starting from a 1969 baseline when almost no mangroves were present. It seems unlikely that the areas shown by Crisp et al. as being occupied by mangroves in 1955-1960 could have been completely infilled or cleared by 1969. Neither Crisp et al. nor Wildland Consultants presented the photographs from which their maps were produced, so the cause of the discrepancy cannot be identified. It may derive from better resolution of the methods used to examine aerial photographs and map mangrove distribution in the later study (which presumably used GIS methods that would not have been available at the time of Crisp et al.'s study). There may also have been differences in interpretation of the images between the two studies.

By 2005 the area of mangroves in the upper Waiuku mapped by Wildland Consultants exceeds that shown in Crisp et al.'s map for 1955-1960, indicating that any losses that may have occurred between 1960 and 1981 have been more than recovered.

4.2 Recent changes in mangrove distribution

Despite the extensive net loss of mangrove area worldwide, there are locations where mangroves are expanding their distribution. Panapitukkul et al. (1998) used aerial photographs from 1966 to 1995 and satellite images from 1985 to 1994 to quantify rates of mangrove progradation over a rapidly-accreting mudflat in southeast Thailand. The average rate of change of the seaward edge of the mangrove forest was ca 39 m yr^{-1}, with a maximal rate between 1966 and 1974 and minimal between 1974 and 1985. Extension of mangroves is also well documented in eastern Australia from Queensland to South Australia (Coleman 1998, Saintilan & Williams 1999, Wilton 2002 and see section 3.6.3).

Avicennia species are generally pioneers in areas where members of the genus coexist with other mangrove genera (Saenger et al. 1977). They are, therefore, likely to be very capable of colonising newly-created areas of suitable habitat. The total area of mangroves in New Zealand is currently estimated to be approximately 22500 ha (LCDB 1996/1997). Numerous studies suggest that this area may be increasing as mangroves consolidate their distribution in areas where they were already present and colonise areas where they did not previously occur. A report by the Nature Conservation Council (1984) presented an inventory of mangrove distribution in estuarine and coastal habitats throughout their range, in the form of maps based on aerial photographs taken between 1970 and 1983, and a summary table. The estimated total area in 1983 was 19343 ha, and the difference (ca 3200 ha) between this value and the current estimate by LCDB may represent a net increase over the past 20 years, although it is also likely to incorporate unknown measurement errors.

The degree of change in mangrove distribution may vary among sites within an estuary or harbour. Creese et al. (1998) found that the extent of mangroves in Whangape Harbour (west coast of Northland) changed little between 1939 and 1968 but that shoals of deposited sediment formed in the Rotokakahi River during this period, forming an island that was subsequently and rapidly colonised by mangroves. This was followed by further development of shoals and presumably these too will eventually be colonised. There was also extensive infilling of the estuary of the Awaroa River between 1968 and 1993. Across the whole harbour mangrove cover has increased by 20% over a period of 53 years (from 280 ha in 1939 to ca 340 ha in 1993: Table 6). Much of this increase (37 ha) seems to have occurred since 1981 (comparing Creese et al's value for the present extent with that in Nature Conservation Council 1984).

There was a 56% increase in the area of mangroves (from 50 ha to 78 ha) in the Puhoi Estuary, north of Auckland between 1941 and 1999 (Kronen 2001). Of this increase, only 4 ha were colonised up to 1989 and the remaining 24 ha between 1989 and 1999 (Table 6). Most expansion occurred in the lower part of the harbour. In Pahurehure Inlet, south Auckland, the area of mangroves was negligible in 1959 but is now about 76 ha (Kingett Mitchell 2005).

Around Auckland, Roper et al. (1994, their Figure 4.2) mapped changes in the distribution of mangroves in the upper Waitemata Harbour between 1940 and 1991, showing consolidation and enlargement of existing areas but relatively little spread to new areas. Morrisey et al. (1999) recorded changes in the areas of mangroves in Lucas Creek (Waitemata Harbour), Mangamangaroa Creek, Mullet Creek (Kaipara Harbour), Okura Estuary (east Auckland), Puhinui Creek (Manukau Harbour) and Whangapoua Harbour (Great Barrier Island)(Table 6). Two of these sites showed a small increase (3.0 ha or 6% in Lucas Creek and 2.5 ha or 18% in Mullet Creek) and the other 4 showed large increases (5.7-74 ha, 54-162%). Of these latter 4, only Okura and Puhinui experienced concurrent changes in catchment landuse (development of plantation forest in Okura and urbanisation in Puhinui) that could be interpreted as causal factors for the change in mangrove distribution. In Lucas Creek, the principle change observed in the estuary was the consolidation of low-density (0-25% cover) mangrove to full cover, with little net increase in area. In Okura and Puhinui there was little change in the extent of low-density mangrove and the observed increase in area mainly involved high-density areas. In Puhinui this increase occurred equally in each of the periods 1939-1969 and 1969-1996. Mangamangaroa and Whangapoua showed increases in the area of all density classes, suggesting that expansion is a continuous and ongoing process. The area of Whangapoua Harbour (Great Barrier Island) occupied by mangroves increased from 88 ha 1945 to 162 ha in 1995. More detailed analysis (NIWA, unpublished data) suggested that most of this change had occurred since 1978.

Wildland Consultants (2006) commented that mangrove expansion in the upper Waiuku arm of the Manukau seemed to be part of a wider regional phenomenon that had occurred in other parts of the Manukau before reaching the upper Waiuku arm around 1980.

Park (2004) has carried out a detailed study of changes in the distribution of mangroves in Tauranga Harbour, revealing extensive increases, most of which has occurred since the late 1970s (Table 6). Boffa Miskell (2002, cited in LaBonte et al. 2003) estimated that there had been a 117% increase in the area of mangroves across the whole of Tauranga Harbour over the past 50 years. Again, there has been considerable variation in the percentage increase among estuaries within the harbour. For example, Tanners Point and Blue Gum Bay both contained ca 0.2 ha of mangroves in 1951 (Table 6). By 2003, however, Tanners Point contained 26 ha but Blue Gum Bay only 2.8 ha.

Another area that has showed a dramatic and rapid increase in the area of mangroves is the southern Firth of Thames. On this area of open coast mudflats have been accreting rapidly since catchment deforestation began (20 mm yr^{-1} over several decades: Swales et al. 2007) and the seaward edge of the mangrove forest has progressed rapidly seaward since the 1950s (200-250 m over the 49 years to 1993: Young & Harvey 1996). By 1960 the mangrove forest was 50 m wide and by 2002 it had expanded to ca 640 m, extending nearly a kilometre seaward of the stopbank at the top of the shore (Swales et al. 2007). Sediment accumulation rates within the seaward edge of mangrove areas has subsequently increased up to 100 mm yr^{-1}.

Table 6

Summary of published information on extent of change (ha) in the distribution of mangroves in New Zealand harbours and estuaries.

Site	**Date**	**Area of mangroves (ha)**					**Saltmarsh (ha)**	**Source**
Northland						**Total mangrove**		
Whangape	1939					280		Creese et al. 1998
	1993					340		
Auckland		**Sparse**	**Low density**	**Medium density**	**High density**	**Total mangrove**		
Pukaki Creek	1964					66.8		Hume & Roper 1986
	1978					78.3		
Puhoi	1941	8	5	23	14	50	13	Kronen 2001
	1960	3	5	28	16	52	13	
	1975	8	2	13	31	54	9	
	1989	5	5	11	33	54	7	
	1999	5	4	15	54	78	4	
		0-25% mangrove	**25-50% mangrove**	**50-75% mangrove**	**75-100% mangrove**	**Total mangrove**	**13**	
Lucas Creek	1950	11.0	3.3	1.2	32.0	47.5	0.9	Morrisey et al. 1999
	1975		7.1		33.2	40.3	0.4	
	1988	1.3	1.6	2.0	43.1	48.0	0.4	
	1996	1.2	7.0	1.2	48.1	50.5	0.6	
Mangamangaroa	1960	0.6	0.9	0.6	8.5	10.5	0.5	Morrisey et al. 1999
	1997	1.9	1.4	0.5	12.5	16.2	0.7	
Mullet Creek	1953	2.8	0.8	1.2	8.9	13.7	0.7	Morrisey et al. 1999
	1996	0.9	0.7	0	14.6	16.2	0.8	
Okura	1951	4.6	1.6	1.9	7.8	15.9	0.1	Morrisey et al. 1999
	1996	3.4	1.4	0.9	19.2	24.9	0.3	
Puhinui	1939	1.6	1.5	3.0	8.4	14.4	30.8	Morrisey et al. 1999
	1969	0.5	0.6	1.2	23.4	25.8	28.1	
	1996	1.6	0.2	3.4	32.5	37.7	19.8	
Great Barrier Is.								
Whangapoua	1960	16.4	1.9	1.0	68.7	88.0	24.6	Morrisey et al. 1999
	1999	24.9	22.8	4.3	110.4	162.4	26.4	
Tauranga		**0-20% mangrove**	**20-50% mangrove**	**50-100% mangrove**		**Total mangrove**		
Welcome Bay	1943	0.00	0.18	0.45		0.63		Park 2004
	1959	0.51	0.19	0.67		1.37		
	1964	0.82	0.23	1.03		2.08		
	1969	0.30	0.35	3.18		3.83		
	1975	0.63	0.50	3.84		4.97		
	1996	0.67	2.69	14.99		18.35		
	1999	0.00	1.87	16.71		18.58		
	2003	0.00	0.00	18.09		18.09		

Table 6 (Cont.)

Site	**Date**	**Area of mangroves (ha)**					**Saltmarsh (ha)**	**Source**
Tauranga (cont.)		**0-20% mangrove**	**20-50% mangrove**	**50-100% mangrove**		**Total mangrove**		
Tuapiro	1948	0.05	0.43	0.01		0.49		Park 2004
	1960	2.09	0.83	0.31		3.23		
	1964	2.11	0.83	0.27		3.21		
	1975	5.60	0.28	1.35		7.23		
	1982	2.42	1.90	1.96		6.28		
	1999	19.41	0.06	16.55		36.02		
	2003	7.77	2.31	20.50		30.58		
Tepuna	1943	1.54	1.61	16.60		19.75		
	1959	3.54	0.69	19.77		24.00		
	1986	0.72	2.34	27.85		30.91		
	1999	0.82	0.00	41.17		41.99		
	2003	0.00	0.72	38.39		39.11		
Waikaraka	1943	0.00	0.76	0.00		0.76		
	1959	0.00	1.58	0.07		1.65		
	1986	0.00	0.20	4.43		4.63		
	1999	0.00	0.00	15.76		15.76		
	2003	0.00	0.05	13.37		13.42		
Tanner Pt North	1943	0.00	0.03	0.25		0.28		
	1959	0.00	0.09	1.16		1.25		
	1986	0.00	4.80	23.48		28.28		
	1993	0.86	0.50	33.47		34.83		
	1999	0.00	1.76	38.38		40.14		
	2003	0.00	1.25	34.39		35.64		
Hunter	1943	0.00	0.00	0.26		0.26		
	1959	0.00	0.00	0.52		0.52		
	1993	0.00	0.81	9.20		10.01		
	1999	0.00	3.21	10.12		13.33		
	2003	0.15	5.76	11.41		17.32		
Blue Gum Bay	1959	0.00	0.00	0.19		0.19		
	1993	0.00	0.00	1.87		1.87		
	1999	0.00	0.23	2.25		2.48		
	2003	0.00	5.69	1.07		6.76		
Waimapu	1959	0.00	0.00	0.22		0.22		
	1999	0.00	0.00	4.16		4.16		
	2003	1.40	0.22	5.68		7.30		

4.3 How does the current expansion compare to historical losses?

Changes in the spatial distribution of mangroves over time have involved losses and gains within and among locations, as discussed above. The lack of quantitative information on the extent of loss of mangrove forests in New Zealand harbours and estuaries makes it impossible to determine net loss or gain up to the present.

In Moreton Bay, southern Queensland, Manson et al. (2003) estimated that 3807 ha of mangrove had been lost over the previous 25 years to both natural disturbances (e.g., storms) and clearance for urban and industrial development, agriculture or aquaculture. During the same period, however, 3590 ha of new mangrove area developed, resulting in a net loss of only 217 ha (1.4% of the total area of mangroves present in 1973: Manson et al.'s Table 3).

4.4 Causes of mangrove spread

The recent expansion of mangrove vegetation observed in many coastal areas of northern New Zealand is now generally recognised as a direct response to estuarine infilling (Nicholls & Ellis 2002, Young & Harvey 1996). Other factors, such as increased inputs of nutrients to estuaries and climate change, may also contribute to the observed changes.

4.4.1 Increased inputs of sediment to estuaries and harbours

The preferred habitat for mangrove is soft, muddy, waterlogged sediments, but they are capable of colonising and growing on a variety of other substrates including fine sands, coral, volcanic rock and soil (Beard 2006). In general, mangrove growth and architecture reflect sediment type, with stunted or dwarf plants developing where propagules are rooted in shallow sediments overlying a hard layer (Crisp et al. 1990; de Lange & de Lange 1994) or where sediments contain less than 50% mud (Ellis et al. 2004). Hofstra et al. (submitted) showed that increased rates of sedimentation into estuaries in the Whitford embayment (east of Auckland) have resulted in increased spread of mangrove communities. In Whangarei Harbour, the main area of mangrove spread between 1942 and 1979 was at Portland where washings from the cement works had accumulated since 1956 (Northland Harbour Board 1985). From 1966, a stand of 1-3-m high mangroves developed occupying ca 75% of a 47-ha area adjacent to the cement works. The correlation between deposition of catchment-derived sediments and mangrove progradation in the inner Firth of Thames is discussed in section 3.2.

Sedimentation rates in many New Zealand estuaries and harbours appear to have increased following human, and particularly European, settlement. 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. Hume & Dahm (1992) examined sediment cores from 3 locations around the Coromandel Peninsula and identified changes in rates of sediment deposition over time using pollen and radiocarbon dating. They concluded that sedimentation rates were generally low (0.1-0.1 mm yr^{-1}) prior to Polynesian settlement. Rates remained unaltered or increased slightly following the first human arrivals, but increased substantially (0.3-2.8 mm yr^{-1}) following European settlement, as a consequence of forest clearance associated with logging, kauri-gum digging, mining, exotic forestry and farming. The increases in sedimentation rates following human settlement were consistent with those reported in other New Zealand estuaries, including the Waitemata Harbour and Nelson Haven (see Table 4.4 of Hume & Dahm 1992). Swales et al. (2007) refer to data collected in 1882 and 1918 indicating that ca 6.9 x 10^6 m^3 of sediment was deposited within a 16-km^2 area around the mouth of the Waihou River, Firth of Thames, and ca 36.7 x 10^6 m^3 over the southern Firth following catchment deforestation associated with logging and mining. Subsequent construction of a system of drainage channels in the Hauraki Plains is likely to have further increased rates of sediment delivery to the Firth.

Urban development has been a more recent cause of increased rates of sediment input to estuaries (Williamson 1993), as demonstrated by the study by Hofstra et al. (submitted), described above. Erosion of exposed soil during the development process, and erosion of stream banks during and following development, results in often-rapid deposition of sediment, particularly following high rainfall events. The sediment delivery ratio (i.e., amount of sediment delivered to the estuary: amount eroded: Novotny & Chesters 1981) will vary with the steepness of the catchment and the length of the drainage system but eventually all or most will arrive at the estuary. Initial deposition often occurs around stream mouths. Once deposited, sediment is subjected to continual resuspension and dispersal to other parts of the estuary and these processes may, in turn, be modified by the presence of mangroves (see section 2.6.1).

Morrisey et al. (1999) reported expansion of mangroves in Okura Estuary and Puhinui Creek (Table 6) coincident with changes in catchment landuse (development of plantation forest in Okura and urbanisation in Puhinui) that could be interpreted as causal factors for the change in mangrove distribution. Other estuaries in the Auckland region, however, showed relatively little change in mangrove distribution over time or, where expansion occurred it did not correspond with any marked change in landuse. In a system like the Waitemata Harbour, however, coupling of landuse change, sediment deposition in the estuary, and changes in mangrove distribution may be altered by import of sediment from other parts of the harbour where sediment inputs are higher. Conversely, the time-lag between landuse change and increased rates of sediment input to the estuary (and subsequent mangrove spread) depends on the retention time of sediment in the stream network.

The rate of mangrove spread in response to increased sediment deposition is dependent upon hydrodynamic parameters, such as the influence of wind-waves that remobilise sediments and reduce net sedimentation rates, leading to a gradient of sedimentation down the length of an estuary. The high sedimentation rates are reflected in surficial sediment characteristics (higher silt/clay content) and mangrove architecture (taller trees, saplings, and seedlings, and higher numbers of seedlings: Hofstra et al. submitted).

4.4.2 Nutrients

Elevated nutrient loadings (particularly nitrogen), by contributing to enhanced growth rates of plants, are also thought to be a determining factor in the acceleration of mangrove spread in some New Zealand estuaries.

Hofstra et al. (submitted) found that the soft sediments from upper-estuary sites, where both sedimentation rate and tree heights were greatest, typically contained higher concentrations of organic matter (measured as % volatile organic matter and as chlorophyll *a*) and nutrients (measured as total nitrogen and total phosphorus) than sites further down the estuary. However, as yet there is no conclusive evidence that nutrients are a main causal factor of the observed mangrove expansion (Schwarz 2002).

4.4.3 Climate change

The earliest confirmed evidence of mangrove presence in New Zealand lies with pollen preserved in sediments dated at approximately 11 000 years BP from the Firth of Thames (North Island) (Pocknall 1989). While the above location lies well within the present range of *Avicennia* in New Zealand, historically, mangrove extended much further south to the Poverty Bay – East Cape region. Pollen in sediments from Sponge Bay and Te Paeroa lagoon, approximately 140 km further south than the present natural limits, indicate a presence of *Avicennia* in this region at the time of the post-glacial climate optimum between 9000 and 7000 years BP (Mildenhall 1994, 2001, Mildenhall & Brown 1987). Mangroves may have extended even further south along the east coast during this period (Mildenhall 1994). Subsequent disappearance of mangrove from these latitudes is estimated to have occurred around 6000 years BP, and has been attributed to loss of habitat caused by rising sea levels and/or tectonic lifting of coastlines, and further to increased occurrence of frost and a climate unsuitable for mangrove survival (Mildenhall 1994).

Several aspects of current and potential future climate change may affect the growth and distribution of mangroves. Increased concentrations of carbon dioxide in the atmosphere and increased average temperatures may lead to increased rates of photosynthesis and growth of many plants, including mangroves (McLeod & Salm 2006). The effects of climate change likely to affect mangroves most strongly, however, are sea-level rise (SLR) and changes in rainfall, through their impact on sediment budgets (Ellison 1994, Field 1995).

At sites where mangroves currently occur, their distribution up and down the shore may change as a result of several interacting factors. Rising sea level may reduce their down-shore range as lower parts of the shore are flooded by the tide more frequently or permanently submerged. This may be exacerbated by erosion of lower parts of the shore at more exposed sites, due to increased frequencies of storms associated with climate change. It has been estimated that worldwide SLR could lead to the loss of up to 22% of coastal wetlands (McCarthy et al. 2001).

In areas where rates of sediment accumulation are high, however, the resulting rise in the level of the shore may keep pace with, or even exceed, the rate of sea-level rise. Studies of shoreline changes during the Holocene indicate that in some parts of the world mangrove forests were able to persist during periods when sea level rose at rates of 8-10 mm yr-1 (Woodroffe 1990). These studies suggest that in areas where sediment inputs to estuaries are large, mangrove forests may be able to keep pace with future SLR.

The current rate of sea-level rise in Auckland is 1.3 mm yr-1, but this is predicted to increase in the future, with sea levels reaching 0.4 m higher than the 1990 level by 2100 (Bell et al. 2001, Ramsay 2006: an average rate of increase of 20 mm yr^{-1}). These values are within the range of sediment accretion rates for some parts of the New Zealand coast where progradation of mudflats and mangroves is occurring, such as the Firth of Thames (accretion rates up to 100 mm yr^{-1}: Swales et al. 2007). In these areas the net effect of SLR may just be a reduction in the rate of seaward mangrove spread. Increased frequency of storms and variability in rainfall associated with future climate change may increase rates of supply of sediment to estuaries (McCarthy et al. 2001), further increasing rates of sediment accretion.

Where sediment accumulation does not keep pace, rising sea level may either reduce the width of the mangrove zone on the shore or cause them to migrate upshore, as higher levels on the shore become flooded more frequently (McCarthy et al. 2001). This migration may occur at the expense of saltmarshes behind the mangroves, unless they too are able to migrate upshore. There is evidence for such upward migration of mangroves during periods of SLR from studies of shoreline changes of glacial/interglacial cycles (Wolanski & Chappell 1996). However, there may be much larger shorter-term variation in sea level (Ramsay 2006), so that even if sedimentation rates or mangrove migration rates are able to keep pace with the average rate of SLR, there may be net loss of mangroves or saltmarsh during these periods of more rapid change. Increased rainfall may allow mangroves to migrate and out-compete saltmarsh vegetation at locations where their distribution up the shore is currently limited by high soil salinity (Harty 2004).

Migration of both mangroves and saltmarshes will be restricted where coastal defences are present – a process referred to as “coastal squeeze”. In parts of Europe, such as the Netherlands and eastern England, this potential loss of coastal habitat has been addressed through a strategy known as “managed realignment”. Rising sea levels are allowed to breach existing sea defences and low-lying areas behind them are flooded and potentially revert to coastal vegetation (Wolters et al. 2005). These areas are generally uneconomic farmland that was formerly created by infilling of the coast. The strategy thus allows the preservation of coastal habitat and avoids the high cost of defending low-value land.

Migration of mangroves to higher latitudes has also been predicted as a result of climate change (McLeod & Salm 2006) as increasing average temperatures allow them to survive at higher latitudes. Expansion of the geographical range of mangroves in New Zealand will depend on whether mangrove propagules can actually reach suitable habitats further south, and may also be limited by periodic extremes of temperature.

All of these potential effects are subject to considerable uncertainty and are likely to be influenced by other coastal changes occurring at the same time. These include changes in coastal geomorphology, water movement and associated patterns of erosion and sedimentation. These factors make it very difficult to predict how mangroves will respond to SLR at any given location or over a particular period of time.

4.4.4 Artificially altered estuarine hydrodynamics

Causeways and other restrictions across estuaries and harbours have the potential to alter estuarine hydrodynamics, resulting in increased sedimentation where water velocity is decreased and scouring where it is increased (Roper et al. 1993). Tidal flows may increase or decrease, leading to changes in water quality, salinity and stratification. Reduced flow can lead to eutrophication, increased algal growth and subsequent hypoxia as algal material decomposes. Changes in the distribution of animals and plants, including mangroves, may result from changes in sediment type and tidal range. Reduced tidal flows may encourage retention of mangrove propagules and increase the probability that propagules will establish successfully.

Increased deposition of sediment following causeway construction may have detrimental effects on existing upstream mangroves, but mangroves may subsequently recolonise rapidly (Blom 1992, Walsby 1992). In Whangarei Harbour, mangroves growing upstream of road and rail embankments and in sandpits have increased in area and percent canopy cover since 1942 (Northland Harbour Board 1985).

Roper et al. (1993) reviewed the environmental effects of 164 causeway crossings of estuaries throughout New Zealand and selected 40 for detailed examination, including 15 within the distributional range of mangroves. Slight increases in mangrove density over time were common, although the total area occupied often remained unchanged. These changes also occurred in areas away from the causeways and were, therefore, assumed not to be a direct of causeway construction. Mangroves substantially increased their areal extent at a number of sites, sometimes, but not always, in association with a general increase in mangrove coverage throughout the estuary. At the road crossing of Pahurehure Inlet (Manukau Harbour) mangroves had spread in the sheltered area upstream of the causeway, apparently as a result of causeway construction. Major catchment development has also occurred in this area, however, and may have contributed to increased sedimentation and mangrove spread.

Mangroves often colonised the flanks of embankments where the causeway provided habitat above the level of the surrounding intertidal flats. Loss of mangroves may occur as an indirect effect of causeway construction when upstream areas are subsequently infilled, as at the entrance to Waireia Creek in Hokianga Harbour (Roper et al. 1993) and in Pukaki Creek (Hume & Roper 1986).

4.5 Factors affecting the likely maximum extent of mangrove spread

As stated above, the recent expansion of mangrove vegetation observed in many coastal areas of northern New Zealand is now generally recognised as a direct response to estuarine infilling (Nicholls & Ellis 2002, Young & Harvey 1996). Historical deforestation, land-use changes and structural modifications in the estuarine environment (e.g., the construction of causeways and reclamation – see section 3.4.4) have caused significant changes in sediment dynamics and input in some estuaries, leading to elevation of intertidal areas and subsequent increases in the amount of habitat suitable for mangroves (Nichol et al. 2000). However, there are a number of factors that influence how much (if any) of this habitat is then colonized by mangroves, and also the likely maximum extent of their growth. These factors include the supply and establishment of propagules in relation to the reproductive success of existing plants, and also successful recruitment to sapling and maturity stages (given suitable habitat and growth conditions). Limitations on spread may also be imposed by the habitat requirements of *A. marina*, as discussed in section 2.2.

4.5.1 Reproductive success of existing plants

Given that *A. marina* does not reproduce by vegetative means, the only way it can colonise new areas is through a supply of propagules and the subsequent establishment of seedlings. Should any stage of the reproductive process be halted due to the effects of an unfavourable environment, disease, or herbivory, then propagule supply and potential for mangrove presence in any given area may be reduced. However, it is important to note that reproductive success, and the continued presence of mangroves, may be achieved even if only relatively few seedlings survive. For example, in estuaries where extensive tidal flushing occurs (i.e., those with less sediment input and little or no accretion occurring), many seedlings may be lost from the system, yet the mangrove stands still survive (Maxwell 1993).

Mangrove seed germination and initial development of the young plants (propagules) takes place while they are attached to the parent plant. This reproductive strategy, termed vivipary (or, in the case of *Avicennia*, cryptovivipary[1]), is advantageous because, given a pre-filtered water supply from the parent plant, it allows both for seed germination in the absence of toxic chloride effects, and reduced salt concentrations in the developing embryo (Bhosale & Mulik 1992, Farnsworth 2000). Vivipary also allows for the rapid rooting and establishment of seedlings in unstable environments (Dawes 1998). At their early stage of development a propagule is effectively a 'packaged seedling' consisting of a developing embryo, rudimentary root and leaf structures, and two fleshy cotyledons, all enclosed by a protective cover (the pericarp). Propagules continue their development while attached to the parent plant for up to five months, after which they are released and drop into water or directly onto the substrate. Being buoyant, they are then disseminated by water (Burns 1982).

The reproductive process may be affected at several stages:

- *Flowering, fertilization, germination:* in New Zealand, full anthesis of mangrove flowers (i.e., development of the flower to full maturity allowing it to either produce viable pollen or undergo fertilisation) may be prevented by low air temperatures, leading to failed germination and no further development of propagules.

  Although some literature supports the idea that mangroves are unable to reproduce at their geographic limits due to climatic constraints on flowering and fertilization (Chapman & Ronaldson 1958, Mildenhall 2001), the presence of propagules on plants at and beyond the natural range of mangrove on both east and west coasts of New Zealand indicates that neither process is completely halted by climate effects (Beard 2006, de Lange & de Lange 1994). However, flower development may be incomplete in a portion of the plants where they are exposed to low winter temperatures (Crisp et al. 1990). Further research would be required to assess what proportion of flowers (if any) is adversely affected.

- *Propagule development:* propagules are particularly vulnerable to the effects of frosts in the early stages of their development. In New Zealand, the likelihood of lethal freezing exposure is high, not only because frosts occur in many areas where mangroves grow but also because the timing of propagule development coincides with the coldest months of the year. New Zealand mangrove have a limited frost tolerance which increases with increasing latitude to a lower limit of around –5°C (Beard 2006), so frosts may not always have a lethal effect on whole mangrove plants. However, new leaves, flowers and developing propagules are more vulnerable than older leaves and branches to freezing damage because younger plant tissues generally have little cold-tolerance (Bannister 1976) and their position (mostly terminal on upper or outer branches) exposes them to the lowest temperatures, particularly in dwarf mangrove forest (Beard 2006).

  Cool winter temperatures (<+5°C) place additional stresses on mangrove photosynthetic processes (Beard 2006, Kao et al. 2004). This compromises

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[1] where the embryo grows to break through the seed coat but not the fruit wall before it splits open.

not only plant performance, health and productivity, but also the ability to replace freeze-damaged or dead parts.

4.5.2 Propagule supply (dispersal)

Dispersal of *Avicennia* propagules is entirely dependant on water, so their distribution and extent are greatly influenced by the action of both tides and currents, and by the buoyancy and longevity of each propagule (Clarke & Myerscough 1991, de Lange & de Lange 1994).

The buoyant nature and robust morphology of *Avicennia* propagules suggests an ability to disperse over long distances. However, data on dispersal movements of *A. marina* propagules in New Zealand and overseas do not entirely support this hypothesis. Observations in southern Australia indicate that dispersal between populations is likely to be a rare event and that gene flow among populations may be fairly limited, with newly-released propagules being moved predominantly on an initial flood tide and stranding at the high tide mark less than 500 m from the point of their release. Very few propagules disperse further than 10 km (Clarke 1993). Allozyme studies suggest that *Avicennia* species in the Indo-West Pacific and eastern North America also have limited gene flow, and that dispersal distances are much shorter than has been commonly believed (Duke et al. 1998b). Preliminary analyses of RAPD (random amplified polymorphic DNA) data indicate that a similar situation may exist amongst New Zealand populations (Beard & Walbert, unpublished data).

4.5.3 Seedling establishment, survival and population recruitment

Several factors determine if and where propagules will establish (anchor) in any given area. Their growth and continued presence is then reliant on favourable physical and biotic factors including climate (air and water temperature, rainfall, wind), light, salinity, nutrients, water depth, wave energy, disease and herbivory, (Clarke & Allaway 1993, Kathiresan & Bingham 2001).

Initial settling of propagules is influenced by water depth, temperature and salinity. A floating propagule will sink when its pericarp (fruit coat) is shed, a process that is stimulated by contact with water, and one that occurs more rapidly at higher temperatures and decreased salinity. Both conditions are common to estuarine rather than oceanic environments, thus providing a greater probability that propagules will sink in shallow, brackish waters where conditions are more conducive to growth. However, this window of establishment opportunity is short because most *Avicennia* propagules will shed their pericarps and sink, regardless of conditions, within 5 days of release. After sinking, propagules may refloat after a few days, although in higher salinity conditions this process takes longer (Burns 1982).

Establishment of roots is only initiated once a propagule is stationary, so the wave climate and water currents must be of sufficiently low energy to allow the propagule to come to rest. The presence of existing mangrove trees may assist this process by helping to dissipate wave and current energy by means of their stems, branches and pneumatophores. Saifullah (1994) showed that propagules have a tendency to cluster either around existing trees or in depressions protected from water movement. Burns (1982) demonstrated that establishment is also influenced by the number of obstacles present to trap propagules. The most effective traps for propagules are pneumatophores, which reach their greatest densities around existing mangrove plants. However, propagule establishment does not occur as readily where the substrate is occupied by macro-algae. For example, an investigation of establishment of *A. marina* propagules in an Australian mangrove system showed that five times more propagules established on clear ground than did when macroalgae were present (Clarke & Myerscough 1993).

Water depth is also a significant factor influencing propagule establishment. It must be shallow enough that sufficient light reaches the leaves for photosynthesis to occur, but also with sufficient tidal range that the plant is exposed for part of the tidal cycle. Young seedlings are intolerant of continuous waterlogging (Clarke & Hannon 1970), and once rooted in the substrate, require regular exposure to air. However, in their first year of growth the depth and length of tidal inundation have little effect on growth and development (other than if conditions are well outside the range in which the plant normally grows). Aerobic respiration can be maintained for several hours in the root tissue during the period when the seedling is isolated from the air by the tide. The optimum period of inundation for seedlings in a natural system is unknown, but under simulated tidal conditions, best growth occurs where the period of inundation is between 2 and 7 hours per tidal cycle (Hovenden et al. 1995).

4.6 Evidence for mangroves colonising other valued habitats

4.6.1 Bird feeding, roosting and breeding habitat

Expansion of the distribution of mangroves may benefit those birds listed in section 2.5.3 as known to use mangroves to feed, roost or breed. Where expansion of mangroves converts more open habitats, such as intertidal flats, into areas suitable for high-tide roosts or providing more concealment, there may be a local net increase in the area of suitable habitat for these birds. This does not necessarily imply a consequent increase in the number of birds, however, because birds may simply redistribute themselves to include new areas of mangroves and there may be other factors impacting on bird abundance.

Monitoring of birds in and around mangroves in Tauranga Harbour has recently started as part of an assessment of effects of mangrove control (Phil Battley, pers. comm.). Data are being collected throughout the tidal cycle (in contrast to the high-tide counts in the Firth of Thames described below, which focus on roosting areas) on distribution of birds in relation to mangroves and standing water. White-faced heron and pukeko use mangrove areas for feeding, and other species feed among seedlings. Banded rails are present in mangroves at all 4 study sites.

Conversely, colonisation of intertidal flats may deprive wading birds of feeding and roosting areas. Loss of roosting areas has been documented in the Firth of Thames (Battley et al. 2006), where dense stands of mangroves have colonised parts of the inner Firth during the period over which annual high-tide censuses of coastal birds have been conducted by the Ornithological Society of New Zealand (1960-present). Use of these roosting sites by shorebirds has steadily decreased and there has been no substantial use of the area since 1990 (Woodley 2004). This change in distribution has been particularly noticeable for wrybills (*Anarhynchus frontalis*), golden plovers (*Pluvialis fulva*), red knots (*Calidris canutus*) and whimbrels (*Numenius phaeopus*). The loss of one particular roosting area, Access Bay in front of the Shorebird Centre at Miranda, has been described in detail (Woodley 2004). This area of mudflat, enclosed by the main shell spit along the Miranda coast, provided the most significant high-tide roost for wading birds in the Firth of Thames (the area regularly held 500-4800 knots: Battley et al. 2006. Mangroves have expanded south along the bay since 1995 and now the whole area is covered in mangroves or their seedlings and is no longer available to roosting wading birds. A nearby area of pools has since become an important roosting site but it too is now experiencing colonisation by mangroves. It is not currently known whether mangrove expansion is also causing a net loss of feeding areas for wading birds in the Firth.

It is important to bear in mind that net habitat loss will only cause a reduction in numbers of birds if habitats within the range of the local populations are at carrying capacity. There is a long-standing debate about the significance of gain or loss of feeding habitat to wading birds at the population level. Effects probably depend on the relative quality of the affected area, among other factors (see, for example, Stillman et al. 2005). Currently, there is not sufficient information available to assess population-level effects. of mangrove expansionon wading birds in New Zealand.

4.6.2 Intertidal flats and seagrass areas

Down-shore colonisation of sandflats by small mangroves (1-1.5 m) has been documented from aerial photographs in Whangapoua Harbour in the Coromandel (NIWA unpublished data). At the low densities of mangroves currently present in these areas, there does not appear to have been any obvious change in the nature of the sediment around them.

Morrisey et al. (2003) examined differences in the substrates and the animals living in them between young (3-12 years) and old (>60 years) mangrove stands in Puhinui Creek, Manukau Harbour. The young sites consisted of areas of with large numbers of saplings (up to 1.6 m tall) and seedlings with relatively small numbers of pneumatophores and soft, muddy sediment. The sediment in these areas was essentially similar to that in surrounding unvegetated areas. The old stands contained mature trees (up to 4.6 m), fewer saplings but large numbers of seedlings and pneumatophores, and with compacted, organically-rich sediment with large amounts of plant detritus on the surface. The average total faunal abundance did not differ between the age classes, but the snail *Potamopyrgus antipodarum* dominated numbers at old sites. When this species was omitted from the comparison, numbers of individuals of the remaining species were larger at the younger sites. Numbers of taxa and numbers of crab (*Helice crassa*) holes were also generally higher at younger sites.

This study indicates that as mangroves colonise mudflats and the stands mature, they may cause a decrease in the abundance and diversity of the animals living in the sediments (even though the sediments are organically richer), perhaps because the reduced frequency of tidal flooding creates more compact sediments and this, and the presence of high densities of tree roots, makes burrowing difficult. Morrisey et al. (2003) did not sample the fauna living on the trees themselves, but suggested that, as stands mature, the focus of faunal abundance and diversity may move from the sediment (as in the unvegetated intertidal areas) to the insect and spider fauna of the trees.

Ellis et al. (2004) compared faunal composition and abundance among mangrove sites with different levels of sedimentation in Mangamangaroa and Waikopua Estuaries and also with nearby mudflats and sandflats in the Whitford embayment, east of Auckland. Sites with higher sedimentation had lower faunal diversity, fewer suspension feeders, and were dominated by deposit-feeding polychaete and oligochaete worms. Faunal abundance and diversity in the mudflats and mangroves were lower than in the nearby sandflats, suggesting that the fauna was responding to the increased muddiness of the sediment, rather than the presence of mangroves. The mangrove stands in this study were less mature than the older stands in the study by Morrisey et al. (2003), with shorter trees and lower densities of pneumatophores. Consequently, the sediment among the mangroves had probably not been modified to the same degree relative to that in adjacent mudflats, and effects on the fauna were less apparent.

Alfaro (2006) sampled faunal diversity and abundance in 6 types of habitat (mangrove stands, pneumatophore zones, seagrass beds, low-tide channels, channel banks, and sandflats) in Matapouri Estuary, Northland. Each habitat had a distinctive faunal assemblage, although some taxa, such as cockles (*Austrovenus stutchburyi*) and pipis (*Paphies australis*) occurred across all habitats. Diversity and total abundance were highest in sandflats and lowest in mangroves. Pneumatophore zones, however, had relatively high abundance and diversity and appear to act as important transition environments between seagrass and mangroves. Although pneumatophore abundances were similar to those in the younger stands in the study by Morrisey et al. (2003), the sediments around them were relatively sandy and faunal abundance and diversity may reflect an interaction between the habitat complexity provided by pneumatophores and the texture of the sediment. Abundances of cockles were lowest, but the individual animals were largest, in the mangrove habitats. Seagrass beds contained large numbers of juveniles, suggesting that they recruit to this habitat but that mangroves and pneumatophore zones may still represent important habitats for this species.

In a separate study, Alfaro (in press) demonstrated that the snail *Turbo smaragdus*, a dominant intertidal grazer in Matapouri Estuary, migrates upshore during high-tide periods, from low-shore seagrass beds to higher-shore pneumatophore and mangrove areas. Movements appeared to be related to the relative abundance of macroalgal food in the different habitats. Abundances were highest in the pneumatophore area during tidal immersion and lowest in the mangroves, but the average size of individuals was largest in the mangroves (and see Taylor 1983). Large snails appeared to feed on filamentous macroalgae and microalgae on the sediments and plant structures. This study again suggests that while mangrove areas may not contain the largest abundances of a given species, they may still be important at the population level. It also implies that low-tide surveys of the faunas of mangroves (and other intertidal habitats) may underestimate their faunal abundance and diversity.

Where seagrass beds occur adjacent to mangroves, as in Matapouri Estuary (Alfaro 2006), any downshore progradation would be expected to invade seagrass beds and eventually exclude them through a combination of shading and effects of increased sedimentation. It is, however, likely that seagrass beds will already have been adversely affected by high concentrations of suspended sediment and sediment deposition in those estuaries and harbours where mangroves are spreading rapidly. For example, Hume & Roper (1986) recorded an increase in the area of mangroves in Pukaki Creek between 1964 and 1978 (Table 6), coincident with modification of the estuary by construction of Auckland Airport (1960-1961) and a causeway across the creek (1964). Reduction in estuarine area and constriction of the inlet resulted in reduced tidal flushing. Urbanisation of the catchment after 1964 probably led to reduced water quality and increased sediment inputs to the creek. Between 1961 and 1965 the area of seagrass at the mouth of the creek varied between 2.8 and 4.3 ha. From 1966, however, all seagrass disappeared. Seagrass decline had been reported in other parts of the Manukau around this time, probably due to disease, which is consistent with the rapid loss of seagrass in Pukaki Creek. Whether seagrass disappearance was due to disease or deteriorating water quality, it seems unlikely that mangrove spread was the direct cause of such a rapid change.

4.6.3 Saltmarsh and fringing wetlands

Saltmarshes are vegetated intertidal flats dominated by low-growing halophytic shrubs, herbaceous plants and rushes. Largely confined to temperate coastlines, they occupy a similar niche to mangrove forests (Frey & Basan 1985). Throughout the upper North Island of New Zealand, saltmarsh and mangrove often intermingle, but the habitats differ in floristics and intertidal position. Where both are present, saltmarsh usually occupies a higher elevation and a more landward position, and as such is subject to fewer tidal inundations than the mangrove areas.

In Australia, expansion of mangrove into saltmarsh habitat is a well-documented phenomenon, and has been attributed to a number of mechanisms including climatic change, altered tidal regimes, sedimentation, subsidence, increased nutrient levels and changes in the salinity of estuarine waters (Coleman 1998, Saintilan & Hashimoto 1999, Saintilan & Williams 1999, 2000, Williams & Meehan 2004). Saintilan & Williams (2000) reviewed photogrammetric surveys of changes in saltmarsh and mangrove distribution at locations in eastern Australia, which showed substantial losses of saltmarsh at 28 locations. The main cause of these changes was the landward expansion of mangroves (mainly *A. marina*), with urban development providing a secondary cause. Wilton (2002) measured changes in the area of mangroves at 9 locations in New South Wales using aerial photographs from the 1940s/1950s to the 1990s. Some sites developed substantial areas of mangroves where none had existed before while other sites that already had large stands of mangroves increased further. One location (Ukerebagh Island, Tweed River), in contrast, showed a decrease in total area between 1948 and 1961 (47.1 ha to 37.7 ha) and a net loss of 1.9 ha between 1948 and 1998. In all sites mangrove expanded landward, in some they also expanded seaward, but in no case did they just expand seaward. Landward expansion generally occurred at the expense of existing saltmarsh communities, with an average 42% reduction in the area of saltmarsh over the period from the 1940s to the late 1990s, most of which was due to mangrove incursion. Coleman (1998) recorded landward expansion of mangroves into saltmarsh (samphires: mixed species of *Sarcocornia* and *Halosarcia*) in South Australia. There was also some seaward expansion and, in addition, samphires colonised some previously bare areas and some areas previously occupied by mangroves. Overall, however, there was a net reduction in the area of saltmarsh over time, notably during the period 1985-1993.

Rogers et al. (2005, 2006) measured changes in shore surface elevation, vertical accretion of sediment and changes in the distribution of saltmarsh and mangroves in 7 estuaries in southeastern Australia. There was a general trend in decreasing area of saltmarsh and increasing area of mangroves at all sites studied but rates of decrease were usually lower in Victoria than in New South Wales. Rates of sediment accretion were faster than corresponding rates of increase in surface elevation, indicating that sediments were compacting as they accumulated. Rates of mangrove expansion into saltmarshes were highest where the rates of increase of saltmarsh surface elevation were low (even though rates of accretion may have been relatively high). In these areas, increasing surface elevation of saltmarshes may have been failing to keep pace with sea-level rise, increasing the frequency of tidal inundation and promoting mangrove expansion. Mangrove expansion is dependent on relative rates of sea-level rise, sediment accretion and sediment compaction or subsidence. Rates of compaction and subsidence are likely to vary among sites, corresponding to differences in soil properties and rainfall.

As mangroves colonise areas landward of their previous distribution in southeast Australia, they extend their elevational range beyond that normally shown (by 0.09-0.74 m: Wilton 2002). This migration seems to have occurred since European colonisation and runs contrary to longer-term patterns of coastal vegetational change in which the upper parts of mangrove forests are replaced by saltmarsh, presumably as frequency of inundation decreases with increasing bed height (Saintilan & Williams 1999). Saintilan & Williams (1999) documented landward migration in a range of geomorphological settings, but noted that it was not a universal phenomenon even within the same locality.

There is little documented evidence of similar landward incursions of mangrove in New Zealand. Park (2004) reported colonisation of the edges of saltmarshes by mangrove in Tauranga Harbour, but this was neither a general pattern throughout the harbour (some boundaries remained stable over the 45-year analysis period), nor was it on a large scale, with edge invasions by mangrove averaging 5-10m during that time. Healthy rush communities appeared to be fairly resistant to mangrove colonisation and in many areas salt marsh had actually increased in area during the analysis period. Greatest mangrove incursions were associated with areas where salt marsh vegetation was sparse, or where channels and substrate allowed propagules to be carried and to establish.

In the Firth of Thames, Graeme (2006) noted that saltmarsh occurs under areas of open, mature mangroves in some areas, increasing floral diversity. The fact that these were mature mangroves suggests that they had coexisted with the saltmarsh for some time or even that saltmarsh had colonised the mangrove areas. The introduced saltmarsh grass *Spartina* sp. was also present in some areas within the mangroves where they had been disturbed, for example by tracks. In Pahurehure Inlet there have been documented changes in the distribution of saltmarshes concurrent with mangrove expansion, but with no net loss of saltmarsh (Kingett Mitchell 2005). Examples of these changes in saltmarsh distribution include the conversion of areas of sandflat to mudflat as a result of sediment deposition, followed by saltmarsh colonisation.

Of the 6 locations examined by Morrisey et al. (1999: see Table 6), only 1 (Puhinui Creek in the Manukau Harbour) showed a clear decrease in the area of saltmarsh (from 30.8 ha in 1939 to 19.8 ha in 1999). This estuary experienced extensive urbanisation of its catchment from the late 1960s and this has been associated with the creation of grassed foreshore reserves, dumping of rubbish at the top of the shore and, on the north side of the inlet, grazing and trampling of upper-intertidal areas by cattle (Morrisey pers. obs.). There was no evidence that mangrove expansion was the cause of saltmarsh loss.

It is not known why landward invasion of saltmarshes by mangroves should be an apparently common event in Australia but almost unknown in New Zealand. It may, of course, simply be due to the relatively small number of detailed studies of changes in mangrove distribution. It may also reflect differences in the history of sedimentation patterns in estuaries between the 2 regions, differences in patterns of rainfall and associated soil compaction, or differences in the composition of the saltmarsh communities and their associated vulnerability to invasion (for example, tall, dense rush communities versus lower, more open samphire communities).

We are not aware of any evidence for invasion of other wetland habitats by mangroves in New Zealand. Freshwater wetlands occur at higher elevations than mangroves and, as indicated above, mangrove expansion in New Zealand almost invariably occurs to seaward. They are therefore unlikely to invade freshwater habitats.

4.6.4 Do mangroves provide habitat for rats?

We are not aware of any quantitative evidence for the use of mangroves by rats. It is very likely that rats would use mangroves as habitats even at high tide, since 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, and concluded that they were feeding on vegetable matter. As far as we know there is no information on predation of 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. Weasels have also been occasionally sighted in mangrove forests (Blom 1992).

4.6.5 Are areas of mangrove expansion reducing biodiversity?

As discussed in sections 3.6.1-3.6.3, mangrove expansion may result in reduced diversity for some components of estuarine biotas. For example, infaunal diversity appears to be generally higher in seagrass beds, sandflats or mudflats than in nearby mangroves, and diversity of birds that feed on intertidal flats also decreases when mangroves colonise their habitat. The diversity of other components, such as insects, spiders and birds living on the mangrove trees themselves may, however, increase but our knowledge of these relative changes is very incomplete. Consequently, it is difficult to assess changes in diversity when a particular area of mudflat or seagrass bed changes to a stand of mangroves. At an estuarine scale, however, it is likely that loss of habitat diversity as a result of mangrove expansion will lead to overall loss of biological diversity. It is also important to bear in mind that loss of habitat diversity, and the diversity of species associated with habitats that are lost, may be caused by the factors that led to mangrove spread, such as increased rates of sediment deposition or reduced water quality, rather than the mangroves themselves (Ellis et al. 2004).

4.7 Does the value of mangroves to the ecosystem vary with their location?

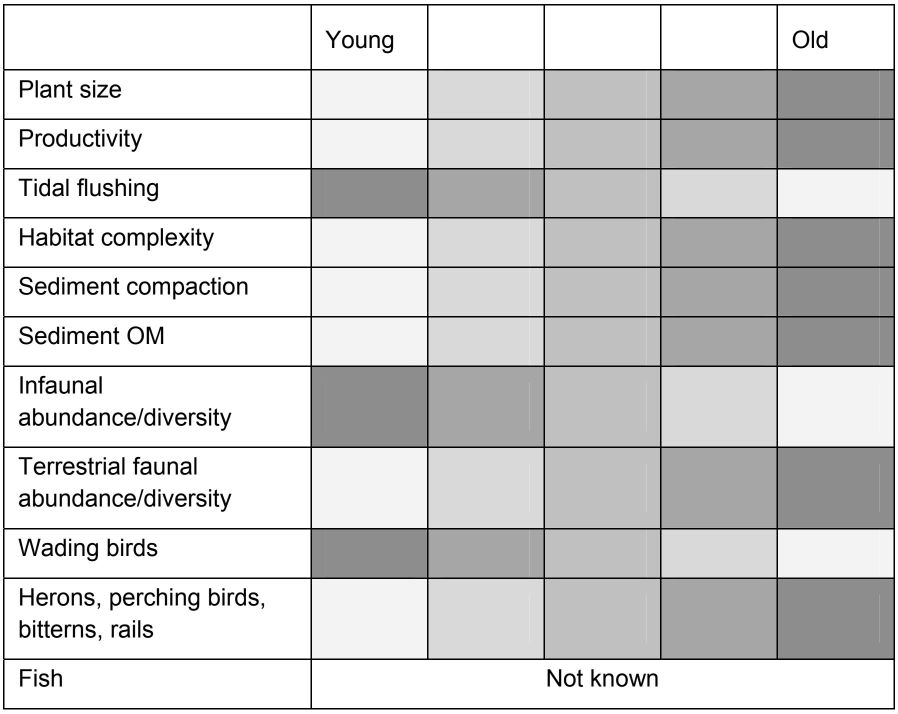
The previous discussions of variation in plant size, architecture and productivity and the diversity and abundance of associated species among different locations suggests that the answer to this question is “yes”. There are a number of different gradients present within mangrove habitats, each of which may influence the characteristics of the mangroves living there, and many of which interact.

4.7.1 Gradients in mangrove age

Age variations in mangrove characteristics that affect their value are summarised in the diagram below. The interaction between plant size, and associated productivity, and tidal flushing may produce areas within the forest that are particularly important in terms of exporting nutrients and organic matter to adjacent habitats. This may be maximal in places where the largest mangroves line the banks of the low-tide channels. Where the largest mangroves are at the top of shore, where tidal immersion occurs in frequently, much of the organic matter may be recycled in situ. In some areas high on the shore dwarfing of mangroves occurs and the size of trees does not reflect their age in these areas.

Variation in faunal diversity across age gradients is difficult to identify because we know so little about the terrestrial fauna (insects, spiders, etc.) of mangroves. Other components of the fauna vary with plant age and size as shown. Eels respond positively to increase benthic habitat diversity (Morrison et al., in prep.), and favour mangrove areas to open mudflats, but there is of course a trade of between complexity and duration of tidal immersion where the largest mangroves lie at the top of the shore. There is little evidence for such a preference in other species.

Summary of environmental and biological variation along gradients of mangrove age (in this and subsequent tables, darker shading indicates an increase in the variable in question).

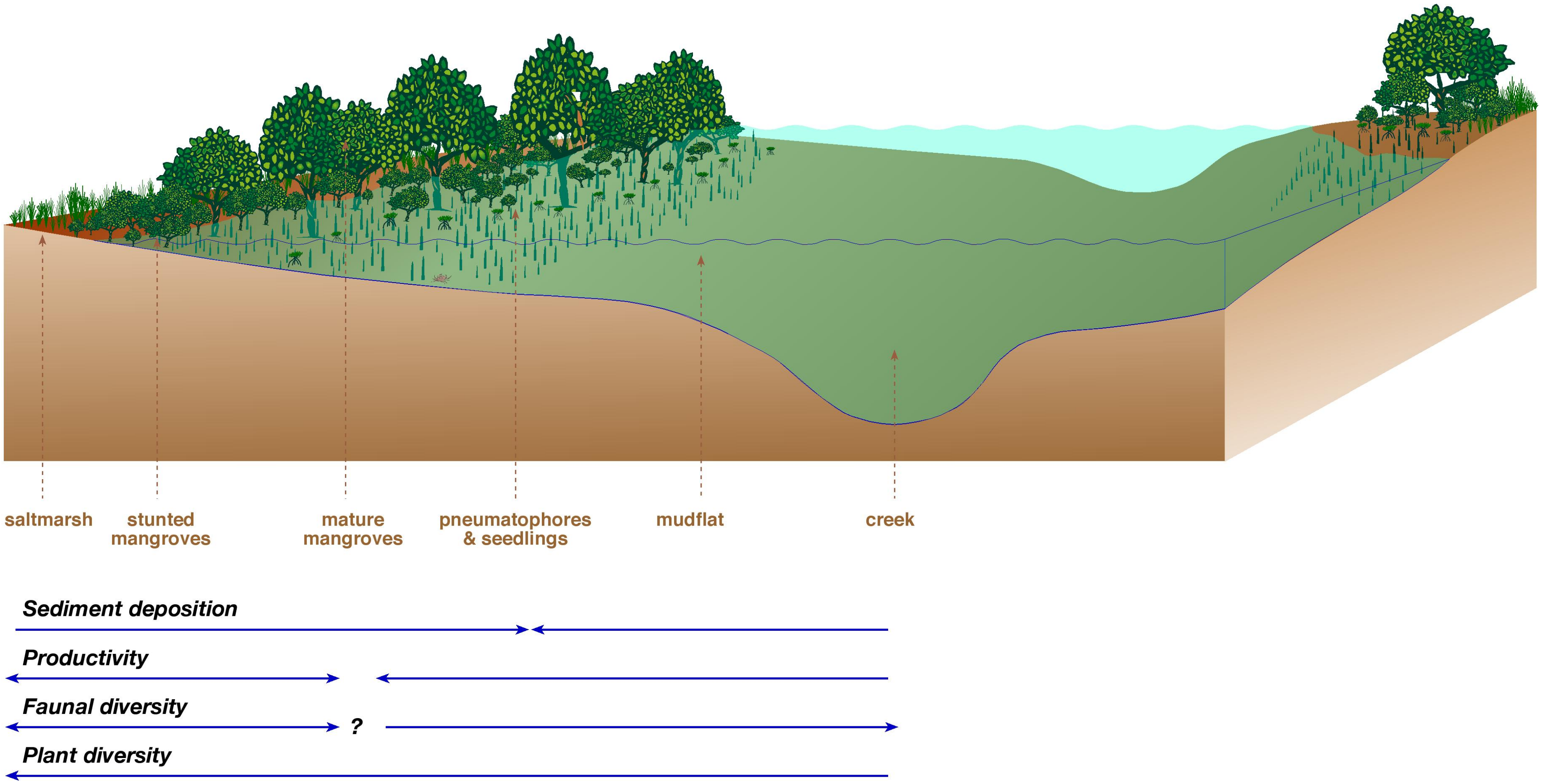


	Young				Old
Plant size	□	░	▒	▓	█
Productivity	□	░	▒	▓	█
Tidal flushing	█	▓	▒	░	□
Habitat complexity	□	░	▒	▓	█
Sediment compaction	□	░	▒	▓	█
Sediment OM	□	░	▒	▓	█
Infaunal abundance/diversity	█	▓	▒	░	□
Terrestrial faunal abundance/diversity	□	░	▒	▓	█
Wading birds	█	▓	▒	░	□
Herons, perching birds, bitterns, rails	□	░	▒	▓	█
Fish	Not known				

4.7.2 Gradients in elevation across the shore

The compaction of the sediment generally increases up the shore, as does the concentration of organic matter in it (Morrisey et al. 2003) and the porewater salinity. Sediment deposition rates tend to be highest among the mangroves and pneumatophores (Young & Harvey 1996). Morrisey et al. (2000) sampled at different heights on the shore at several locations in each of 2 mangrove-lined estuaries but found no evidence that concentrations of sediment-associated contaminants were higher within the mangrove or pneumatophores zones (although they did not sample at more than one height within the mangroves). Mangrove size shows several patterns in relation to elevation. In areas bordering low-tide channels the largest (and most productive mangroves) often occur along the creek banks, with a zone of pneumatophores in front of them. Where the intertidal area is wide, intertidal flats may lie behind the mangroves, occupied by stunted trees bounded at the upper level by saltmarsh or terrestrial vegetation. In other places, including many where mangroves have expanded rapidly down-shore, the oldest and largest trees are at the back of the shore, with progressively younger, and smaller trees down the shore. As with gradients of age (with which the elevation gradient is highly correlated), the interaction between plant size and tidal flushing may produce areas within the forest that are particularly important in terms of exporting nutrients and organic matter to adjacent habitats. These gradients are summarised in Figure 11 and the table below. There is little or no information available on how differences in fish use of mangroves at different heights on the shore.

Figure 11
Cross section through a mangrove-lined creek showing distribution of habitats, relative rates of sediment deposition and primary production, and relative biological diversity.



Summary of environmental and biological variation across the shore.

	Low		Mid		High
Tidal flushing	█	▓	▒	░	□
Sediment porewater salinity	□	░	▒	▓	█
Sediment compaction	□	░	▒	▓	█
Plant size, productivity and habitat complexity (large trees at top of shore) **OR**	□	░	▒	▓	█
Plant size, productivity and habitat complexity (large trees along creek banks)	█	▓	▒	░	□
Sediment OM	□	░	▒	▓	█
Infaunal abundance/diversity	█	▓	▒	░	□
Terrestrial faunal abundance/diversity	□	░	▒	▓	█
Wading birds	█	▓	▒	░	□
Herons, perching birds, bitterns, rails	□	░	▒	▓	█
Fish	Not known				

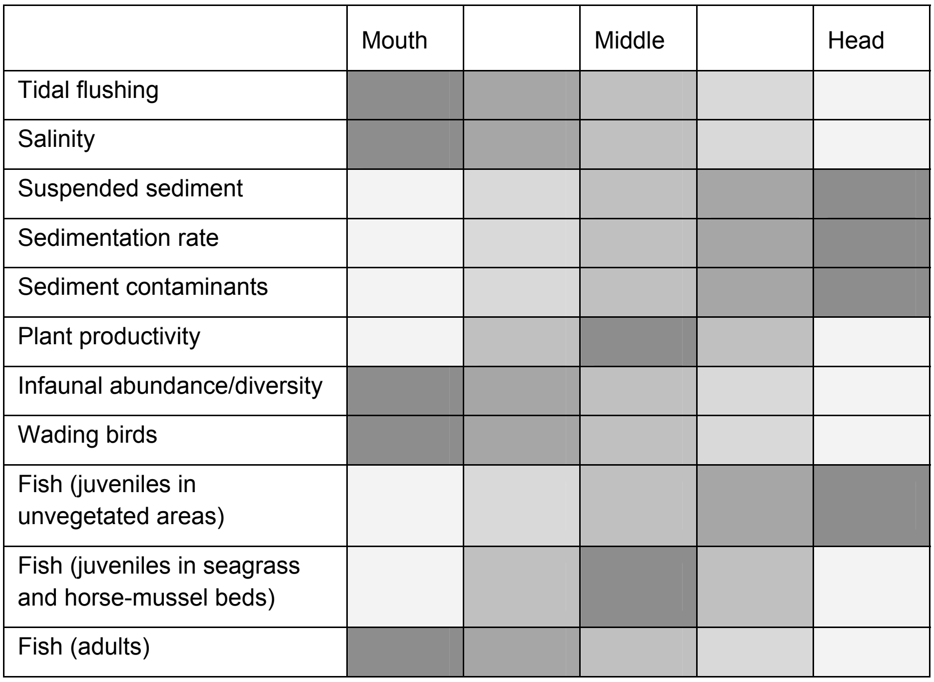
4.7.3 Gradients along an estuary

The strongest environmental gradients along an estuary are those of salinity and suspended sediment. Salinity increases seaward while suspended sediment concentrations increase upstream. Sediment deposition rates are highest at the head of the estuary, where mixing of fresh and saltwater causes flocculation and deposition of suspended particles. Contaminants associated with suspended sediment also accumulate in the upper reaches of the estuary (Williamson & Morrisey 2000). As emphasised above, at any point along the length of the estuary there will be interacting gradients, such as variation in physical environmental factors across the shore.

The optimal salinity range for *A. marina* is ca 50% of seawater (Beard 2006 and see section 2.2), and productivity and growth is likely to be highest in this part of the gradient. Plant size and structure, however, will vary considerably at any point along the estuary depending on height on the shore and other factors. Faunal diversity generally decreases upstream, partly in response to the decreasing and more variable salinity (a pattern common to estuarine biotas in general) and partly in response to increasing rates of sediment deposition (Ellis et al. 2004), as observed in the Whitford embayment (Nicholls & Ellis 2002). Productivity and diversity increase again in freshwater habitats, but these are beyond the range of mangrove distribution and are not considered here. Human developments also tend to be focussed at the heads of estuaries, and environmental degradation may therefore be more severe in these areas, further decreasing productivity and biological diversity (see section 3.7.4).

Numbers of wading birds may be larger on wider intertidal flats near the mouth of the estuary. While overall diversity and abundance of small fish often increases with turbidity and 'muddiness' up to a point (independent of mangrove presence/absence, as evidenced by sampling of estuaries without mangroves), most of the more valued recreational and commercial fish species (e.g., snapper, trevally, kahawai, and small coastal sharks) prefer cleaner water and/or three-dimensional benthic biogenic habitats (e.g., seagrass and horse mussel beds for juvenile snapper and trevally), especially as juveniles. Fish living in and around mangroves, such as yellow-eyed mullet, smelt, and triple-fins, tend to be small and of little commercial value (with the exception of grey mullet, eels, and yellow-belly flounder). Several small species that favour these general muddy environments and that are highly abundant e.g., anchovies and speckled soles (not found in mangroves), may prove to be important 'forage' fish' for larger fish and birds at later adult stages, when they move off-shore, but the importance of mangroves (if any) in this possible relationship is unclear.

Summary of environmental and biological variation along an estuary.



	Mouth		Middle		Head
Tidal flushing	█	▓	▒	░	
Salinity	█	▓	▒	░	
Suspended sediment		░	▒	▓	█
Sedimentation rate		░	▒	▓	█
Sediment contaminants		░	▒	▓	█
Plant productivity		▒	█	▒	
Infaunal abundance/diversity	█	▓	▒	░	
Wading birds	█	▓	▒	░	
Fish (juveniles in unvegetated areas)		░	▒	▓	█
Fish (juveniles in seagrass and horse-mussel beds)		▒	█	▒	
Fish (adults)	█	▓	▒	░	

4.7.4 Gradients of human impact and environmental degradation

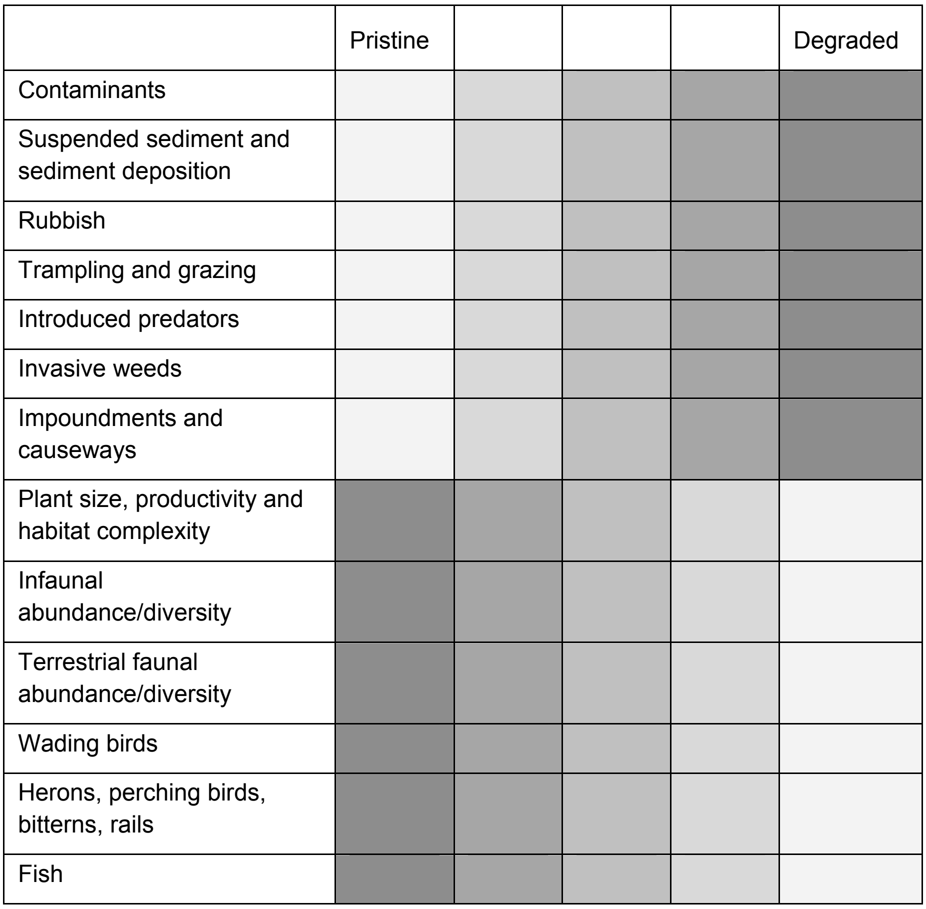
In Whangateau Harbour, Blom (1992) found that mangrove stands receiving landfill leachate were stunted, showed reduced growth and contained less diverse benthic macrofaunal assemblages than control areas. Stands that experienced altered patterns of water movement as the result of construction of a causeway suffered initial damage due to increased rates of siltation, but mangroves subsequently recolonised the area. Grazing by cattle on mangroves in Puhoi Estuary resulted in reduced size of trees, densities of pneumatophores and abundance and diversity of macrofauna (Blom 1992, Kronen 2001). Of 79 sites assessed in Puhoi Estuary, only 24 (30%) were unaffected by cattle grazing or borer (*Oemona hirta*) infestation (Kronen 2001).

Causeways for roads and railways and other obstructions to tidal flow are more common at the heads of estuaries, where they are nearer to other human developments and where the distance to be spanned is shorter. Dick & Osunkoya (2000) found that rates of decomposition of *A. marina* litter were slower landward of floodgates on a tidal channel in New South Wales. They concluded that litter on the tidal side of the obstruction contributed more strongly to the estuarine food web than that on the landward side.

Causeways often lead to increased sediment deposition on the landward side (Roper et al. 1993). Although mangroves are relatively tolerant of sediment deposition, and are able to colonise intertidal areas where high rates of sedimentation have raised the elevation to the critical height for mangrove survival, excessive deposition of sediment can be detrimental to them (Blom 1992, Walsby 1992, Ellison 1998). There are several reported cases of *A. marina* in Saudi Arabia, Queensland and northwest Australia dying or showing reduced "vitality" following deposition of silt or sand. Causes of increased sedimentation included causeway construction and dumping of dredge spoil. Death of *A. marina* seems to occur when the depth of deposited sediment is sufficient to cover the pneumatophores (ca 10 cm), but there are also cases where death has occurred despite only partial burial. The rate of burial is clearly important in determining mangrove response, since sedimentation rates of up to 100 mm yr^{-1} in the Firth of Thames have been associated with the spread of mangroves (Swales et al. 2007). Subsequent recolonisation following burial can be rapid. Walsby (1992, p. 56) presented a photograph of the dead remnants of a mangrove stand after construction of a causeway in Whangateau Harbour and another taken 10 years later showing the area once again full of mangroves 1-2 m tall. Causeways and other restrictions to the flow of water may restrict access by fish to mangrove areas upstream and reduce the export of organic matter to downstream areas.

Since levels of human impact tend to increase towards the heads of estuaries, and up the shore (where access is easier), gradients of impact will often correlate very strongly with other, natural factors that vary along these gradients.

Summary of environmental and biological variation along human impact and environmental degradation.



	Pristine				Degraded
Contaminants	⬜	░	▒	▓	█
Suspended sediment and sediment deposition	⬜	░	▒	▓	█
Rubbish	⬜	░	▒	▓	█
Trampling and grazing	⬜	░	▒	▓	█
Introduced predators	⬜	░	▒	▓	█
Invasive weeds	⬜	░	▒	▓	█
Impoundments and causeways	⬜	░	▒	▓	█
Plant size, productivity and habitat complexity	█	▓	▒	░	⬜
Infaunal abundance/diversity	█	▓	▒	░	⬜
Terrestrial faunal abundance/diversity	█	▓	▒	░	⬜
Wading birds	█	▓	▒	░	⬜
Herons, perching birds, bitterns, rails	█	▓	▒	░	⬜
Fish	█	▓	▒	░	⬜

4.7.5 How do mangroves at either end of the estuarine gradient compare to the other habitat values present?

Our very limited knowledge of the absolute and relative ecological values (such as productivity and biological diversity) of mangroves and other estuarine habitats makes it difficult to draw any general conclusions about relative values of different habitats along the estuarine gradient. There are also value-judgements involved in assessing, for example, the relative importance of the suite of species associated with one type of habitat with that of another. The previous section of this report suggests that productivity and health of mangroves may be reduced in relatively degraded habitats, and the diversity of the associated biota may also be lower. Productivity and diversity in such areas is, however, likely to be relatively low whether or not mangroves are present, and in some cases mangrove growth may be enhanced in degraded areas, such as those where mangrove spread is occurring in response to increased rates of sedimentation.

The relative productivity of different habitats may vary along the gradient from the mouth to the head of the estuary with, for example, freshwater wetlands becoming relatively more important at the head and seagrass beds at the mouth. The importance of their exported plant material to nearby habitats may vary correspondingly but this is not certain because it depends on the extent of connections among habitats. For example, freshwater wetlands behind the shore in the upper estuary may have higher productivity than nearby mangroves or saltmarsh, but their importance as sources of organic matter and nutrients to estuarine mudflats may be much less if they are not closely connected via water movement. In terms of fish, mangroves in more pristine systems, and that are immediately adjacent to seagrass beds, are likely to have different fish assemblages (and associated fish habitat values) from those remote from seagrass beds (see Jelbart et al. 2007, discussed in section 2.5.2, for an Australian example; there is some limited evidence for such landscape effects from Rangaunu Harbour, New Zealand).

In addition to productivity per unit area, the relative area of different habitats also affects their overall contribution to the functioning of the estuarine ecosystem. To date, there have not been any comparative studies with sufficient spatial resolution to address this issue.

The relative importance of mangroves at different heights on the shore, in terms of contribution to nearby habitats, will also depend on a combination of productivity and degree of connection. Saltmarsh productivity may be comparable to, or exceed, that of stunted, high-shore mangroves but because both are infrequently flooded by the tide, export of material to lower-shore habitats will be restricted relative to that of mangroves further down the shore. Faunal and floral diversity of high-shore habitats, such as saltmarshes and fringing terrestrial vegetation, may be higher than that of mangrove stands. Mangroves nevertheless represent an important zone of transition between terrestrial and estuarine or coastal biota, making simple comparisons of diversity less useful indicators of “value”.

Soliman (2004) did not find any differences in concentrations of zinc among sediments from mangroves, seagrass beds or sandflats in Matapouri Estuary, nor between mangrove and seagrass leaves. The type of response of mangroves to gradients of human impact is probably similar to that of other habitats, such as seagrass beds, saltmarshes and intertidal flats, although the size of response may vary. Seagrasses, for example, are likely to be more sensitive to poor water quality, high inputs of nutrients and high suspended-sediment loads than mangroves (e.g., Hauxwell et al. 2003, Terrados et al. 1998). Trampling, infilling and other physical disturbance of habitats bordering urban or industrial areas is probably also similar for mangroves and saltmarsh. Determining the effect of environmental quality on the relative values of mangroves and other habitats is confounded by the presence of other environmental gradients. It is inevitably highly site-specific and, given our very poor understanding of the issues, likely to be dealt with best, from a management perspective, on a case-by-case basis.

4.8 Minimal “critical mass” of mangroves required to retain a sustainable mangrove ecosystem

There may be a minimum critical size required to sustain a mangrove stand in terms of, for example, the amount of organic matter produced and exported to surrounding areas and the diversity of animals and plants that it contains but this issue is very poorly understood for New Zealand mangroves.

In the case of seagrass patches in New Zealand estuaries, Turner et al. (1999) found that patch size was a poor explanatory variable for infaunal differences. They suggested that this was partly due to the dynamic nature of seagrass patches, which vary in size, density of cover and other properties over reasonably short time scales (for example, seasons). At a larger spatial scale, environmental variables such as distances among patches and complexity of shape were important explanatory variables. Mangrove stands are less dynamic than seagrass patches, but we do not have the necessary information to identify critical sizes.

Critical size may, in any case, vary with the definition of sustainability. In contrast to tropical mangrove assemblages, where several species of mangroves and associated vascular plants occur in the same stand, New Zealand mangrove stands are generally monospecific. Vascular plant diversity is therefore not a major concern when assessing ecological sustainability. The dispersal capabilities of the mangroves themselves ensure that a stand is likely to persist even if it does not produce enough of its own recruits to maintain itself, as long as there are other stands within dispersing distance. The same argument probably holds for the fauna, including infauna living in the sediment, marine and terrestrial epifauna living on the trees, fish and birds. None of these occurs exclusively in mangroves and all are likely to be able to recruit from surrounding areas in sufficient numbers to maintain populations in the stand. On the other hand, the contribution of the stand to surrounding habitats may be proportional to its size or some derivative of this, such as the ratio of area to perimeter.

4.9 Mangrove management initiatives in New Zealand

4.9.1 Background

Attitudes toward mangrove in New Zealand have undergone a number of changes since the first occupation of these islands. The first Pacific settlers held the mangrove “Manawa” and its associated habitat in high regard as a source of food, fuels and medicines (Crisp et al. 1990). Although some of these values still persist through to the present day, attitudes changed radically with European settlement in the late 1800’s. Mangroves were considered useless, with little in the way of aesthetic or economic value. These attitudes were particularly prevalent where mangrove occupied potential reclamation 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, for example the Hokianga, approximately 34% of mangrove were destroyed (Chapman 1978). By the late 1970’s perceptions of mangrove in New Zealand changed again; a move championed largely by Professor V.J. Chapman whose work, along with others, emphasised the unique ecological and economical values of mangrove. 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). Of these, only four are full reserves (Mom 2005).

The Resource Management Act (1991) allows governing bodies to uphold protection of mangroves against indiscriminate destruction and/or reclamation. However, concerns over recent expansion of mangrove areas, coupled with a push to preserve the ecology of adjacent habitats (e.g., saltmarsh, seagrass beds and open mudflats), has 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 polarized, 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 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 the North Island have removed mangroves from estuaries in protest at controls and perceived inaction.

4.9.2 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 mangrove-occupied areas, 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 this 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 mangrove form a significant component of the protected foreshore vegetation are Motu Manawa (Pollen Island) marine reserve in the Waitemata Harbour, and Te Matuku marine reserve, Waiheke Island; both managed by the 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, whereby seedling mangrove plants may be removed from newly colonized mudflats (a seedling being defined as a mangrove plant with 2-12 leaves, one stem and between 5 and ca 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 pre-determined baseline. The main aims of this approach are to preserve the ecology of habitats threatened by mangrove encroachment (for example; saltmarsh, eelgrass beds, open mudflat); to restore aesthetic values in an estuary (for instance; 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 substrate 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 since there is a general acceptance that mangrove expansion is a response to increased sediment input into harbours and estuaries. 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 to provide physical works, services and advice to landowners to reduce the risk of soil erosion and flooding, reduce the amount of sediment getting into waterways, 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 (Mom 2005, Nichol et al. 2000).

4.9.3 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. However, impacts of human disturbance (i.e., clearance) in mangrove forests elsewhere in the world may provide some answers. Research indicates 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). 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 and/or compaction of soft sediments. These processes affect the ability of organisms to re-establish in the substrate 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, this 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).

Sediment grain size may also be altered following mangrove removal, as a result of changes to runoff, and current and tidal flows brought about by the absence of the trees and pneumatophores. Sediments in highly altered mangrove areas in 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 substrate following mangrove clearance may increase the possibility of erosion and transport of sediments to other areas that, 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.

On-going monitoring of mangrove areas before and after removal in two North Island 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 et al. 2005, Wildland Consultants 2005).

4.9.4 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. Of the approximately 90 countries that have mangrove vegetation, around 20 have undertaken rehabilitation initiatives (Field 1998), establishing nurseries and attempting afforestation of previously uncolonised mudflats and re-planting 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 to the present day, albeit on a much smaller scale (Crisp et al. 1990 and see section 3.1). Even though mangrove 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 (for example, Mohakatino, Mokau and Urenui river mouths), 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 in the first place are removed or discontinued. In some cases, mangrove wetlands will then self-repair if the necessary natural processes, such as seedling recruitment and hydrology, are still intact. Otherwise, given appropriate environmental conditions (for example; wave energy, salinity, pH, nutrient concentrations, substrate composition, inundation etc.), successful rehabilitation may be a long-term process dependant on human assistance and ongoing active management (including re-planting and weed control)(Gilman et al. 2006).

4.9.5 Effectiveness of mangrove management initiatives

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

Research has established that, regardless of which approach is decided upon, 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 proved inadequate not only for communities seeking guidance or action on mangrove management, but also for the governing agencies responsible for providing those services.

Recognition of the need for further research and communication, coupled with increasing pressure from community groups, led to the formation of the Mangrove Steering Group in 2001. The group was established to identify knowledge gaps and facilitate information exchange between all concerned parties. It includes representatives from Northland, Auckland, Waikato, and Bay of Plenty Regional councils, Department of Conservation, Universities, Landcare Research, NIWA, Royal Forest and Bird Protection Society and Iwi.

4.9.6 Regulatory approaches to mangrove management

Four Regional Councils (Northland, Auckland, Waikato and Bay of Plenty) have responsibility for regulating mangrove-control activities with a view to managing adverse effects on the environment. Decisions on resource consents and whether to allow or prohibit specific activities are made on the basis of the principles of the Resource Management Act (RMA), the national policy of the New Zealand Coastal Policy statement (NZCPS), and the objectives, policies and rules of the relevant Regional Coastal Plan and Regional Policy Statement. The consent authority (i.e., the Regional Council, or, for specific cases, the Minister for Conservation) holds the decision on whether or not to grant consent, and to impose conditions.

A number of regulatory approaches to mangrove management are currently in place in the rules and policies of the four upper North Island Regional Councils (Table 7). There are six types of activity status that can be used by a Council to control a persons activity in the coastal marine area – permitted, controlled, restricted discretionary, discretionary, non-complying and prohibited. Activities regarding mangroves are variously classified, depending on the type of activity proposed, as either requiring no resource consent (i.e., permitted activities) or as requiring resource consent (i.e., controlled, discretionary, restricted discretionary, or restricted coastal activities), or as strictly prohibited. Additional conditions apply to each of those categories for which resource consent is a requirement. The regulations allow for the possibility of a variety of mangrove management practices, from pruning of mature trees to several degrees of removal specific to the growth stage of the plants (i.e., seedling, sapling or mature trees).

5 Future research

Public interest in mangroves in New Zealand has waxed and waned over time, and with it the pressure to management 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 in New Zealand. This report has highlighted the need to assess the appropriate management actions for a given area of mangroves, or a given estuary, on a case-by-case basis because of the large variation among areas indicated by existing studies. The information that would allow us to make the assessments is, however, often lacking. The usefulness of applying conclusions from the large body of overseas work needs to be treated with caution. Important differences between the ecology of tropical mangroves and those in New Zealand, 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 preceeding discussion. A critical eye is needed even when comparing information from studies of *A. marina* forests in other temperate parts of the world with those in New Zealand, 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 of New Zealand mangroves.

Current work addressing some of the issues has been discussed above, but there are many other aspects that still need to be investigated. For example, our current 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 (such as terrestrial invertebrates) is extremely limited.

As our understanding of different estuarine habitats and their assemblages (plants, invertebrates, fish, 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 is especially relevant to the potential influence of human activities, which speed up the 'aging' and infilling of estuaries. For instance, Saintilan (2004) showed that as New South Wales (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 this estuarine habitat landscape dynamic, and need to be assessed in this context, as new information becomes available. Numerous recent/current projects by different research groups in New Zealand are generating the sorts of information needed for such an approach. An integration of this new knowledge, and how it might be integrated into management initiatives and future research directions, would be timely.

Table 7

Summary of Regional Council rules for mangrove removal. Note: only the rules relating to vegetation removal are presented (Hill et al. 2005, NRC 2006).

Northland Regional Council	Auckland Regional Council	Environment Bay of Plenty	Environment Waikato
Northland Regional Council Coastal Plan The Northland Regional Coastal Plan sets out rules for the removal or pruning of mangrove trees in its six marine management areas. In summary: The removal of mangroves from artificial drainage channels for the purpose of avoiding flooding of adjacent land (subject to controls on the extent of mangrove removal) is: a permitted activity in Marine 2 (conservation) and Marine 6 (wharves); a controlled activity in Marine 1 (protection), Marine 3 (marine farming) and Marine 5 (port facilities); a restricted discretionary activity in Marine 4 (moorings). The removal or pruning of mangroves where the progressive growth or proliferation of these has led to the obstruction of existing public access to and along the coastal marine area; or interferes with the reasonable or safe use or operation of authorised structures or facilities on adjoining land or in the coastal marine area is: a permitted activity in Marine 6, a controlled activity in Marine 3 and 5 a restricted discretionary activity in Marine 1, 2 and 4.	*Auckland Regional Plan: Coastal* The removal of indigenous vegetation is permitted for the purposes of gaining access to a lawful structure, other than in a Coastal Protection Area (CPA) 1 (subject to conditions). The removal of indigenous vegetation from a lawful structure is permitted (subject to conditions). The removal of indigenous vegetation that does not comply with the permitted activities is a restricted discretionary activity. The removal of indigenous vegetation for the purpose of maintaining or gaining access to a lawful structure in a CPA 1 is a discretionary activity, as is the removal of vegetation for the purposes of habitat or geopreservation site enhancement. The removal of indigenous vegetation from within any CPA 1, other than to maintain or gain access to a lawful structure is a prohibited activity. The removal of indigenous vegetation that was classified as a discretionary activity and extended over an area equal or greater than 10 hectares, or extended 10,000 metres over the foreshore and seabed, is a restricted coastal activity.	*Environment Bay of Plenty Coastal Plan* The removal, damage, modification or destruction of indigenous vegetation that is growing in the foreshore or seabed, is a discretionary activity. Applicants are required to provide details of what the works will entail, where they will be located, alternatives considered, any actual or potential effects, measures which will be used to avoid, remedy or mitigate any likely, actual or potential adverse effects on the environment, details of consultation undertaken by the applicant and outcomes, and any other information necessary to demonstrate that the proposed activity will comply with all relevant objectives, policies, rules and other methods of implementation contained within the plan. In the case of works affecting an area greater than 4 hectares, the activity is a restricted coastal activity and the approval of the Minister of Conservation is required.	*Environment Waikato Regional Coastal Plan* The removal of vegetation is a permitted activity in the Coastal Marine Area (CMA) provided it complies with the conditions stated in Rule 16.2.1. The conditions are: The removal is undertaken by iwi for traditional harvesting purposes. The removal is undertaken for the sole purpose of maintaining an existing boat access, clearing an existing navigational channel, or an existing boat launching site and the vegetation to be removed in any one year covers a ground area of less than 10 square metres. The vegetation is removed by Transit NZ in response to visual road safety concerns and the vegetation to be removed covers a ground area less than 10 square metres in accordance with section 55 of the Transit New Zealand Act 1989. In all cases, except the activities provided for in Rule 16.6.23, the vegetation to be removed shall not be identified as a conservation value within the ASCV areas marked on maps in Appendix III and described in Appendix IV of the Plan. The removal is undertaken for the purpose of maintaining existing drainage canal outlets, floodgate outlets and stopbanks as provided for in Rule 16.6.23. The removal or eradication of any indigenous plant species in the CMA that does not comply with the conditions for a permitted activity in Rule 16.2.1 is a discretionary activity. A range of criteria is provided for assessing any application for the removal or eradication of indigenous vegetation.

Northland Regional Council	Auckland Regional Council	Environment Bay of Plenty	Environment Waikato
The pruning or removal of live mangroves trees that is not otherwise a restricted discretionary activity is: a prohibited activity in Marine 1, a discretionary activity by default in the other marine management areas. Where controlled or restricted activity resource consents are required, NRC has retained control over/restricted its discretion to a range of matters, including the duration of the permit, the area of removal/pruning, the timing of the work, methods employed, and the ecological effects and alternatives (in Marine 1 and 2). The Northland Regional Council has recently notified a plan change to provide for the removal of mangroves in all areas as a short term management tool where mangroves are encroaching on communities' abilities to provide for their social, cultural, and economic needs. This is in response to recognition that the expansion of mangrove forests is the result of more favourable environmental conditions affording them increased habitat as a result of increased nutrient and sediment loads entering Northland's harbours and estuaries – which will require long-term solutions.	**Proposed Auckland Regional Plan: Air Land and Water** Applies only in respect of the provisions that relate to indigenous vegetation removal on the landward side of the coastal marine area. The removal of up to 30 square metres of mangroves in any 12-month period to maintain or gain access to a lawful structure is a permitted activity (Rule 7.5.11). More extensive clearance is provided for as a permitted activity if hand held removal or chemical spraying is used (7.5.12). Where removal cannot meet the permitted activity terms, removal of indigenous vegetation is either: a controlled activity where the work is undertaken for stormwater management purposes; a restricted discretionary activity for most other purposes including enhancement of a lake, natural stream or wetland management area or by handheld methods in these high value areas; or otherwise a non complying activity where removal is for purposes other than enhancement in a lake, natural stream or wetland management area. It is noted that the mangrove provisions of the Air, Land and Water Plan are subject to appeals and may be changed through the process of resolving these appeals.		

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