# Effects of mangrove removal on benthic communities and sediment characteristics at Mangawhai Harbour, northern New Zealand

#### 65

70

# **Q1** Andrea C. Alfaro\*

<sup>10</sup> Faculty of Health and Environmental Sciences, School of Applied Sciences, Auckland University of Technology, Private Bag 92006, Auckland 1020, New Zealand

\*Corresponding Author: tel: +64 9 9219999 ext. 8197; fax: +64 9 9219627; e-mail: andrea.alfaro@aut.ac.nz.

Alfaro, A. C. Effects of mangrove removal on benthic communities and sediment characteristics at Mangawhai Harbour, northern 75 15 New Zealand. – ICES Journal of Marine Science, doi:10.1093/icesjms/fsq034.

Received 19 August 2009; accepted 14 March 2010.

The spread of mangroves at many locations in temperate northern New Zealand provides a stark contrast to the well-documented trend in mangrove forest decline recorded through the tropics and subtropics. To explore this difference, improved understanding is <sup>80</sup>

- <sup>20</sup> needed of New Zealand's mangrove ecosystems and how they respond to anthropogenic disturbance. The effect of mangrove removal on the community ecology of mangrove stands and adjacent habitats was investigated within Mangawhai Estuary, northern New Zealand, between March 2004 and September 2006. The vegetation, benthic macrofauna, and sediments were sampled within habitats (marshgrass, mangrove stands, pneumatophore zones, sandflats, and channels) at a treatment site (mangroves 85
- 25 removed) and two undisturbed sites, before and after mangrove-removal activities. Mature mangrove habitats had less total abundance and fewer taxa than all the other habitats sampled and were dominated by pulmonate snails (*Amphibola crenata*) and mud crabs (*Helice crassa*). Whereas faunal composition varied seasonally as a result of life-history dynamics, temporal changes could be attributed to mangrove-removal activities. Mangrove eradication was followed by immediate changes in the sediment from a muddy to sandier environment, which favoured an overall increase in the abundance of crabs, snails, and bivalves. <sup>90</sup>
- <sup>30</sup> However, unexpected topographic catchment reconfigurations in late 2005 may have caused a subsequent increase in the delivery of silt and organic content to the study area and an overall decrease in faunal density in March and September 2006. The study provides direct evidence of the effect of mangroves on sediment and benthic faunal characteristics and the importance of catchmentderived imports to estuarine ecosystems.

35 Keywords: Avicennia marina australasica, benthic fauna, biodiversity, estuarine ecology, mangrove removal, sediment characteristics.

#### Introduction

- <sup>40</sup> Vascular plants have a strong influence on coastal community structure, function, and successional patterns (Bertness, 1991, 1992; Snelgrove *et al.*, 2000; Bortolus *et al.*, 2002; Levin and Talley, 2002). Earlier studies on plant–animal interactions focused on the effect of plants as (i) sediment modifiers (e.g.
- light, temperature, and chemistry regulators of benthic habitats;
  Bertness and Hacker, 1994; Alongi *et al.*, 2000; Levin and Talley, 2002), (ii) a food source (e.g. fresh and detrital organic matter;
  Peterson *et al.*, 1985; Kieckbusch *et al.*, 2004; Alfaro *et al.*, 2006; Levin *et al.*, 2006), and (iii) structural support (e.g. nursery habi-
- tats, coastal stabilization, and run-off filtration; Gleason et al., 1979; Warren and Neiring, 1993; Valiela et al., 2001). However, the specific mechanism by which vascular plants shape these ecosystem-level processes is still not fully understood. A major difficulty in advancing knowledge in this field is the rarity of manip-
- <sup>55</sup> ulative experiments owing to the often protected status of wetlands. A few manipulative studies have been possible alongside recovery and restoration programmes within saltmarshes (Levin and Talley, 2002; Gratton and Denno, 2005; Pagliosa and Lana,

2005; Whitcraft and Levin, 2007) and mangrove habitats (Botero 100 and Salzwedel, 1999; Sherman *et al.*, 2000; Macintosh *et al.*, 2002; Gladsone and Schreider, 2003). However, studies often are limited by constrained experimental designs, low replication, and a lack of suitable controls.

Research on tropical and subtropical mangrove-dominated <sup>105</sup> estuaries have resulted in a wealth of information regarding the diversity and ecological value of these habitats (Lindegarth and Hoskin, 2001; Valiela *et al.*, 2001; Ashton and Macintosh, 2002; Bouillon *et al.*, 2002; Macintosh *et al.*, 2002; Bosire *et al.*, 2004). Therefore, mangroves in subtropical and tropical regions are regarded as biologically important areas that provide food and shelter for a diversity of organisms and result in rich ecosystems (Laegdsgaard and Johnston, 2001; Valiela *et al.*, 2001; Diop, 2003; Duke *et al.*, 2007). Nevertheless, some areas around the world have been cleared of mangroves to give way to aquaculture farms and coastal development or to provide firewood and other mangrove-derived products for local residents (Stonich, 1992; Valiela *et al.*, 2001; Diop, 2003). It is estimated that one-third of the world's mangrove forests have been lost in the past 50 years

<sup>&</sup>lt;sup>60</sup> © 2010 International Council for the Exploration of the Sea. Published by Oxford Journals. All rights reserved. For Permissions, please email: journals.permissions@oxfordjournals.org

(Alongi, 2002). In places, the destruction and degradation of mangrove habitats has prompted conservation and rehabilitation

- 125 efforts. Mangrove-management projects have been undertaken and documented in many parts of the world (Spurgeon, 1998; Tri *et al.*, 1998; Botero and Salzwedel, 1999; Franks and Falconer, 1999; Barbier, 2000). These projects often involve extensive quantification of benthic fauna, mangrove vegetation, and
- 130 physical parameters of the water and sediment (Kelaher *et al.*, 1998; Ashton *et al.*, 2003). Some of these studies also included comparisons with adjacent estuarine habitats (Kitheka, 1997; Davis *et al.*, 2001; Dittmar *et al.*, 2001; Lindegarth and Hoskin, 2001) and seasonal contrasts (Gordon *et al.*, 1995; Crowe, 1999).
- In general, tropical rehabilitated areas have shown an increase in species abundance and biodiversity associated with mangrove plantations (Botero and Salzwedel, 1999; Sherman *et al.*, 2000; Macintosh *et al.*, 2002). For example, Macintosh *et al.* (2002) recorded generally greater macrofaunal diversity, abundance, and
- biomass in conserved and replanted mangrove sites compared with sites cleared of mangroves in the Ranong Province, Thailand. New Zealand's temperate mangrove ecosystems may differ significantly from their tropical counterparts, in that their biodiversity and ecological value may not be as high as previously thought
- 145 (Alfaro, 2006). In the 1970s, a strong movement to preserve mangroves developed on the assumption that New Zealand's and subtropical and tropical mangrove forests had comparably high ecological value because they shared similar physical and biological properties (Chapman, 1976). To date, there is insufficient scienti-
- 150 fic information to clearly evaluate the ecological importance of New Zealand's mangroves. Nevertheless, a conservation movement still exists that advocates protection of mangrove habitats. On the other hand, many community groups and environmental managers have raised concerns regarding the unrestricted spread
- 155 of mangroves over other habitats (e.g. seagrass beds, sandflats), which they argue has detrimental ecological and socio-economic effects (Green *et al.*, 2003; Schwarz, 2003).

Based on aerial photographs and maps, rapid mangrove spread has been documented in many estuaries throughout northern New

- 160 Zealand, such as Whangape Harbour, Puhoi Estuary, Kaipara, Manukau, Waitemata, and Tauranga Harbours (references in Morrisey *et al.*, 2007). Other sites have experienced little or no increase in mangrove area, mostly because of the small size of the estuary or elevation limits on their landward sides (Morrisey
- 165 *et al.*, 2007). Nationwide, a total net gain of  $\sim$ 3200 ha of mangroves has been estimated for the 20-year period between 1984 and 1996/1997 (Morrisey *et al.*, 2007). Mangroves also are seen as an unwanted species in Hawaii, where introduction of *Rhizophora mangle* in the early 1900s initiated a dramatic change
- in the native habitat of endangered Hawaiian waterbirds (Allen, 1998; Cox and Allen, 1999; Rauzon and Drigot, 2002).
   Subsequent mangrove-removal activities within the wetlands of Nu'upia Ponds, Mokapu Peninsula, Hawaii, resulted in successful restoration and recolonization by native birds (Rauzon and
- 175 Drigot, 2002). However, it is important to note that contrary to mangroves in Hawaii, Avicennia marina australasica is endemic to New Zealand and may require a different management system. In New Zealand, studies of mangrove habitats have focused largely on the effects of sedimentation, or infilling of estuaries
- 180 owing to mangrove spread (Woodroffe, 1982, 1985; Young and Harvey, 1996), and on the production of mangrove leaf litter as a source of nutrients to the ecosystem (Woodroffe, 1982, 1985; May, 1999). More recently, investigations on the role of associated

flora and fauna within these habitats have increased in number (Morrisey et al., 2002; Alfaro, 2006; Alfaro et al., 2006). Morrisey 185 et al. (2002) conducted a comparative study of benthic fauna within young (3-12-year old) and old (>60 years) mangrove stands in Manukau Harbour, New Zealand. Their findings suggest that, as mangrove stands mature, the abundance and biodiversity of the associated benthic fauna tend to decrease. This 190 decrease in benthic biota was proposed to be a response to increased compaction of sediments around older mangroves (Morrisey et al., 2002). Although studies of benthic associations in different types of mangrove stands may aid management decisions, the ecological importance of mangrove habitats, relative 195 to adjacent estuarine habitats, also needs to be addressed for New Zealand mangroves. Alfaro (2006) investigated the community composition of benthic fauna within mangrove, seagrass, sandflat, and channel habitats at Matapouri Estuary, northern New Zealand. Mangrove habitats had significantly less benthic abun- 200 dance and biodiversity than adjacent seagrass beds and subtidal channels, but pneumatophore areas at the fringe of the mangrove stands contained a high diversity of organisms (Alfaro, 2006). At that study site, the dominant benthic fauna within the ecosystem derive nutrients from a variety of sources, such as bacteria and 205 brown algae, but mangrove-derived nutrients have only a localized effect on the foodweb, with little export of organic matter to adjacent habitats, such as sandflats (Alfaro et al., 2006).

Within Mangawhai Harbour, northern New Zealand, an environmental permit (CON20031099401) was granted in 210 August 2003 by the Northland Regional Council to remove a 0.26-ha fringe of mangrove trees for water access. This permit provided the unusual opportunity to evaluate the ecological effects of mangrove removal on the estuarine ecosystem. The aims of this study were to quantify the effect of mangrove-removal activities 215 on benthic abiotic and biotic components. Disturbed and undisturbed mangrove areas, adjacent pneumatophore zones, marshgrass, sandflats, and subtidal channels were monitored over time to test the hypotheses that (i) mangrove removal would alter sediment characteristics, (ii) mangrove removal would change the 220 benthic faunal composition, and (iii) variations in sediment characteristics and faunal composition would differ among habitats (i.e. mangrove areas, pneumatophore zones, marshgrass, sandflats, and subtidal channels) and over time. To quantify the long-term effects of this anthropogenic activity, ecological data 225 were collected before mangrove removal and subsequently at 6-month intervals over a period of 3 years.

#### Material and methods

The study site  $(36^{\circ}7'0''S \ 174^{\circ}34'0''E)$  is located in central 230 Mangawhai Harbour, northern New Zealand, at the northeastern corner of the Molesworth Causeway, ~2 km from Mangawhai Heads and ~4 km from Mangawhai Village (Figure 1). This part **Q2** of the estuary consists of a wide channel (~10 m near the bridge), with mangrove trees (*A. marina australasica*) and sand/ 235 mudflats on both sides of the channel. The 0.26-ha area of mangrove removal is located on the east side of the causeway, just north of the bridge (Figure 1).

The ecological study was conducted between March 2004 and September 2006, with sampling once before and five times after 240 the April 2004 mangrove tree-removal activities. Characterization of vegetation, macrofauna (epifauna and infauna), and sediment was undertaken within the mangrove-removal area and adjacent habitats (treatment site; Figure 1, Site 1). In addition, two control



Figure 1. Map of Mangawhai Estuary (Middle Harbour). Sampling sites include a mangrove-removal site (G1, M1, P1, S1, and C1), a control site across the channel (G2, M2, S2, and C2), and another control site on the west side of the causeway (G3, M3, P3, S3, and C3). Habitats within sites include marshgrass (G1, G2, and G3), mangroves (M1, M2, and M3), pneumatophores (P1 and P3), sandflats (S1, S2, and S3), and 325 channel (C1, C2, and C3). G, marshgrass; M, mangrove; P, pneumatophore; S, sandflat; and C, channel. Numbers 1, 2, and 3 refer to mangrove-removal site (1) and two control sites (2 and 3). Note that there was no pneumatophore habitat in Site 2.

sites were identified and sampled. The first control site is located just south of the treatment site, across the channel (Figure 1, Site 2), and the second west of the treatment site, on the other side of the cause-

- 270 the second west of the treatment site, on the other side of the causeway (Figure 1, Site 3). It is recognized that Sites 2 and 3 are not true control sites (not randomly chosen relative to the treatment site), but are similar enough to the treatment site to provide comparative undisturbed sites. Although the potential exists for exchange effects
- 275 of sediment and organisms among sites, this is likely to be minimal owing to the strong physical barriers (tidally dominated channel and causeway) between sites. Within each sampling site, several unique habitats were identified between the edge of the catchment and the subtidal channel. The habitats, or zones, were identified
- 280 according to their unique vegetation, inundation time, and general faunal characteristics and previously reported ecological differences (cf. Alfaro, 2006). Slight variations exist among equivalent habitats (e.g. different pneumatophore lengths among sites), but the results from earlier studies suggest comparability of habitats (cf.
- 285 Alfaro, 2006). The habitats within each site included marshgrass, mangrove, pneumatophore (aerial roots), sand/mudflat, and channel, except for Site 2 which did not have a pneumatophore habitat.
- The marsh habitat is dominated by jointed rush, *Leptocarpus similis*, with other small terrestrial grasses and plants among the rushes. Pneumatophores from nearby mangroves also extend into the marshgrass habitat. The mangrove habitat is densely covered with mature mangrove trees (*A. marina australasica*) 4-5 m high. The top 5 cm of sediment is characterized as a silty
- <sup>295</sup> mud layer, and there is a dense mat of fibrous mangrove roots (>20 cm deep) below this layer. This habitat was removed from Site 1 in April 2004. The pneumatophore habitat is a zone of dense mangrove pneumatophores next to the fringing mangrove trees at all three sites. However, the pneumatophore zone at Site
- 300 2 was too narrow (<1 m) to sample. Sandflat habitats were found within all three sites, although their sediment composition varied slightly. Subtidal channel habitats were dominant features of the study location. The main channel constricts as it approaches the bridge to the east (Site 3), then divides into two branches

 $_{305}$   $\sim$  50 m to the east, just past the bridge. All samples within these

habitats were taken during low tide, at a water depth of  ${\sim}20-$  50 cm. \$330

# Sampling of the vegetation

A survey of the vegetation was conducted within all mangrove habitats for the three sites. The survey included quantification of 335 trees (mangroves taller than 0.5 m and >2.5 cm in stem diameter) and saplings (mangroves taller than 0.5 m, but <2.5 cm in stem diameter) within five quadrats of 25 m<sup>2</sup>. The mean height and diameter at breast height (dbh) of ten random mangrove trees, anywhere in the habitat, also were recorded. The density of man-340 grove seedlings (mangroves shorter than 0.5 m), propagules, and pneumatophores in mangrove, and pneumatophore habitats were determined using five replicate quadrats of area 0.25 m<sup>2</sup>. The percentage cover of mangrove leaf litter and marshgrass inside each of five quadrats of 0.25 m<sup>2</sup> within mangrove, pneuma-345 tophore, and marshgrass habitats also were recorded. All measurements were standardized to an area of 1 m<sup>2</sup> to compare among parameters.

#### Sampling of the macrofauna

350

Macrofauna (infauna and epifauna) densities were determined within each habitat and site. Five randomly placed sediment cores  $(25 \times 25 \text{ cm}^2 \text{ area}, 5 \text{ cm depth})$  were used to collect macrofauna within each habitat during low tides. Each replicate sediment sample was sieved through a 2-cm and then a 0.5-mm 355 mesh. The 0.5-mm mesh sieve was used to determine the density and distribution of juvenile species (e.g. bivalves) and worms. Preliminary samples at the study sites indicated that most infauna (~98% of all individuals) were within the top 5 cm of the sediment within mangrove and marshgrass habitats. 360 Hence, a sampling depth of 5 cm provided an accurate representation of the density of infauna in these habitats and minimized the arduous task of sieving through dense root systems. This 5 cm depth was used for all cores within all habitats to standardize the samples. All live animals found in all samples were enumer- 365 ated, recorded, and standardized to a volume of 1 m<sup>3</sup>. Samples

were kept refrigerated until sieving could be completed, within 3 d of each sampling event.

# 370 Sampling of the sediment

Three replicate sediment samples  $(15 \times 15 \text{ cm}^2 \text{ area, 5 cm depth})$  were taken from each habitat at each site, a total of 45 samples per sampling event. All sediment samples were first refrigerated, then analysed within 3 d of collection. They were used to determine

- 375 grain-size and organic content. Grain-size characterization was done by sieving each dried sample through several sieves of different mesh sizes (mud  $\leq 150 \ \mu m$ , fine sand  $= 150 - 300 \ \mu m$ , medium sand  $= 300 - 600 \ \mu m$ , coarse sand  $\geq 600 \ \mu m$ ) and calculating the proportions. Total organic content was obtained
- through weight differences before and after total combustion at 450°C after acidification to a pH of 2 (Parrish, 1998). Sediment compaction was determined by measuring the depth of penetration of a sharpened steel rod (50 cm long, 0.7 cm diameter, 150 g weight) when dropped from a distance of 1.2 m above the
- 385 sediment surface (Morrisey *et al.*, 2002). Compaction relates to the porosity and permeability of the sediment. Variations in these properties may create microhabitats with different soil chemistry and biological activity.

#### 390 Statistical analyses

Multiple factor ANOVAs were used to test vegetation differences among sites, habitats, and dates, and individual three-way ANOVAs with Tukey tests were performed to test benthic faunal differences among sites, habitats, and dates. Multiple dimension

- <sup>395</sup> scaling (MDS) plots were constructed, based on similarities of correlation matrices, to detect groupings of habitat type for each sampling date. Principal component analysis (PCA) was used to detect habitat differences, based on sediment characteristics for each sampling date. Data that did not meet the requirements for
- <sup>400</sup> parametric analyses were transformed with an arcsine or square root x + 0.5 transformation to meet these requirements. Statistica 6.0 and Primer 6 software were used for statistical analyses.

#### 405 **Results**

The three mangrove habitats had similar vegetation parameters (i.e. mean densities of mangrove trees, saplings, seedlings, propagules, pneumatophores, and tree height and dbh) before mangrove removal (two-way ANOVA; habitat, p > 0.001; vegetation, p <0.001), and these parameters continued to be consistent through the sampling period in the remaining two mangrove stands (three- 430 way ANOVA; habitat, p > 0.001; vegetation, p < 0.001; date, p >0.001; Table 1). However, sapling, seedling, and pneumatophore densities varied considerably between March 2004 and September 2006 in the mangrove habitat (M1) after tree removal (two-way ANOVA; vegetation, p < 0.001; date, p > 0.001; 435 Figure 2). Sapling and seedling densities increased throughout the sampling period, although saplings were only present in March 2004 and in March and September 2006. Only a few propagules were present in this habitat in March 2005 and 2006. Pneumatophore density increased sharply from March to 440 September 2004, then decreased steadily until the end of the sampling period (Figure 2). Marshgrass habitats were similar in vegetation composition among sites, except for Site 1, which was slightly more elevated than the other two sites and had a greater density of marshgrass reed cover throughout the sampling 445 period (ANOVA; p < 0.001; Tukey test, Site 1 differs from Sites 2 and 3; Table 1). The pneumatophore habitats had different densities of pneumatophores; Site 3 had higher mean densities than Site 1 throughout the sampling period (Table 1). As expected, the mean percentage of mangrove leaf litter inside random quad- 450 rats was higher in the mangrove habitats (Table 1).

Overall, mangrove habitats had less total abundance and fewer total numbers of taxa than any of the other habitats sampled within all sites (Figure 3; Appendix). Individual three-way ANOVAs and Tukey tests, with date, site, and habitat (excluding 455 pneumatophore habitats) as fixed factors, were performed for total numbers of individuals and for total number of taxa (Table 2). Significant differences were observed among date, site, and habitat factors, signalling the high spatial and temporal variability of the area. Significant interactions among main factors 460 suggest that different ecological processes (e.g. differential seasonal effects, variations in habitat preferences) are responsible for the faunal distribution and abundance at the study site. Hence, detailed variations among dates, sites, and habitats were necessary (Tukey tests, in Table 2). These analyses specifically highlight the 465 significant temporal variability for some taxa. The MDS analyses revealed clear separation between the sandflat/channel habitats and the rest of the habitats for all sites and sampling dates (Figure 4). Generally, the pneumatophore habitats clustered 470

410

**Table 1.** Mean ( $\pm$  s.e.) values for plant parameters recorded from marshgrass (G), mangrove (M), and pneumatophore (P) habitats within three estuarine sites (Site 1, mangrove-removal area; Sites 2 and 3, control sites) in Mangawhai Estuary, New Zealand, for the sampling period March 2004–September 2006.

		Site 1		Site	2	Site 3				
<sup>5</sup> Plant characteristic	G	м	Р	G	м	G	м	Р		
Marshgrass (% cover $m^{-2}$ )	348.0 ± 9.6	_	_	164.4 ± 18.4	-	222.0 ± 21.2	-	_		
Mangrove trees (number $m^{-2}$ )	-	$0.5\pm0.0^{a}$	_	-	$0.6\pm0.0$	-	$0.6\pm0.0$	-		
Mangrove tree height (m)	-	$4.2\pm0.4^{a}$	_	_	$4.6\pm0.8$	-	4.9 ± 0.9	_	40	
Mangrove tree dbh (cm)	-	$5.7\pm0.4^{a}$	_	_	5.8 ± 0.7	-	5.0 ± 0.6	-	40	
Saplings (number $m^{-2}$ )	-	$0.0\pm0.0$	_	_	$0.0\pm0.0$	-	$0.1\pm0.0$	_		
Seedlings (number $m^{-2}$ )	$0.0\pm0.0$	31.6 ± 5.6	$2.8\pm2.0$	$0.4\pm0.0$	$0.0\pm0.0$	$0.0\pm0.0$	1.2 ± 1.2	14.0 ± 4.0		
Propagules (number $m^{-2}$ )	$0.0\pm0.0$	$0.4\pm0.4$	$0.8\pm0.4$	$0.0\pm0.0$	$0.0\pm0.0$	$0.0\pm0.0$	$0.8\pm0.8$	$1.2 \pm 0.4$		
Pneumatophores	$0.4\pm0.4$	102.0 $\pm$ 8.8	$75.2 \pm 10.8$	$5.2 \pm 2.8$	68.4 ± 10.4	39.6 ± 16.4	66.0 ± 12.0	152.4 ± 28.0		
(number $m^{-2}$ )									48	
5 Leaf litter (% cover $m^{-2}$ )	$0.0\pm0.0$	4.8 ± 1.6	$0.0\pm0.0$	$1.2 \pm 0.4$	22.0 ± 12.4	$0.4\pm0.0$	24.0 ± 12.4	$0.4\pm0.0$		

<sup>a</sup>Sampling during March 2004 only (before mangrove removal). Note that there was no pneumatophore habitat at Site 2.



Figure 2. Mean abundance ( $\pm$  s.e.) of saplings, seedlings, propagules, and pneumatophores in the mangrove habitat (M1; mangrove-removal area) from March 2004 to September 2006.

between the sandflat/channel habitats and the marshgrass/ 510 mangrove habitats. All mangrove habitats clustered before mangrove removal (March 2004), but M1 separated from M2 and M3 on all other sampling dates, except for March 2005 (Figure 4). The marshgrass habitat in Site 1 separated from those in Sites 2 and 3 during all sampling dates. The range of 515 stress values for all MDS plots was low (0.02–0.05), strongly

supporting the groupings. The abundance of the dominant macrofauna in each habitat

was plotted for each site between March 2004 and September 2006 to identify spatial and temporal variations and to elucidate ecological differences between mangrove-removal and control

- <sup>520</sup> ecological differences between mangrove-removal and control sites (Figures 5–8). The most abundant organism, *Potamopyrgus antipodarum*, had an overall mean density ( $\pm$ s.e.) of 1.33  $\pm$ 0.01 m<sup>-3</sup>, but was present only in the marshgrass and mangrove habitats (Figure 6). Polychaete and oligochaete worms were the
- 525 next most abundant organisms, with overall mean densities  $(\pm s.e.)$  of  $0.04 \pm 0.00$  and  $0.23 \pm 0.01 \text{ m}^{-3}$ , respectively (Figure 8). The snail *Zeacumantus lutulentus* was found in all habitats, with an overall density of  $0.38 \pm 0.00 \text{ m}^{-3}$ , but was most common in the pneumatophore, sandflat, and channel habitats
- 530 (Figure 5). The mud crab *Helice crassa* was generally present in all habitats, except for the channel, whereas the mud snail *Amphibola crenata* was found mostly in the marshgrass and mangrove habitats (Figures 5 and 6). The overall mean densities  $(\pm s.e.)$  for *H. crassa* and *A. crenata* were  $0.05 \pm 0.00$  and
- 535  $0.30 \pm 0.02 \text{ m}^{-3}$ , respectively. The cockle Austrovenus stutchburyi was common within mangrove, pneumatophore, sandflat, and channel habitats, and the pipi Paphies australis was found in sandflat and channel habitats only (Figure 7). The overall mean densities ( $\pm$  s.e.) for A. stutchburyi and P. australis were 0.11  $\pm$
- 540 0.01 and  $0.14 \pm 0.01 \text{ m}^{-3}$ , respectively. Individual three-way ANOVAs and Tukey tests, with date, site, and habitat (excluding pneumatophore habitats) as fixed factors, were performed for all major macrofauna (Table 2). Significant effects and interactions were observed for most fauna, but *post hoc* tests revealed a range
- 545 of significant date pairs, indicating high temporal variability (Table 2). In general, mangrove removal appeared to result in an immediate increase and subsequent decrease in crab, snail, and bivalve abundance in surrounding areas, with polychaetes following the inverse pattern.

There were consistent differences in sediment characterization 550 among habitats. The mean depth of the penetrometer was consistent among sites and over time, although there were distinct differences among habitats. The mean penetration depth  $(\pm s.e.)$  was lower in the marshgrass  $(5.6 \pm 1.3 \text{ mm})$ , sandflat  $(14.6 \pm$ 1.0 mm), and channel  $(4.7 \pm 0.6 \text{ mm})$  habitats than in the man- 555 grove  $(15.6 \pm 0.9 \text{ mm})$  and pneumatophore  $(15.9 \pm 1.1 \text{ mm})$ habitats (ANOVA; p > 0.001). Grain-size analyses of sediments within all habitats and sites revealed similar characteristics across sites, fine and medium sandy sediments being the most abundant sediments in most habitats (Figure 9). Comparisons 560 among habitats generally revealed marsh habitats to display a greater proportion of coarse sand sediments, mangrove and pneumatophore habitats to exhibit more muddy sediments, and sandflat and channel habitats to have greater fine and medium sediments (Figure 9). The temporal patterns in grain-size compo- 565 sition indicate that Site 1 experienced a general decrease in fine sand from March to September 2004, especially for the mangrove, pneumatophores, and sand habitats (but not the channel in Site 1), and an increase in finer sediments from September 2005 to September 2006 (Figure 9). For Sites 2 and 3, an increase in 570 both fine and coarser sediments was observed during the later part of the study period.

The PCA ordination of sediment characteristics revealed clear habitat clustering for mangrove, marshgrass, and pneumatophore habitats at the beginning of the study (Figure 10; March 2004). 575 Therefore, sediment conditions within these habitats were similar among sites at the start of the study. A distinct separation of mangrove habitat at Site 1 (mangrove-removal site) was found at and after September 2004, which agrees with the increase in sand composition there immediately after mangrove removal 580 (Figure 9). Marshgrass habitats generally clustered throughout the study period, whereas greater separation and mobility was observed in the rest of the habitats, especially in the sandflats and channel (Figure 9). The variable loadings for principal components 1-3 accounted for 100% of the variation for all sampling 585 dates. In general, component 1 had a high (positive or negative) loading for fine and coarse sand, whereas component 3 was mostly associated with mud. Component 2 was highly variable in its loading composition. Component 1 explained ~40-60% of the variation, component 2  $\sim$ 20-40%, and component 3 590 almost 20% of the total variation.

There was generally greater organic content for mangrove and pneumatophore habitats than for marshgrass, sandflat, and channel habitats (Figure 11). Distinctive spatial and temporal differences were observed across habitats and sites. At Site 1, the 595 organic content in all habitats, but especially in the mangroves and pneumatophores, increased slightly immediately after mangrove removal (Figure 11). This trend was followed by a general decrease in organic content in sediment samples, and a sharp increase between March 2005 and September 2006. At Sites 2 600 and 3, the temporal changes were less pronounced. A three-way ANOVA resulted in significant date and habitat factors (p < 0.001) and non-significant site factor and all interactions (p > 0.001).

### 605

## **Discussion** Mangrove ecosystems

Although many ecological studies of subtropical and tropical mangroves have revealed high species diversity and abundances 610



**Figure 3.** Mean abundance ( $\pm$ s.e.) of total individuals and total taxa within different habitats at three sites (Site 1, mangrove-removal area; Sites 2 and 3, control sites) from March 2004 to September 2006 (mangrove removal illustrated by vertical dashed line). Note that there was no pneumatophore habitat at Site 2 and that the *y*-axes have different scales. 720

660

(Dittmann, 2000; Ashton and Macintosh, 2002; Macintosh *et al.*, 2002), the mangrove habitats found in temperate New Zealand may differ in various aspects, including sedimentation rate and water characteristics (i.e. temperature, salinity, inundation time, rate of nutrient recycling), arboreal architecture, and species com-

665 rate of nutrient recycling), arboreal architecture, and species composition of associated flora and fauna. Although mangrove densities in many tropical areas are declining (Laegdsgaard and Johnston, 2001; Valiela *et al.*, 2001; Diop, 2003), New Zealand mangroves are spreading dramatically in some locations, mostly

<sup>670</sup> a consequence of accelerating sedimentation rates from anthropogenic catchment modifications (Hume and Dahm, 1992; Ellis *et al.*, 2004). In addition, cooler temperatures and shorter periods of tidal inundation within New Zealand coastal areas appear to decrease the decomposition rate, which dampens the reincorporation of organic matter into the foodweb compared 725 with tropical and subtropical mangrove ecosystems (Alfaro, 2006). A lack of intertidal plant competitors also may facilitate mangrove spread in New Zealand. In Hawaii, where mangroves (*R. mangle*) also are spreading rapidly, a high propagule production rate (Cox and Allen, 1999) and a lack of propagule predators (Steel *et al.*, 1999) have been suggested as two potential reasons for the success of mangroves there (Chimner *et al.*,

Table 2. Statistical analyses (three-way ANOVAs) for total number of individuals and taxa, and major macrofauna for six dates between<br/>March 2004 and September 2006 (M4, S4, M5, S5, M6, and S6), three sites (Site 1, mangrove-removal area; Sites 2 and 3, controls), and four<br/>735 habitats (G, marshgrass; M, mangrove; S, sandflat; C, channel).735

	Source	d.f.	Mean square	F-value	<i>p-</i> value	d.f.	Mean square	F-value	<i>p-</i> value
			Total indi			Tota	taxa <sup>b</sup>		
	Date (D)	5	1 818.48	3.61	0.003	5	19.02	14.42	0.001
	Site (S)	2	86 011.32	170.95	0.001	2	13.04	9.88	0.001
740	Habitat (H)	3	275 953.01	548.45	0.001	3	55.25	41.87	0.001
	$D \times S$	10	4 229.31	8.40	0.001	10	18.81	14.25	0.001
	$D \times H$	15	584.10	1.16	0.303	15	3.09	2.34	0.003
	S  imes H	6	91 116.54	181.09	0.001	6	13.67	10.36	0.001
	$D \times S \times H$	30	868.21	1.73	0.013	30	2.19	1.66	0.019
745	Error	288	503.32			288	1.32		
/ 15			Helice c		Zeacumantı	ıs lutulentus <sup>d</sup>			
	Date (D)	5	3.13	1.55	0.173	5	10.05	4.98	0.001
	Site (S)	2	25.43	12.62	0.001	2	72.31	35.83	0.001
	Habitat (H)	3	46.06	22.85	0.001	3	123.61	61.25	0.001
	$D \times S$	10	1.84	0.91	0.523	10	2.72	1.35	0.203
750	$D \times H$	15	1.09	0.54	0.915	15	5.07	2.51	0.002
	S  imes H	6	20.14	9.99	0.001	6	34.16	16.93	0.001
	$D \times S \times H$	30	1.04	0.52	0.984	30	3.35	1.66	0.019
	Error	288	2.01			288	2.01		
			Potamopyrgus (	antipodarum <sup>e</sup>			Amphibo	la crenata <sup>f</sup>	
755	Date (D)	5	84.00	0.26	0.936	5	59.24	3.32	0.006
155	Site (S)	2	45 025.11	137.78	0.001	2	543.34	30.42	0.001
	Habitat (H)	3	165 631.60	506.86	0.001	3	3 900.91	218.40	0.001
	D × S	10	199.22	0.61	0.805	10	24.83	1.39	0.184
	$D \times H$	15	91.90	0.28	1.000	15	33.00	1.85	0.028
	S  imes H	6	43 639.21	133.54	0.001	6	382.34	21.41	0.001
760	$D \times S \times H$	30	202.17	0.62	0.943	30	20.13	1.13	0.301
	Error	288	326.80			288	17.86		
			Austrovenus s	stutchburyi <sup>g</sup>			Paphies		
	Date (D)	5	54.76	8.71	0.001	5	20.363	2.7070	0.021
	Site (S)	2	8.53	1.36	0.259	2	154.269	20.5085	0.001
765	Habitat (H)	3	959.75	152.61	0.001	3	606.669	80.6503	0.001
705	$D \times S$	10	10.19	1.62	0.100	10	11.559	1.5367	0.126
	$D \times H$	15	18.35	2.92	0.001	15	7.652	1.0172	0.437
	S  imes H	6	16.57	2.63	0.017	6	51.514	6.8482	0.001
	$D\timesS\timesH$	30	14.96	2.38	0.001	30	4.493	0.5973	0.955
	Error	288	6.29			288	7.522		
770			Polych	aetes <sup>i</sup>			Oligoo	haetes <sup>j</sup>	
	Date (D)	5	9.68	2.66	0.023	5	77.35	3.5029	0.004
	Site (S)	2	7.00	1.92	0.148	2	2.63	0.1193	0.888
	Habitat (H)	3	94.88	26.07	0.001	3	2 630.25	119.1209	0.001
	D × S	10	4.54	1.25	0.260	10	11.31	0.5124	0.881
775	$D \times H$	15	3.50	0.96	0.495	15	55.15	2.4978	0.002
,15	S  imes H	6	5.90	1.62	0.141	6	97.55	4.4180	0.001
	$D\timesS\timesH$	30	1.64	0.45	0.994	30	10.17	0.4606	0.993
	Error	288	3.64			288	22.08		

Tukey tests for appropriate comparisons are shown. Significant *p*-values are emboldened.

<sup>a</sup>Non-significant Tukey tests: M4 × S4, M4 × S6, S4 × M5, S4 × S5, S4 × M6, S4 × S6, M5 × S5, M5 × M6, M5 × S6, S5 × M6, S5 × S6, M6 × S6. <sup>780</sup> <sup>b</sup>Non-significant Tukey tests: M4 × S4, M4 × S5, M4 × S6, S4 × S5, S4 × M6, M5 × M6, S5 × S6.

<sup>c</sup>Non-significant Tukey tests: All date pairs are non-significant; Sites:  $1 \times 2$ ; habitats: G  $\times$  S.

<sup>d</sup>Non-significant Tukey tests: M4  $\times$  S4, M4  $\times$  M5, M4  $\times$  S5, M4  $\times$  M6, M4  $\times$  S6, S4  $\times$  M5, S4  $\times$  S5, S4  $\times$  M6, M5  $\times$  S5, M5  $\times$  M6, S5  $\times$  M6, M6  $\times$  S6; Sites: 1  $\times$  2; habitats: G  $\times$  M.

<sup>e</sup>Non-significant Tukey tests: All date pairs are non-significant; habitats: M  $\times$  S, M  $\times$  C, S  $\times$  C.

<sup>f</sup>Non-significant Tukey tests: M4 × S4, M4 × M5, M4 × S5, M4 × M6, M4 × S6, S4 × M5, S4 × S5, S4 × M6, S4 × S6, M5 × S5, M5 × M6, S5 × M6, M6 × <sup>845</sup> S6; Sites: 2 × 3; habitats: S × C.

<sup>g</sup>Non-significant Tukey tests: M4  $\times$  M5, S4  $\times$  M5, S4  $\times$  S5, S4  $\times$  M6, S4  $\times$  M6, S4  $\times$  S6, M5  $\times$  S5, M5  $\times$  M6, S5  $\times$  M6, S5  $\times$  S6, M6  $\times$  S6; Sites: 1  $\times$  2, 1  $\times$  3, 2  $\times$  3; habitats: G  $\times$  M.

<sup>h</sup>Non-significant Tukey tests: M4 × S4, M4 × M5, M4 × S5, M4 × M6, M4 × S6, S4 × M5, S4 × S5, S4 × M6, S4 × S6, M5 × S5, M5 × M6, M5 × S6, S5 × M6, M6 × S6; Sites: 1 × 3; habitats: G × M, S × C1.

<sup>i</sup>Non-significant Tukey tests: M4 × S4, M4 × M5, M4 × S5, M4 × S6, S4 × M5, S4 × S5, S4 × M6, S4 × S6, M5 × S5, M5 × M6, M5 × S6, S5 × M6, S5 × S6, <sup>850</sup> M6 × S6; Sites: 1 × 2, 1 × 3, 2 × 3; habitats: G × M, S × C.

<sup>j</sup>Non-significant Tukey tests: M4  $\times$  S4, M4  $\times$  M5, M4  $\times$  M6, S4  $\times$  M5, S4  $\times$  S5, S4  $\times$  M6, S4  $\times$  S6, M5  $\times$  S5, M5  $\times$  M6, M5  $\times$  S6, S5  $\times$  M6, S5  $\times$  S6, M6  $\times$  S6; Sites: 1  $\times$  2, 1  $\times$  3, 2  $\times$  3; habitats: G  $\times$  M, S  $\times$  C.



Figure 4. Non-metric MDS plots of habitats based on faunal assemblages at Mangawhai Harbour. Habitats include (G, marshgrass; M, mangroves; P, pneumatophores; S, sandflats; and C, channel) at three sites (Site 1, mangrove-removal area; Sites 2 and 3, control sites) from March 2004 to September 2006. Note that there was no pneumatophore habitat at Site 2.

- 2006). New Zealand's *A. marina* also produces a large number of resilient propagules, which appear to have few predators. The viviparous nature of these propagules allows for continuous development and growth throughout the dispersal stages, with no physiological control to inhibit or delay embryonic development
   900 (Fountain and Outred, 1991). In addition, few grazers on man-
- 900 (Fouritain and Outred, 1991). In addition, rew grazers on mangrove propagules or leaves have been reported in New Zealand. In fact, Alfaro (2006) suggested that the low abundance of mangrove grazers (i.e. crabs) in New Zealand, compared with tropical mangrove habitats, may result in a minimal transfer of nutrients
- 905 from mangroves to the rest of the estuarine ecosystem, so locking high vegetative biomass within this specific habitat. Based on these ecological differences, and whatever the cause, New Zealand (and Hawaiian) mangrove habitats are being subjected to management and control of their spread, rather than 910 undergoing the replanting and protection that is underway for
- some tropical mangrove areas.

## Faunal distribution

The overall abundance patterns of benthic fauna among habitats 915 and sites indicates that mature mangrove habitats have less total abundance and fewer total numbers of taxa than any of the other habitats studied (although not during all sampling events). These differences may be related to mature trees tending to form dense mats of fibrous roots, which may not provide a suitable habitat for many macroinvertebrates. Indeed, Morrisey et al. 960 (2002) found that although mature stands of mangroves in the Manakau Harbour had higher concentrations of organic matter, they had fewer associated taxa, and many species were less abundant, than in younger mangrove stands nearby. Oxic respiration in mangrove habitats is increased by tidal influence, crab bioturba- 965 tion, and physiological activities of the roots; nonetheless, mangrove respiration rates are lower than in other coastal areas, such as saltmarshes (Alongi et al., 2000). This intrinsic characteristic of older mangrove stands may make it difficult for benthic fauna to inhabit these areas, as suggested by Alfaro (2006). Greater quan- 970 tities of leaf litter within mangrove habitats also may cause a decrease in benthic fauna, because tannins from leaf litter have been identified as a cause of low species diversity in mangrove habitats in Australia (Alongi, 1987).

The species composition within each habitat in the Mangawhai 975 study tended to be similar for all sites, and dominant species



**Figure 5.** Mean abundance ( $\pm$  s.e.) of *H. crassa* and *Z. lutulentus* within different habitats where these species were found at three sites (Site 1, mangrove-removal area; Sites 2 and 3, control sites) from March 2004 to September 2006 (mangrove removal illustrated by vertical dashed <sup>1085</sup> line). Note that there was no pneumatophore habitat at Site 2 and that the *y*-axes have different scales.

generally had clearly defined ranges. Among all species encountered during the study period, the snail *P. antipodarum* was the most abundant, and it clearly dominated marsh habitats. However, its abundance was low or non-existent in the mangrove

- However, its abundance was low or non-existent in the mangrove habitats. This trend is consistent with the benthic abundance and distribution studies of Alfaro and McDowell (2003), Alfaro (2006), and Alfaro *et al.* (2006) in Matapouri Estuary, northern New Zealand. However, Morrisey *et al.* (2002) found *P. antipodarum*
- 1035 in greater numbers in older mangrove stands in the Manakau Estuary, Auckland, New Zealand. At Mangawhai, the pulmonate snail *A. crenata* was found in greatest numbers along the transition

between marshgrass and mangrove habitats. That snail has been reported to live in the muddy substrata of mangrove habitats (May, 1999; Morrisey *et al.*, 2002; Ellis *et al.*, 2004). However, in 1090 the current study, both juveniles and adults of this species were found in greater numbers in the sandy substrata of the marshgrass habitats. At Mangawhai, the scavenger snail *Z. lutulentus* was found predominantly in the sandflat, channel, and pneumatophore habitats, although its distribution tends to be patchy and 1095 dependent on food sources. Other than polychaete and oligochaete worms, which were found throughout the study sites, the mud crab *H. crassa* had the widest distribution range. This small





**Figure 6.** Mean abundance (±s.e.) of *P. antipodarum* and *A. crenata* within different habitats where these species were found at three sites (Site 1, mangrove-removal area; Sites 2 and 3, control sites) from March 2004 to September 2006 (mangrove removal illustrated by vertical dashed line). Note that there was no pneumatophore habitat at Site 2 and that the *y*-axes have different scales.

crab, of  $\sim 10-20$  cm in carapace width, was found in all habitats, but predominantly in mangroves. It has been reported to feed on mangrove leaves (May, 1999), but it is more likely that it is a scavenger on different types of organic matter, including other dead invertebrates (Alfaro *et al.*, 2006).

Two bivalves were dominant in this study. The cockle *A. stutch-*1145 *buryi* was abundant in sandflats and subtidal channels. Its tolerance to muddy sediments is reflected by its extended distribution, in lesser numbers, into the mangrove habitats. Although little is known about where it recruits in New Zealand estuaries (Stewart and Creese, 2002; Marsden, 2004), juveniles

1150 often were found in the sandflat and channel habitats. The pipi *P. australis* was recorded almost exclusively in channel and sandflat habitats, although its numbers were generally low.

## **Temporal changes**

1155 A significant increase in overall faunal composition was observed 6 months after the removal of mangrove trees at Site 1, especially within mangrove and pneumatophore habitats. This increase in population density was reflected by a higher mean number of individuals, number of taxa, and dominant species (i.e. crabs, snails, bivalves) within that site. These biological changes were 1200 accompanied by changes in sediment composition, from high silt to coarser sediment immediately after removal, and an increase in total organic content in the sediment. Although all mangrove trees were removed from the site, the results from the September 2004 sampling event showed a greater number of pneumatophores 1205 within the mangrove and pneumatophore habitats, probably a consequence of the removal of the uppermost sediments by water motion, which could have uncovered shorter pneumatophores. Another possible explanation for this pattern is that pneumatophores continued to grow for a short time, although the trees 1210 were removed, because many pneumatophores have photosynthetic tissue.

Subsequent faunal and sediment samples from March 2005 to September 2006 indicate similar temporal changes among sites, although many were more pronounced at Site 1. The general biological pattern was of an increase in species abundance just after mangrove removal, followed by a sharp decrease in species abundance in March and September 2006. These biological changes appear to be related to an increase in silt and organic content, which was most noticeable at Site 1, but was apparent too in 1220





**Figure 7.** Mean abundance ( $\pm$  s.e.) of A. *stutchburyi* and *P. australis* within different habitats where these species were found at three sites (Site 1, mangrove-removal area; Sites 2 and 3, control sites) from March 2004 to September 2006 (mangrove removal illustrated by vertical dashed line). Note that there was no pneumatophore habitat at Site 2 and that the *y*-axes have different scales.

- pneumatophore, sandflat, and channel habitats at Sites 2 and 3. It is likely that these physical changes were the result of intensive catchment activity just above Site 1, where a new building development is underway. Disturbance of buried peat within catchment soils, as a result of topographic reconfiguration by bulldozing, may have resulted in the increased organic content recorded in
- <sup>1275</sup> adjacent coastal sediments (J. Lockwood, pers. comm.). Although these changes in sediment structure may have been the major contributors to the faunal changes observed over time, reproductive cycles and seasonal migration patterns are likely to have been superimposed on the ecological trends. For example,

at Matapouri Estuary in northern New Zealand, Alfaro (2006)

found distinctive abundance and biodiversity patterns within <sup>1330</sup> specific estuarine habitats, which often were related to recruitment and migration patterns.

Highly mobile species, such as the crab *H. crassa*, dramatically increased in abundance following mangrove removal at Site 1, then slowly decreased in subsequent sampling dates. The pattern suggests that it may have migrated to the site to take advantage of the increase in organic content following the disturbance. Although it may exhibit intraspecific competition for food, it does show gregarious behaviour within favourable muddy habitats (Morrisey *et al.*, 1999; Sivaguru, 2000). This aggregation behaviour also may be responsible for its high densities in the marshgrass and



1395

Figure 8. Mean abundance ( $\pm$ s.e.) of polychaetes and oligochaetes within different habitats at three sites (Site 1, mangrove-removal area; Sites 2 and 3, control sites) from March 2004 to September 2006 (mangrove removal illustrated by vertical dashed line). Note that there was no pneumatophore habitat at Site 2 and that the y-axes have different scales. 1460

mangrove habitats. For other species, such as the mud snail A. crenata, the affinity to marsh and muddy substrata in the upper intertidal clearly define the distribution patterns (Pilkington and Pilkington, 1982). Although abundances were similar within Sites 2 and 3 throughout the sampling period, mangrove clearance at Site 1 resulted in a sharp increase in that snail's



**Figure 9.** Frequency of grain-size distribution (mud,  $<150 \mu$ m; fine sand,  $150-300 \mu$ m; medium sand,  $300-600 \mu$ m; coarse sand,  $>600 \mu$ m), at three sites (Site 1, mangrove-removal area; Sites 2 and 3, control sites) for marshgrass, mangrove, pneumatophore, sandflat, and channel habitats between March 2004 and September 2006 (mangrove removal was between March and September 2004). Note that there was no pneumatophore habitat at Site 2.





**Figure 10.** PCA plots of sediment (percentage mud and fine, medium, and coarse sand) across habitats (G, marshgrass; M, mangroves; P, pneumatophores; S, sandflats; C, channel) and sites (Site 1, mangrove-removal area; Sites 2 and 3, control sites) between March 2004 and September 2006 (mangrove removal was between March and September 2004).

1640 abundance within marshgrass and mangrove habitats. These results suggest that the mangrove trees themselves may not enhance snail population densities, but that the muddy sediment and high organic content may facilitate growth and survival. Another pulmonate snail (*P. antipodarum*) exhibited stable, high

where it often feeds on cockles and other dying invertebrates. A slight increase followed by a decrease in population density over time for this species was apparent for Sites 1 and 2, probably a consequence of their normally patchy distribution around food sources, which vary in time and space.

1700

1705

1645 densities in marshgrass habitats, but its density decreased in the mangrove habitat at Site 1 over time. The scavenger Z. lutulentus was most abundant in sandflat and channel habitats at Site 3, The dominant bivalves, *A. stutchburyi* and *P. australis*, both had generally constant densities throughout the sampling period, with a distinct decrease in population density in September 2006,



Figure 11. Mean percentage organic content ( $\pm$ s.e.) in sediment samples from five habitats within three sites (Site 1, mangrove-removal area; Sites 2 and 3, control sites) between March 2004 and September 2006 (mangroves removal was between March and September 2004). Note that the *y*-axes have different scales.

compared with previous sampling events. This decrease in density coincided with the increase in fine sediments and organic content observed, which can be attributed to catchment reworking. In addition, the abundance and distribution patterns of these species coincide with seasonal reproductive patterns (Hooker, 1995; Stewart and Creese, 2002). Finally, polychaete and oligo-

- 1755 chaete worms were most abundant in sandflat, channel, and pneumatophore habitats for all sites throughout the sampling period. Generally, polychaetes decreased in density immediately following mangrove removal at Site 1, and similar changes also were observed for oligochaetes. Although the densities of both groups
- 1760 of worm varied over time, no dramatic temporal changes was observed at Sites 2 and 3 (except for some instances at Site 3), indicating their success within muddy/sandy habitats.

### Habitat modifications

1765 It has been suggested that natural and anthropogenic changes to the structure of mangrove stands have a direct impact on the physical processes operating within the habitat and their associated fauna (Wolanski *et al.*, 1992). For example, the creation of canopy gaps may cause changes in soil characteristics (Clarke and Kerrigan,

2000) and promote the growth of saplings (Sherman et al., 2000). 1810 Moreover, significant changes in the abundance and composition of associated taxa take place after disturbances of mangrove architecture (Schrijvers et al., 1995; Skilleter, 1996; Kelaher et al., 1998; Skilleter and Warren, 2000; Bosire et al., 2004). The results of this study show that removal of mangroves altered the sediment charac- 1815 teristics and abundance of macrofauna within the habitat, suggesting that the transformation from mangrove to mudflat habitat immediately increased species abundance and diversity. However, these faunal characteristics continued to change over the next 2.5 years and could not be fully separated from further anthropogenic catch-1820 ment activities at the study site. In western Kincumber Broadwater, New South Wales, Australia, dramatic changes in benthic faunal composition and increased community structure variability took place after mangrove canopy pruning (from 5 to 1 m height; Gladsone and Schreider, 2003). However, that study evaluated 1825 faunal effects only once, 5 years after the event, and the authors interpreted the ecological changes based on comparisons with nearby undisturbed stands. In this study, faunal and sediment characteristics were recorded before and after the clearance event, monitored for 3 years, and compared with undisturbed sites. In addition, 1830

ecological effects on adjacent habitats (i.e. sandflats, subtidal channels) also were investigated.

In summary, this study provides a comprehensive evaluation of the effects of mangrove removal on faunal and sediment character-

- istics in a mangrove-dominated estuary. The results also suggest that ecological changes may extend beyond the immediate area  $(\sim 100 \text{ m})$  and into other habitats and that the effects may persist for 3 or more years after the event. The results may provide valuable ecological information for environmental man-
- 1840 agers seeking to control the spread of mangroves in the estuaries of northern New Zealand.

## Acknowledgements

- This work would not have been possible without the field and laboratory assistance of numerous community volunteers and students, including E. Beatson, A. Goldsmith, F. Thomas, S. Dewas, and L. Sergent. Special thanks are also due to the LaBonté's for their support with field logistics and scientific discussions. Further field support was provided by J. Wintle and the Mangawhai
- <sup>1850</sup> Harbour Restoration Society, and technical support by C. Whyburd, C. Silvester, and B. Jacomb of the School of Applied Sciences, Auckland University of Technology. I thank K. Campbell and anonymous reviewers for their scientific and editorial comments. The research was financially supported by Gracefields and
- <sup>1855</sup> Company Ltd and an AUT Contestable Research Grant.

#### References

1860

- Alfaro, A. C. 2006. Benthic macro-invertebrate community composition within a mangrove/seagrass estuary in northern New Zealand. Estuarine, Coastal and Shelf Science, 66: 97–110.
- Alfaro, A. C., and McDowell, M. 2003. Benthic ecology of estuarine habitats at Matapouri, northern New Zealand. New Zealand Marine Sciences Conference, Auckland, New Zealand.
- Alfaro, A. C., Thomas, F. C. M., Sergent, L., and Duxbury, M. 2006. Identification of trophic interactions within an estuarine food
- 1865 Identification of trophic interactions within an estuarine food web (northern New Zealand) using fatty acid biomarkers and stable isotopes. Estuarine, Coastal and Shelf Science, 70: 271–286.
  - Allen, J. A. 1998. Mangroves as alien species: the case of Hawaii. Global Ecology and Biogeography Letters, 7: 61–71.
- Alongi, D. M. 1987. The influence of mangrove-derived tannins on <sup>1870</sup> intertidal meiobenthos in tropical estuaries. Oecologia, 71: 537–540.
  - Alongi, D. M. 2002. Present state and future of the world's mangrove forests. Environmental Conservation, 29: 331–349.
- Alongi, D. M., Tirendi, F., and Clough, B. F. 2000. Below-ground
- 1875 decomposition of organic matter in forests of the mangroves *Rhizophora stylosa* and *Avicennia marina* along the arid coast of Western Australia. Aquatic Botany, 68: 97–122.
- Ashton, E. C., and Macintosh, D. J. 2002. Preliminary assessment of the plant diversity and community ecology of the Sematan mangrove forest, Sarawak, Malaysia. Forest Ecology and Management, 166: 111–129.
- Ashton, E. C., Hogarth, P. J., and Macintosh, D. J. 2003. A comparison of brachyuran crab community structure at four mangrove locations under different management systems along the Melaka Straits-Andaman Sea Coast of Malaysia and Thailand. Estuaries, 26: 1461–1471.
- Barbier, E. B. 2000. Valuing the environment as input: review of applications to mangrove–fishery linkages. Ecological Economics, 35: 47–61.
  - Bertness, M. D. 1991. Zonation of *Spartina patens* and *Spartina alterniflora* in New England salt marsh. Ecology, 72: 138–148.
- 1890 Bertness, M. D. 1992. The ecology of a New England salt marsh. American Scientist, 80: 260–268.

- Bertness, M. D., and Hacker, S. D. 1994. Physical stress and positive associations among marsh plants. American Naturalist, 144: 363–372.
- Bortolus, A., Schwindt, E., and Iribane, O. 2002. Positive plant-1895 animal interactions in the high marsh of an Argentinean coastal lagoon. Ecology, 83: 733–742.
- Bosire, J. O., Dahdoug-Guebas, F., Kairo, J. G., Cannicci, S., and Koedam, N. 2004. Spatial variation in macrobenthic fauna recolonisation in a tropical mangrove bay. Biodiversity and Conservation, 13: 1059–1074.
- Botero, L., and Salzwedel, H. 1999. Rehabilitation of the Cienaga Grande de Santa Maria, a mangrove–estuarine system in the Caribbean coast of Colombia. Ocean and Coastal Management, 42: 243–256.
- Bouillon, S., Koedam, N., Raman, A. V., and Dehairs, F. 2002. Primary 1905 producers sustaining macro-invertebrate communities in intertidal mangrove forests. Oecologia, 130: 441–448.
- Chapman, V. J. 1976. Mangroves and salt marshes of the Kaipara Harbour: a study with proposals for preservation of areas supporting the harbour ecosystem. Department of Lands and Surveys, Auckland. 28 pp. <sup>1910</sup>
- Chimner, R. A., Fry, B., Kaneshiro, M. Y., and Cormier, N. 2006. Current extent and historical expansion of introduced mangroves on O'ahu, Hawai'i. Pacific Science, 60: 377–383.
- Clarke, K. R., and Kerrigan, R. A. 2000. Do forest gaps influence the population structure and species composition of mangrove 1915 stands in northern Australia? Biotropica, 32: 642–652.
- Cox, E. F., and Allen, J. A. 1999. Stand structure and productivity of the introduced *Rhizophora mangle* in Hawaii. Estuaries, 22: 276–284.
- Crowe, T. 1999. Limits to generality: seasonal and temporal variation in dispersal of an intertidal gastropod. Journal of Experimental Marine Biology and Ecology, 232: 177–196.
- Davis, S., Childers, D., Day, J., Rudnick, D., and Sklar, F. 2001. Nutrient dynamics in vegetated and unvegetated areas of a southern Everglades mangrove creek. Estuarine, Coastal and Shelf Science, 52: 753–768.
- Diop, S. 2003. Vulnerability assessment of mangroves to environmental change. Estuarine, Coastal and Shelf Science, 58: 1–2.
- Dittmann, S. 2000. Zonation of benthic communities in a tropical tidal flat of north-east Australia. Journal of Sea Research, 43: 33–51.
- Dittmar, T., Lara, R., and Kattner, G. 2001. River or mangrove? Tracing major organic matter sources in tropical Brazilian coastal waters. Marine Chemistry, 73: 253–271.
- Duke, N. C., Meynecke, J. O., Dittmann, S., Ellison, A. M., Anger, K., Berger, U., Cannicci, S., *et al.* 2007. A world without mangroves? Science, 317: 41–42.
- Ellis, J., Nicholls, P., Craggs, R., Hofstra, D., and Hewitt, J. 2004. Effects of terrigenous sedimentation on mangrove physiology and associated macrobenthic communities. Marine Ecology Progress Series, 207: 71–82.
- Fountain, D. W., and Outred, H. A. 1991. Germination requirements 1940 of New Zealand native plants: a review. New Zealand Journal of Botany, 29: 311–316.
- Franks, T., and Falconer, R. 1999. Developing procedures for the sustainable use of mangrove systems. Agricultural Water Management, 40: 59–64.
- Gladsone, W., and Schreider, M. J. 2003. Effects of pruning a temperate mangrove forest on the associated assemblages of macroinvertebrates. Marine and Freshwater Research, 54: 683–690.
- Gleason, M. L., Elmer, D. A., Pien, N. C., and Fisher, J. S. 1979. Effects of stem density upon sediment retention by salt marsh cordgrass. Estuaries, 2: 271–273.
- Gordon, D. M., Bougher, A. R., and LeProvost, M. I. 1995. Use of models for detecting and monitoring change in a mangrove

1950

1930

1990

ecosystem in Northwestern Australia. Environment International, 21: 605–618.

- 1955 Gratton, C., and Denno, R. F. 2005. Restoration of arthropod assemblages in a *Spartina* salt marsh following removal of the invasive plant *Phragmites australis*. Restoration Ecology, 13: 358–372.
  - Green, M., Ellis, J., Schwarz, A., Green, N., Lind, D., and Bluck, B. 2003. For and against mangrove control. NIWA Information Series, 31. 8 pp.
  - Hooker, S. H. 1995. Life history and demography of the pipi, *Paphies australis* (Bivalvia: Mesodesmatidae) in northeastern New Zealand. MSc thesis, University of Auckland, New Zealand. 231 pp.
- Hume, T. M., and Dahm, J. 1992. An investigation of the effects of Polynesian and European land use on sedimentation in Coromandel estuaries. Consultancy Report No. 6104, Department of Conservation, Hamilton Regional Office, Hamilton, New Zealand. 56 pp.
- Kelaher, B. P., Chapman, M. G., and Underwood, A. J. 1998. Changes in benthic assemblages near boardwalks in temperate urban mangrove forests. Journal of Experimental Marine Biology and Ecology, 228: 291–307.
- Kieckbusch, D. K., Koch, M. S., Serafy, J. E., and Anderson, W. T. 2004. Trophic linkages among primary producers and consumers in fringing mangroves of subtropical lagoons. Bulletin of Marine Science, 74: 271–285.
  - Kitheka, J. U. 1997. Coastal tidally-driven circulation and the role of water exchange in the linkage between tropical coastal ecosystems. Estuarine, Coastal and Shelf Science, 45: 177–187.
- Laegdsgaard, P., and Johnston, C. 2001. Why do juvenile fish utilise
   mangrove habitats? Journal of Experimental Marine Biology and Ecology, 257: 229–253.
  - Levin, L. A., Neira, C., and Grosholz, E. D. 2006. Invasive cordgrass modifies wetland trophic function. Ecology, 87: 419-432.
- Levin, L. A., and Talley, T. S. 2002. Natural and manipulated sources of heterogeneity controlling early faunal development of a salt marsh. Ecological Applications, 12: 1785–1802.
  - Lindegarth, M., and Hoskin, M. 2001. Patterns of distribution of macro-fauna in different types of estuarine, soft sediment habitats adjacent to urban and non-urban areas. Estuarine, Coastal and Shelf Science, 52: 237–247.
- Macintosh, D. J., Ashton, E. C., and Havanon, S. 2002. Mangrove rehabilitation and intertidal biodiversity: a study in the Ranong Mangrove Ecosystem, Thailand. Estuarine, Coastal and Shelf Science, 55: 331–345.
- 1995 Marsden, I. 2004. Effects of reduced salinity and seston availability on growth of the New Zealand little-neck clam Austrovenus stutchburyi. Marine Ecology Progress Series, 266: 157–171.
- May, D. 1999. Spatial variation in litter production by the mangrove *Avicennia marina* var. *australasica* in the Rangaunu Harbour, Northland, New Zealand. New Zealand Journal of Marine and Freshwater Research, 33: 163–172.
- Morrisey, D. J., Beard, C., Morrison, M., Craggs, R., and Lowe, M. 2007. The New Zealand mangrove: review of the current state of knowledge. Auckland Regional Council Technical Publication, 325.
- 2005 Morrisey, D. J., DeWitt, T. H., Roper, D. S., and Williamson, R. B. 1999. Variations in the depth and morphology of burrows of the mud crab *Helice crassa* among different types of intertidal sediments in New Zealand. Marine Ecology Progress Series, 182: 231–242.
- Morrisey, D. J., Skilleter, G. A., Ellis, J. I., Burns, B. R., Kemp, C. E., and Burt, K. 2002. Differences in benthic fauna and sediment among mangrove (*Avicennia marina* var. *australasica*) stands of different ages in New Zealand. Estuarine, Coastal and Shelf Science, 56: 581–592.

- Pagliosa, P. R., and Lana, P. D. 2005. Impact of plant cover removal on macrobenthic community structure of a subtropical salt marsh. 2015 Bulletin of Marine Science, 77: 1–17.
- Parrish, C. 1998. Lipid biogeochemistry of plankton, settling matter and sediments in Trinity Bay, Newfoundland. 1. Lipid classes. Organic Geochemistry, 29: 1531–1545.
- Peterson, B. J., Howarth, R. E., and Garritt, R. H. 1985. Multiple stable isotopes used to trace the flow of organic matter in estuarine food webs. Science, 227: 1361–1363.
- Pilkington, M. C., and Pilkington, J. B. 1982. The planktonic veliger of *Amphibola crenata* (Gmelin). Journal of Molluscan Studies, 48: 24–29.
- Rauzon, M. J., and Drigot, D. C. 2002. Red mangrove eradication and 2025 pickleweed control in a Hawaiian wetland, waterbird responses, and lessons learned. *In* Turning the Tide: the Eradication of Invasive Species, pp. 240–248. Ed. by C. R. Veitch, and M. N. Clout. IUCN SSC Invasive Species Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK. 414 pp.
- Schrijvers, J., Van Gansbeke, D., and Vinex, M. 1995. Macrobenthic <sup>2030</sup> infauna of mangroves and surrounding beaches at Gazi Bay, Kenya. Hydrobiologia, 306: 53–56.
- Schwarz, A. 2003. Spreading mangroves: a New Zealand phenomenon or a global trend? Water and Atmosphere, 11: 8–10.
- Sherman, R. E., Fahey, T. J., and Battles, J. J. 2000. Small-scale disturb- 2035 ance and regeneration dynamics in a neotropical mangrove forest. Journal of Ecology, 88: 165–178.
- Sivaguru, K. 2000. Feeding and burrowing in a North Island New Zealand population of the estuarine mud crab, *Helice crassa*. PhD thesis, University of Auckland, New Zealand.
- Skilleter, G. A. 1996. Validation of rapid assessment of damage in urban mangrove forests and relationships with molluscan assemblages. Journal of Marine Biological Association of the UK, 76: 701-716.
- Skilleter, G. A., and Warren, S. 2000. Effects of habitat modification in mangroves on the structure of mollusk and crab assemblages. 2045 Journal of Experimental Marine Biology and Ecology, 244: 107–129.
- Snelgrove, P. V. R., Austen, M. C., Boucher, G., Heip, C., Hutchings, P. A., King, G. M., Koike, I., *et al.* 2000. Linking biodiversity above and below the marine sediment-water interface. BioScience, 50: 1076–1088.
- Spurgeon, J. 1998. The socio-economic costs and benefits of coastal habitat rehabilitation and creation. Marine Pollution Bulletin, 37: 373–382.
- Steel, O. C., Ewel, K. C., and Goldstein, G. 1999. The importance of propagule predation in a forest of non-indigenous mangrove 2055 trees. Wetlands, 19: 705–708.
- Stewart, M. J., and Creese, R. G. 2002. Transplants of intertidal shellfish for enhancement of depleted populations: preliminary trials with the New Zealand little neck clam. Journal of Shellfish Research, 21: 21–27.
- Stonich, S. C. 1992. Struggling with Honduran poverty: the environmental consequences of natural resource-based development and rural transformation. World Development, 20: 385–399.
- Tri, N. H., Asger, W. N., and Kelly, P. M. 1998. Natural resource management in mitigating climate impacts: the example of mangrove restoration in Vietnam. Global Environmental Change, 8: 2065 49-61.
- Valiela, I., Bowen, J. L., and York, J. K. 2001. Mangrove forests: one of the world's threatened major tropical environments. BioScience, 51: 807–815.
- Warren, R. S., and Neiring, W. A. 1993. Vegetation change on a northeast tidal marsh: interaction of sea-level rise and marsh accretion.
   Ecology, 74: 96–103.
- Whitcraft, C. R., and Levin, L. A. 2007. Regulation of benthic algal and animal communities by salt marsh plants: impact of shading. Ecology, 88: 904–917.

2140

- 2075 Wolanski, E., Mazda, Y., and Ridd, P. 1992. Mangrove hydrodynamics. In Tropical Mangrove Ecosystems, pp. 43–62. Ed. by A. I. Robertson, and D. M. Alongi. AGU Press, Washington. 330 pp.
  - Woodroffe, C. D. 1982. Litter production and decomposition in the New Zealand mangrove, *Avicennia marina* var. *resinifera*. New Zealand Journal of Marine and Freshwater Research, 16: 179–188.
  - Woodroffe, C. D. 1985. Studies of a mangrove basin, Tuff Crater, New Zealand: I. Mangrove biomass and production of detritus. Estuarine, Coastal and Shelf Science, 20: 265–280.
- Young, B. M., and Harvey, L. E. 1996. A spatial analysis of the 2085 relationship between mangrove (*Avicennia marina* var.

*australasica*) physiognomy and sediment accretion in the Hauraki Plains, New Zealand. Estuarine, Coastal and Shelf Science, 42: 231–246.

## Appendix

List of the taxa found inside and outside cores within each of six different habitats (G, marshgrass; M, mangroves; P, pneumatophores; S, sandflats; and C, channel) within three estuarine sites (Site 1, Q4 mangrove-removal area; Sites 2 and 3, control sites) in Mangawhai Estuary, New Zealand, between March 2004 and September 2006. 2145 Note that there was no pneumatophore habitat at Site 2.

	Site 1					Site 2					Site 3			
Taxon	G	м	Р	s	с	G	м	s	с	G	м	Р	s	с
Polychaeta		1	1	1	1		1	1	1	1		1	1	1
Oligochaeta	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Sipuncula					1			1	1					1
Polyplacophora														
Chiton glaucus				1	1				1				1	
Sypharochiton pelliserpentis			1		1								1	
Gastropoda														
Amphibola crenata	1	1	1	1		1	1			1	1	1		
Bulla quoyii		1	1											
Cominella glandiformis	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Cominella maculosa		1										1		
Diloma subrostrata		1	1	1				1	1			1	1	
Lepsiella scorbina			1				1				1			
Melagraphia aethiops		1	1								1			
Nerita atramentosa							1				1			
Ophicardelus costellaris	1	1	1			1				1	1			
, Potamopyrgus antipodarum	1	1	1			1				1	1	1		
Turbo smaragdus			1				1				1			
Zeacumantus lutulentus		1	1	1	1		1	1	1	1	1	1	1	1
Zeacumantus subcarinatus	1	1	1	1	1	1	1	1	1		1	1	1	1
Bivalvia														
Austrovenus stutchburvi		1	1	1	1		1	1	1		1	1	1	1
, Felaniella zelandica				1										
Macomona liliana		1		1				1				1	1	
Nucula hartvigiana			1	1	1			1					1	
Paphies australis				1	1			1	1				1	1
Saccostrea cucullata				-	-		1	-	-		1	1	-	-
Venericardia purpurata				1	1		-	1	1		-	-		1
Xenostrobus pulex				-	-		1	-	-		1	1		-
Cirripoda							•				•	•		
Chaemaesipho brunnea		1	1	1			1				1	1	1	1
Chaemaesipho columna		1	1		1		1		1		1	1		•
Amphipoda		-			,		,		-		-			
Corophium acutum				1	1			1	1				1	1
Unidentified	1	1	1	1	1	1	1	✓	1	1	1	1	1	
Isopoda		-			,		,	•	-	~	-			•
lsocladus armatus				1	1			1					1	1
Unidentified		1	1	-	•			1	1				1	•
Decapoda		-	2					•	•					
Elamena producta								1				1		
Helice crassa	1	1	1	1		1	1		1	1	1		1	
Palaemon affinis	•	÷	•	•	1	•	•		•		-	•	•	1
Cirripoda					•			•						•
Chaemaesinho brunnea		1	1				1				1	1		
Chaemaesipho columna		, ,	1				1				1	1		
Helmsi scanha		•		1	1		•	1	1		•	1	1	
Osteichthyes			•	•	•			•	*			•	•	