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Invasive mangroves alter macrofaunal community structure and facilitate opportunistic exotics

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ABSTRACT: Mangroves were introduced to the Hawaiian Islands in 1902, providing an unusual opportunity to examine the impacts of introduced vascular plants on coastal ecosystems. Despite >100 yr residence in Hawaii, little is known regarding how mangroves alter coastal ecosystem structure. We conducted a case study of 2 *Rhizophora mangle* habitats in Hawaii, comparing habitat parameters and macrofaunal community structure in introduced mangroves and nearby control sandflats at a similar tidal elevation. Mangrove sediments had finer sediments and higher organic carbon concentrations and porewater salinities than sandflats. Emergent mangrove roots were colonized by the introduced barnacles *Chthamalus proteus*, *Balanus reticulatus*, and *B. amphitrite* and the introduced sponges *Suberites zeteki*, *Sigmadocia caerulea*, and *Gelloides fibrosa*. Higher densities of non-native macrofauna were found in mangrove transects than in sandflat controls, indicating that invasive mangroves facilitate the persistence of non-native fauna in Hawaii. Mangrove habitats also had higher macrofaunal species richness and diversity, as well as greater dominance by subsurface deposit feeders. Introduced mangroves substantially altered benthic community structure, in part by enhancing the structural complexity of the Hawaiian coastal environment. Because macrobenthos provide a variety of ecosystem services, e.g. serving as prey for fish and birds and promoting detrital decomposition, mangrove-induced changes in sediment community composition will likely have far-reaching consequences in Hawaii. Similar consequences of mangrove invasion are likely in other regions, as mangrove habitats expand with climate warming and increased coastal sedimentation.

KEY WORDS: Ecosystem modification · Mangrove · *Rhizophora mangle* · Benthos · Plant invasion · Non-native species · Hawaii

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INTRODUCTION

Mangrove introduction history in Hawaii

In 1902, *Rhizophora mangle*, a mangrove broadly distributed in North and South America and the South Pacific, was introduced to Molokai, Hawaii, to stabilize the shoreline (MacCaughey 1917). *R. mangle* has developed monospecific stands throughout the main Hawaiian Islands due to continuous propagule production combined with a paucity of mangrove herbivores and seed predators (Allen 1998, Cox & Allen 1999, Steele et al. 1999). *R. mangle* has colonized the full marine tidal range, including the high intertidal, where it typically is outcompeted by other mangroves in native forests (Lugo & Snedaker 1974). Despite the dominance of mangroves in large coastal areas in Hawaii (Chimner et al. 2006), little is known regarding ecosystem structure and function in Hawaiian mangrove habitats.

Ecosystem consequences of mangrove invasion

The impacts of plant introductions on tidal wetlands have been primarily examined in temperate environments (Bertness et al. 2002, Neira et al. 2006), even though coastal plant invasions are occurring on a glo-

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bal scale (Callaway & Josselyn 1992, Ruiz et al. 1997), including in tropical and subtropical habitats (Allen 1998, Chen et al. 2008). Prior to mangrove introduction, Hawaii essentially lacked marine vascular plants (Wester 1981), despite the availability of suitable habitats (Egler 1942). Vascular plants can alter wetland habitat characteristics and faunal community structure through a variety of direct and indirect mechanisms, acting as major ecosystem engineers (Orth 1977, Orth et al. 1991, Jones et al. 1997, Crooks 2002). Introduced *Rhizophora mangle* is likely to act as a major ecosystem engineer in the Hawaiian intertidal, causing increased availability of hard substrata for encrusting organisms, higher porewater salinities, and reduced light levels and rates of water flow (e.g. Alongi 1987a, Shokita et al. 1989, Levin & Talley 2000, Whitcraft & Levin 2007). By reducing water flow, the root structure traps fine and organic-rich sediments transported by currents or produced *in situ* from mangrove litter (Chapman & Ronaldson 1958, Bird 1971). Decreased particle size and increased organic content can lead to enhanced densities of deposit-feeding animals, while reduced water flow can depress the feeding rates and densities of suspension feeders (Peterson et al. 1984, Lana & Guiss 1991). In addition, mangrove detritus has low nutritional value compared to other marine detrital sources because of high carbon:nitrogen ratios and lignin content (Robertson et al. 1992), and it is rich in tannins, which are known to inhibit digestive enzymes of many organisms (Mahadevan & Muthukumar 1980, Alongi 1987b). Introduction of tannin-rich detritus to benthic food webs in Hawaii may inhibit the feeding of native detritivores previously unexposed to significant amounts of tannin-rich vascular plant detritus. Thus infaunal community structure and function within mangrove communities are likely to be influenced by mangrove root structure, sediment grain size, organic content, and detrital input, and consequently differ from non-mangrove, unvegetated sandflat habitats (e.g. Neira et al. 2005, Levin et al. 2006).

Native mangroves in other regions have been shown to harbor a specific fauna with limited species overlap with sand or mud-flat biotopes (Sasekumar 1974, Frith 1977, Sheridan 1997). Because mangroves were very recently introduced to Hawaii, the native fauna is likely to be poorly adapted to this new habitat. For example, the endangered Hawaiian stilt typically forages within sandflats and on the seaward edge of mangrove forests, but generally does not forage within mangrove prop roots (Rauzon & Drigot 2002), possibly as a consequence of variations in microhabitat and prey abundance (e.g. Greenberg 1983, Clout & Gaze 1984). In addition, mangrove forests provide a habitat for waterbird predators, including introduced rats, Indian mongooses, and cattle egrets (Allen 1998). Because mangroves in Hawaii represent habitat loss to endangered waterbirds, they may restrict the recovery of waterbird populations (Allen 1998).

Alternatively, mangroves may have a positive influence on Hawaiian marine ecosystems through facilitation (e.g. Bulleri et al. 2008), e.g. by providing nursery grounds or predation refuges for commercially important fishes and invertebrates such as the Samoan crab *Scylla serrata* (Kay 1987). However, preliminary work on Hawaiian mangroves indicated that they were substantially ecologically underutilized (Walsh 1967), i.e. that they contained a variety of open niches. Such open niches may be readily colonized by invading species with broad tolerances (Orians 1986). Thus mangroves could provide invader 'footholds', facilitating the establishment of exotic species in Hawaii, which in turn threaten the ~500 species of marine and estuarine invertebrates endemic to the Hawaiian archipelago (Kay 1987, Eldredge & Miller 1997).

In order to evaluate *Rhizophora mangle* impacts on Hawaiian coastal communities, we conducted field sampling to test the following hypotheses:

(1) Mangrove invasion significantly alters the physical and chemical environment of unvegetated tidal flats by increasing belowground plant biomass, decreasing sediment grain size, and increasing porewater salinities and sediment organic carbon content.

(2) Hawaiian mangrove benthic communities have lower infaunal densities and species richness than adjacent sandflats and other coastal Hawaiian sandflats.

(3) Hawaiian mangroves harbor a higher proportion of non-native species compared to non-mangrove sandflats.

Because the tropical–subtropical habitat range of mangroves is expanding due to climate warming (IPCC 2007), our results are likely to provide important insights into mangrove invasion impacts in other regions.

MATERIALS AND METHODS

Study sites. Samples were collected in mature *Rhizophora mangle* mangrove communities located in Kaneohe Bay, Oahu (21° 27′ 42″ N, 157° 50′ 29″ W), and near Kapuaiwa Grove, Molokai (21° 05′ 52″ N, 157° 03′ 10″ W), Hawaii (Fig. 1). Kaneohe Bay was colonized by *R. mangle* in ~1930 and has some of the largest mangrove stands on Oahu (Devaney 1982). *R. mangle* was introduced to the south shore of Molokai in 1902, and this island has the oldest, most extensive mangrove stands in the Hawaiian archipelago. Specific mangrove stands were selected because they represented relatively mature forests. Paired control sandflats (non-mangrove sites) were also chosen on both islands, located 1.5 km from the nearest mangrove stand.

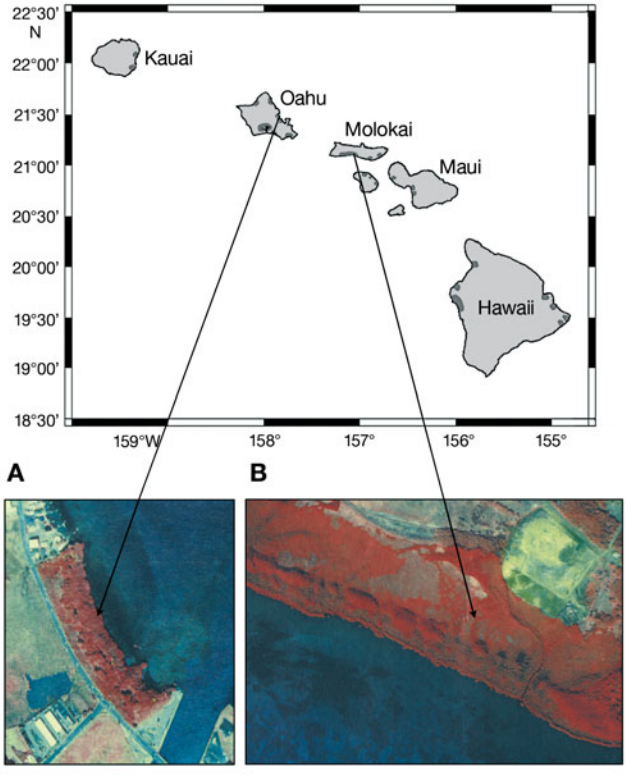

Fig. 1. Aerial photos (infra-red images; courtesy of R. Cannerella, Division of Aquatic Resources, Hawaii DLNR, Honolulu, HI) of mangrove sites on (A) Oahu and (B) Molokai. Dark shaded areas in upper panel indicate current mangrove distribution (Allen 1998)

Mangrove stands and control sandflat sites were chosen to have roughly comparable habitat size, tidal elevation, wave exposure, and coastal location (i.e. within the same bay for Kaneohe Bay and on the same south coast for Molokai). The 4 sites (2 mangrove forests and 2 unvegetated sandflat controls) were selected to represent case studies of extensive mature mangrove stands in Hawaii, providing insights into the intensity of mangrove impacts on Hawaiian coastal ecosystems. In addition, 2 mangrove forests (Waiawa and Pouhala, both in Pearl Harbor) and 1 additional control site (Paiko Lagoon) were sampled for a subset of environmental parameters: particle size, belowground plant biomass, and prop-root density. All control sites are suitable habitat for *R. mangle*, but have remained mangrove-free due to seed and seedling removal by the state of Hawaii and/or private individuals.

Sample collection and preparation. Infaunal and epifaunal benthos and sediments were sampled in each of 3 habitats: mangrove stands, adjacent sandflats, and sandflats at distances >1.5 km from mangrove stands. Samples were collected along 3 randomly located transects running perpendicular to the mangrove forest edge. Samples were taken at 6 points along each transect: at distances of 8, 2, and 0.5 m from the forest edge within the mangrove forest, and at similar distances from the forest edge on the adjacent sandflat. Each non-vegetated sandflat control was sampled along 3 randomly located transects established at the same tidal elevations as for sampled mangrove habitats, and samples were collected at 6 distances along these transects: 3 along the same tidal elevation as interior mangrove stations (control upper) and 3 along the same tidal elevations as sampling sites in the mangrove-adjacent sandflats (control lower). Densities of epifauna and mangrove roots were counted within 0.5 m^2 quadrats placed over each sampling point along a transect (Sasekumar 1974). Salinity was measured using a refractometer (±2 psu) for porewater extracted from syringe samples taken in the upper 5 cm of sediment at low tide.

Two sediment cores were collected from each of the 6 distances along each transect for infaunal analysis and sediment properties. In total, 36 cores were collected from each site, 18 each for infaunal and sediment analysis. Sediment cores (33 cm^2 in area and 5 cm deep) for macrofaunal analysis were preserved in 10% formalin prior to sieving. Cores were sampled to 5 cm depth because pilot sampling indicated that 98% of the macrofauna occurred within the upper 5 cm, and some control sandflats could not be cored deeper than 5 cm. In the laboratory, samples were washed on 500 µm sieves to allow comparison to previous mangrove studies (Sheridan 1997, Morrisey et al. 2003, Ellis et al. 2004). Animals retained on sieves were sorted under a dissecting microscope, identified to the lowest possible taxon, and transferred to 80% ethanol for storage. After identification, animals were briefly blotted and weighed using a microbalance to determine wet weight biomass. Hardparts of molluscs were manually removed prior to weighing. Macrofaunal species were assigned to trophic groups based on Barnard (1969), Barnes (1980), Fauchald & Jumars (1979), Kukert & Smith (1992), and Sheridan (1997). Belowground plant material was removed from macrofaunal cores, dried at 60°C for ~1 to 2 d to a constant weight, and weighed to determine belowground biomass (Neira et al. 2005).

The top 5 cm of sediment cores were extruded for analyses of sediment grain-size distribution, sediment organic carbon and total nitrogen content; the sediment was then homogenized, subsampled for analyses, and frozen at –20°C. Organic carbon and total nitrogen content of the sediments were determined using a Carlo Erba 1108 CHN Analyzer after carbonate material was dissolved using sulfurous acid (as in Verardo et al. 1990). A portion of sediment for grain-size analysis was digested with hydrogen peroxide to remove organic material and subsequently wet sieved through 2000 µm (to separate rubble and/or large grain sizes) and 63 µm

sieves. Size fractions (>2000 µm, 63 to 2000 µm, and <63 µm) were dried at 60°C for 1 to 2 d, weighed, and percent rubble (>2000 µm), sand (63 to 2000 µm), and silt/clay (<63 µm) calculated (Neira et al. 2005).

In order to evaluate Hawaiian mangroves as a habitat for introduced and/or cryptogenic macrofauna (Hypothesis 3), species lists for Hawaiian mangroves were compared with existing lists of introduced species for the state of Hawaii (Eldredge & Miller 1997, Eldredge & DeFelice 2000). The abundances and proportions of introduced and/or cryptogenic species were also compared among mangrove stands, adjacent sandflats, and sandflat controls.

Statistical analysis. One-way ANOVA with *a posteriori* Tukey's HSD tests were used to examine differences within and among sites (4 sites: Oahu mangrove and control transects, and Molokai mangrove and control transects) over the full tidal elevation range from 8 m within mangroves to 8 m out onto adjacent sandflats. All distances are given from the forest boundary for mangrove transects or corresponding boundary for sandflat controls. Within a mangrove site, paired comparisons were made between locations occurring at equal distances from the mangrove boundary; e.g. 8 m inside mangrove versus –8 m outside on the adjacent sandflat. Negative distances correspond to sampling locations on adjacent, lower tidal elevation sandflats. Paired comparisons were also made between mangrove and control transects at similar tidal elevations; e.g. 8 m inside mangrove versus 8 m control upper, 2 m inside mangrove versus 2 m control upper, etc. *F*-tests were used to determine significant differences in all measured variables between mangrove and control sandflat sites, and within sites (i.e. inside mangroves versus adjacent sandflats) for each island (Molokai and Oahu) ($\alpha = 0.05$). Comparisons of macrofaunal and environmental variables between islands, sites (mangrove versus control sandflats), and elevations were made using a nested ANOVA (elevations nested within 4 sites). All data were tested for normality and heteroscedasticity using Shapiro-Wilk and Levene's tests (Sokal & Rohlf 1995). As a result of these tests, particle-size data were arcsin-square-root transformed and macrofaunal densities were square-root transformed prior to statistical analysis to achieve homogeneity of variances. For mangrove root density, belowground plant biomass, salinity, total organic carbon, total nitrogen, macrofaunal biomass, and trophic groups, a non-parametric Wilcoxon test was used because transformed data failed to meet parametric assumptions. All data presented in tables and figures are untransformed means, and faunal data have been converted to a per square meter basis for comparative purposes. ANOVA, *a posteriori* tests, and Wilcoxon tests were performed using SPSS Statistical Software 16.0.

Macrofaunal diversity was examined with PRIMER Statistical Software 6.0 (Clarke & Warwick 2001) using species richness (*S*, number of species), normalized species richness per core ($d = S - 1/\ln(N)$, where N is the number of individuals), Shannon-Wiener index (H'; log base 2), and evenness (J') per core. Similarities and differences in macrofaunal communities were examined using non-metric multidimensional scaling (NMDS), based on Bray-Curtis similarity indices. Pair-wise comparisons were made between mangrove and control transects in each of the 4 sites using analysis of similarities (ANOSIM). Similarity percentages (SIMPER) determined the percent dissimilarity and the taxa responsible for differences between groups. All multivariate analyses were performed using PRIMER Statistical Software on square-root transformed macrofaunal data in order to allow all macrofauna species to contribute to the similarity while also retaining the importance of more abundant species (Clarke & Warwick 2001).

RESULTS

Plant modification of mudflat sediment characteristics

Nested ANOVA revealed significant island, mangrove versus control sandflats, and elevation effects in several of the environmental characteristics (Table S1, available as supplementary material at www.int-res.com/articles/suppl/m404p051_app.pdf). To explore these significant patterns in more detail, 1-way ANOVA paired with non-parametric analyses were applied and results are presented here.

Aboveground root densities within mangroves ranged from 4 to 75 roots m^{-2}. There were no significant differences in root densities (Wilcoxon, $\chi^2 = 79.5$, $p = 0.596$; Table 1); however, Oahu mangroves had significantly greater belowground plant biomass than Molokai mangroves (Table S1). Comparable root densities and belowground root biomass were found in the additional mangrove sites sampled in Pearl Harbor, Oahu (Table S2 in the supplement). Mangrove-adjacent sandflats and non-vegetated sandflat controls had neither roots nor belowground plant biomass, except for the presence of belowground plant biomass at –0.5 m on Oahu. Total organic carbon in sediments was ~2 to 3 times higher in mangrove than in adjacent sandflat sediments for Oahu (Wilcoxon, 2 m vs. –2 m: $\chi^2 = 6.0$, $p = 0.050$) and Molokai (8 m vs. –8 m and 2 m vs. –2 m: $\chi^2 = 6.0$, $p = 0.050$). Total organic carbon in Molokai mangrove sediments was ≤2 times higher than in Oahu sediments ($\chi^2 = 226.0$, $p < 0.001$). Total nitrogen was similar among sites on Oahu, but significantly higher in Molokai mangroves than adjacent

Table 1. Mean (±1 SE, n = 3) values for sediment and environmental variables measured from sampled mangrove and sandflat control transects. DW: dry weight

Variable	Distance from boundary (m)					
	8	2	0.5	−0.5	−2	−8
Oahu						
Root density (no. m^{-2})	35.3 ± 3.5	74.7 ± 20.5	45.3 ± 18.8	0.0	0.0	0.0
Belowground biomass (g DW m^{-2})	1246.7 ± 96.7	1920.1 ± 339.2	2027.4 ± 207.7	791.7 ± 356.5	0.0	0.0
Salinity (psu)						
Mangrove	29.3 ± 1.2	27.7 ± 0.3	28.0 ± 0.6	27.7 ± 1.5	26.3 ± 0.7	26.3 ± 0.3
Sandflat	16.0 ± 2.1	16.3 ± 1.3	16.7 ± 1.7	17.0 ± 1.5	16.7 ± 1.7	16.0 ± 2.3
% Mud						
Mangrove	7.3 ± 1.1	10.3 ± 1.3	9.8 ± 2.2	5.3 ± 1.6	5.9 ± 1.4	5.5 ± 1.3
Sandflat	11.4 ± 2.6	8.6 ± 0.4	6.3 ± 1.0	7.8 ± 0.8	7.2 ± 2.3	7.0 ± 1.4
% Sand						
Mangrove	92.1 ± 1.3	89.7 ± 1.3	89.5 ± 2.9	93.1 ± 0.1	94.1 ± 1.4	93.8 ± 1.2
Sandflat	69.4 ± 6.5	79.0 ± 4.2	65.0 ± 9.1	79.1 ± 6.1	53.7 ± 18.1	74.1 ± 5.1
% Rubble						
Mangrove	0.6 ± 0.6	0.0 ± 0.0	0.7 ± 0.7	1.5 ± 1.5	0.0 ± 0.0	0.8 ± 0.1
Sandflat	19.3 ± 7.5	12.5 ± 4.1	28.7 ± 8.9	13.0 ± 5.3	39.1 ± 20.4	18.8 ± 5.9
Total organic carbon (mg g^{-1})						
Mangrove	12.65 ± 2.95	20.95 ± 10.18	20.92 ± 14.04	8.33 ± 1.15	7.16 ± 1.24	5.91 ± 0.68
Sandflat	7.65 ± 0.05	6.30 ± 0.11	8.70 ± 0.08	7.23 ± 0.08	6.82 ± 0.06	6.62 ± 0.07
Total nitrogen (mg g^{-1})						
Mangrove	1.07 ± 0.19	1.49 ± 0.35	0.97 ± 0.42	0.93 ± 0.21	0.92 ± 0.23	0.79 ± 0.18
Sandflat	1.04 ± 0.20	0.84 ± 0.12	0.77 ± 2.20	0.73 ± 1.09	0.86 ± 0.54	0.82 ± 0.99
Molokai						
Root density (no. m^{-2})	75.3 ± 6.8	54.7 ± 2.9	32.0 ± 14.4	0.0	0.0	0.0
Belowground biomass (g DW m^{-2})	1727.3 ± 175.0	1353.5 ± 620.6	484.8 ± 87.5	0.0	0.0	0.0
Salinity (psu)						
Mangrove	38.3 ± 0.7	37.0 ± 1.0	37.5 ± 2.4	34.3 ± 1.5	35.3 ± 0.9	35.7 ± 0.7
Sandflat	26.0 ± 5.6	26.7 ± 2.9	28.3 ± 2.4	28.0 ± 2.5	27.7 ± 2.6	29.7 ± 0.9
% Mud						
Mangrove	63.7 ± 6.5	36.3 ± 4.2	6.8 ± 3.2	4.6 ± 0.6	5.9 ± 0.3	5.8 ± 1.3
Sandflat	2.3 ± 1.1	3.1 ± 1.1	2.6 ± 0.4	3.2 ± 1.0	3.4 ± 0.8	3.3 ± 0.8
% Sand						
Mangrove	31.0 ± 7.0	57.0 ± 4.5	84.6 ± 8.3	90.7 ± 1.5	90.6 ± 1.6	91.4 ± 0.2
Sandflat	96.8 ± 1.7	96.9 ± 1.1	96.9 ± 0.6	96.4 ± 1.4	96.0 ± 1.1	96.4 ± 1.1
% Rubble						
Mangrove	5.3 ± 2.7	6.7 ± 4.9	8.6 ± 5.3	4.7 ± 1.9	3.5 ± 1.6	2.8 ± 1.5
Sandflat	0.9 ± 0.7	0.0 ± 0.0	0.5 ± 0.3	0.3 ± 0.3	0.6 ± 0.4	0.3 ± 0.3
Total organic carbon (mg g^{-1})						
Mangrove	34.02 ± 12.20	27.08 ± 1.89	17.33 ± 2.85	13.54 ± 1.23	13.64 ± 2.19	15.72 ± 0.55
Sandflat	25.91 ± 5.44	27.50 ± 1.99	24.02 ± 2.69	21.61 ± 6.01	18.28 ± 5.70	28.83 ± 2.61
Total nitrogen (mg g^{-1})						
Mangrove	3.16 ± 0.64	2.34 ± 0.27	0.77 ± 0.09	0.59 ± 0.11	0.59 ± 0.07	0.51 ± 0.05
Sandflat	0.22 ± 0.04	0.22 ± 0.04	0.25 ± 0.09	0.28 ± 0.05	0.30 ± 0.07	0.29 ± 0.09

sandflats (8 m vs. −8 m and 2 m vs. −2 m: $\chi^2 = 6.0$, $p = 0.050$) and sandflat controls ($\chi^2 = 190.0$, $p < 0.001$).

Overall, mangrove sediments had finer grain sizes and higher porewater salinities than control sandflats (Table S1). Oahu mangrove sediments had more sand (particles >63 µm) than sandflat controls (ANOVA, $F_{1,34} = 39.0$, $p < 0.001$), whereas sandflat controls had significantly more rubble than mangrove sites ($F_{1,34} = 64.2$, $p < 0.001$, Table 1). Sediments collected in Pearl Harbor, Oahu, also were characterized by fine grain sediments (Table S2), whereas the additional sandflat site in Paiko Lagoon had more sand and rubble than fine mud (Table S2). Molokai mangrove sediments were composed of more silt/clay and less sand then adjacent sandflats ($F_{1,5} = 45.576$, 8 vs. −8 m: $p < 0.001$ for silt/clay and sand; 2 vs. −2 m: $p < 0.001$ for silt/clay, $p = 0.007$ for sand). Mangrove porewater salinities were higher than in sandflat controls (Wilcoxon, Oahu:

χ^2 = 171.0, p < 0.001; Molokai: χ^2 = 175.0, p < 0.001). However, despite a trend toward increased porewater salinities found in mangrove sediments, there was no significant difference between mangrove and adjacent sandflat porewater salinities for either Oahu or Molokai mangrove transects.

NMDS and ANOSIM analysis of sediment and vegetation parameters revealed significant differences among the environments for mangrove and control transects. For Oahu, mangrove sediments versus adjacent sandflats and sandflat controls were equally dissimilar (ANOSIM, R = 0.561 for mangroves vs. adjacent sandflats, R = 0.617 for mangroves vs. sandflat controls, p = 0.001, SIMPER dissimilarity ≈ 20%, Fig. 2A). On Molokai, mangroves were also distinct from adjacent sandflats and sandflat controls (ANOSIM, R = 0.736 for mangroves vs. adjacent sandflats, R = 0.375 for mangroves vs. sandflat controls, p = 0.001, SIMPER dissimilarity = 20 to 24%). The presence of mangroves was associated with enhancement of root material, increased belowground plant biomass, higher porewater salinities and sediment organic carbon content, and reduced sediment grain size; these parameters were responsible for 98% (SIMPER) of the environmental differences found between mangroves and non-vegetated control transects on both islands.

Mangrove faunal associates: abundance, composition, and diversity

Epifauna utilizing mangrove roots consisted of a variety of introduced species, including the barnacles *Chthamalus proteus*, *Balanus reticulatus*, and *B. amphitrite* (Table S3 in the supplement). Total barnacle densities were highest in the Oahu mangroves (233.3 barnacles root^{-1}; data are given in units of per root because the surface area of the roots was very difficult to assess). The introduced crab *Panopeus lacustris* was also found in Oahu mangrove roots. Sponges found attached at the base of mangrove roots included the introduced *Suberites zeteki*, *Sigmadocia caerulea*, and *Gelloides fibrosa*. The introduced mangrove crab *Scylla serrata* was observed and collected within the mangrove forests (Demopoulos et al. 2007) but not within the sampled transects. Native epifauna included *Metapograpsus* sp. and *Zooanthus pacificus* (Table S3). Epifauna observed on adjacent sandflats and sandflat controls included unidentified species of amphipods, gobies, medusae, and penaid shrimp. We were not able to collect these highly mobile taxa for identification. Overall, a greater variety of epifauna were observed in mangroves than on adjacent sandflats or sandflat controls.

Nested ANOVA of macrofaunal parameters also revealed distinct among-site and elevation differences

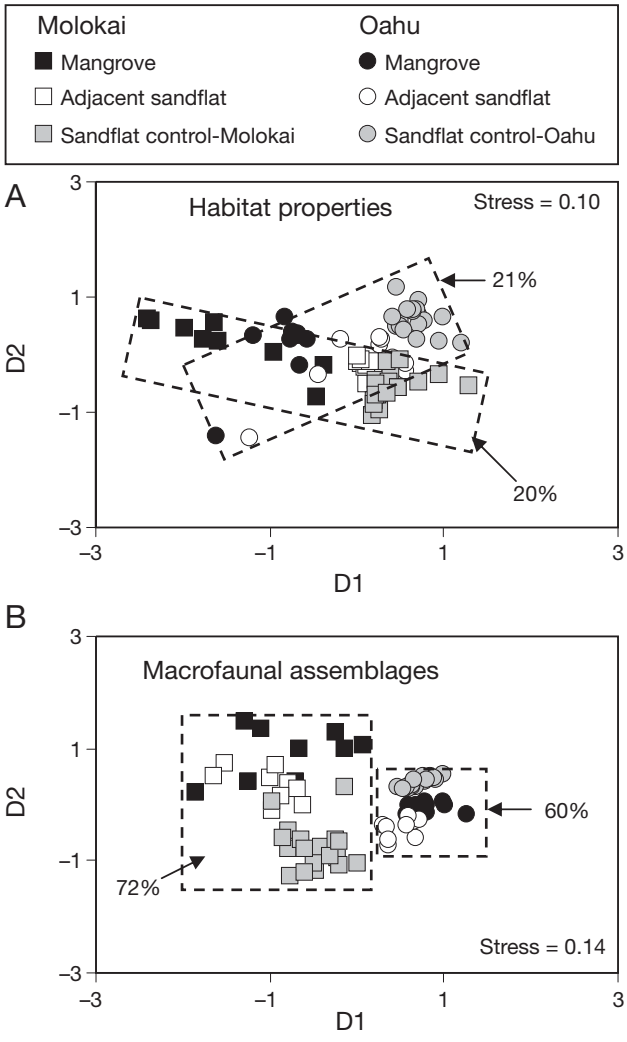

Fig. 2. Non-metric multidimensional scaling results of (A) environmental variables and (B) macrofaunal assemblages from mangroves, adjacent sandflats, and sandflat controls. Each point represents the data from 1 core. Environmental variables include percent organic carbon, percent organic nitrogen, percent mud content, salinity, and belowground plant biomass. The stress value measures how well the 2-dimensional plot represents the multidimensional distances among the data; values <0.20 are considered to yield a useful 2-dimensional representation of the data (Clarke & Warwick 2001). Dashed rectangles represent within-island SIMPER comparisons between mangrove and sandflat control transects

(Table S1). Densities of total sediment macrofauna were higher within mangrove sediments than in adjacent sandflats (Fig. 3) on Oahu (ANOVA, $F_{5,17}$ = 5.06, p = 0.010) and Molokai ($F_{5,17}$ = 29.05, p = 0.007), with the greatest densities occurring at 2 m inside of the mangrove fringe (mean ± SE = 136 363 ± 16 467 and 53 333 ± 3869 ind. m^{-2} for Oahu and Molokai, respectively). The highest densities overall occurred in the mangrove and sandflat control sites on Oahu, with

densities at sandflat control sites on average exceeding those from mangrove sites on Oahu ($F_{11,35}$ = 3.24, p = 0.008). For Oahu transects, total macrofaunal biomass was significantly higher at 2 m inside mangroves than 2 m on adjacent sandflats (Wilcoxon, χ^2 = 6.0, p = 0.050) and at 8 m in the control upper sandflats than on mangrove transects at the same tidal elevation (χ^2 = 6.0, p = 0.050) (Table 2). However, biomass did not differ significantly between habitats for the Molokai transects.

On Oahu, major macrofaunal groups within mangrove sediments included oligochaetes (10 to 72% of total abundance), amphipods (17 to 58%), and polychaetes (10 to 36%; Fig. 4). There was a shift in dominance from oligochaetes (3 species, 72%) in mangroves to a mixture of amphipods (43%), polychaetes (37%) and 1 species of oligochaete (*Ainudrilus* sp., 20%) in adjacent sandflats. Taxa found at 8 m within the mangrove forest included *Ainudrilus* spp., *Marionina coatesae*, Phallodrilinae sp., *Potamilla* sp. 1 and 2, *Capitella capitata*, *Corophium insidiosum*, *Neomicrodeutopus* cf. *makena*, hydrozoans, and nemerteans. In contrast, at 8 m on adjacent sandflats, *M. coatesae*, hydrozoans, and nemerteans were absent. However, many of the same species remained within the top 10 taxa (Table 3). Additional dominant taxa in adjacent sediments included Insect sp. D and the polychaetes *Marphysa corallina*, *Exogone* sp. E, and *Typosyllis cornuta*. These taxa were also present in mangrove sediments, but generally in smaller densities. Sandflat controls shared many taxa with mangrove transects (Table 3), but the sandflat community dominants at all elevations were sabellid polychaetes (62 to 80%).

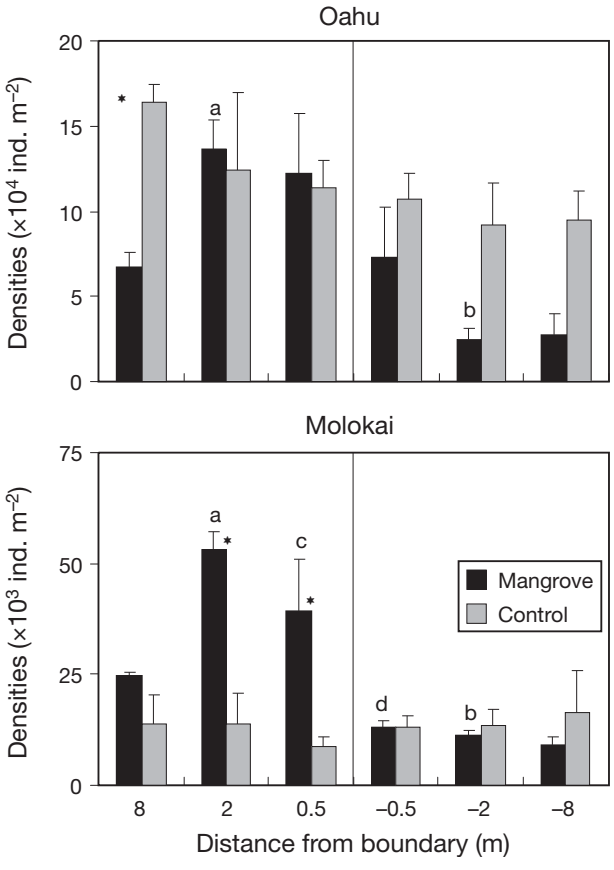

Fig. 3. Mean (±1 SE, n = 3) macrofaunal densities in sediments from Oahu and Molokai. Vertical line corresponds to the boundary between mangrove and adjacent sandflats or control upper and control lower elevations. Lowercase letters indicate significant differences (ANOVA, p < 0.05) between distance pairs from the mangrove fringe, i.e. between 2 and –2 m and between 0.5 and –0.5 m along the mangrove transect. * Significant differences between mangrove and control sandflat transect samples at the same tidal elevations (ANOVA, p < 0.05)

In contrast to Oahu mangrove forests, the sediment macrofauna on Molokai mangrove transects was typically dominated by polychaetes (several species, 33 to 70%) and oligochaetes (19 to 62%), rather than amphipods (Fig. 4). Dominant polychaetes included 7 species exclusively found in mangrove forests in the present study (Table 3): *Pseudopolydora corallicola*, *Carazziella* cf. *reishi*, *Polydora* sp. 1, *Amphiglena mediterranea*, *Monticellina* sp. 2 and 3, and *Paraonella* sp. A. Adjacent sandflats were similar in major taxonomic composition, i.e. dominated by polychaetes (30 to 47%) and oligochaetes (33 to 55%), but contained an additional suite of amphipods (1 to 5%, *Neomicrodeutopus* cf. *makena*, *Eriopisella sechellensis upolu*) and polychaetes (*Pionosyllis spinesetosa*, *Typosyllis cornuta*). Taxa absent from adjacent sandflats included Enchytraeidae sp. 2 and *Ainudrilus* spp. Molokai sandflat control sediments were dominated by a mixture of polychaetes (32 to 76%) and amphipods (9 to 42%). All adjacent sandflats and sandflat controls lacked enchytraeid oligochaetes.

NMDS and ANOSIM analysis of macrofaunal assemblages for all 4 sites and elevations revealed significant differences in macrofaunal assemblages between mangrove and sandflat control transects (Fig. 2B; Table S4 in the supplement). For Oahu, mangrove and sandflat control transects were dissimilar (ANOSIM, R = 0.735, p = 0.002, dissimilarity = 60%). There were 3 species responsible for ~50% of the community differences: *Corophium insidiosum* (absent from sandflat control transects) and *Potamilla* sp. 1 and 2 (found in higher densities in sandflat controls).

On Molokai, mangrove infaunal composition differed from adjacent sandflats (ANOSIM, R = 0.419, p = 0.001, SIMPER dissimilarity = 72%) and sandflat controls (R = 0.854, p = 0.002, SIMPER dissimilarity = 82%). Species responsible for ~50% of the dissimilarity between mangrove transects and sandflat controls included oligochaetes (*Thalassodrilides* cf. *gurwitschi*, *Tectidrilus* cf. *bori*) and polychaetes (*Potamilla* sp. 1, *Armandia intermedia*, *Exogone* sp. E, *Capitella capitata*, *Pseudopoly-*

Table 2. Mean (±1 SE, n = 3) macrofaunal biomass, taxon richness (*S*, *d*), evenness (*J′*), and Shannon-Wiener diversity index (*H′*) for mangrove and sandflat control transects. *S*: number of species per core (33 cm^2); $d = S - 1/\log(N)$. WW: wet weight

Variable	Distance from boundary (m)					
	8	2	0.5	–0.5	–2	–8
Oahu						
Biomass (g WW m^{-2})						
Mangrove	2.01 ± 0.30	5.57 ± 1.03	5.74 ± 2.00	5.06 ± 2.44	1.34 ± 0.17	1.93 ± 0.37
Sandflat	3.25 ± 0.03	3.38 ± 0.38	4.12 ± 1.23	2.86 ± 0.51	3.33 ± 0.52	7.86 ± 3.63
S						
Mangrove	8.7 ± 1.9	14.7 ± 1.9	16.0 ± 2.0	11.7 ± 3.3	7.3 ± 0.3	9.3 ± 0.3
Sandflat	11.0 ± 1.7	9.3 ± 0.9	10.0 ± 1.0	8.7 ± 0.7	11.3 ± 1.3	11.7 ± 0.3
d						
Mangrove	1.43 ± 0.36	2.33 ± 0.28	2.51 ± 0.22	1.94 ± 0.45	1.46 ± 0.01	1.95 ± 0.12
Sandflat	1.59 ± 0.27	1.45 ± 0.24	1.53 ± 0.19	1.32 ± 0.11	1.86 ± 0.32	1.87 ± 0.06
J′						
Mangrove	0.56 ± 0.11	0.65 ± 0.04	0.57 ± 0.07	0.61 ± 0.11	0.67 ± 0.07	0.69 ± 0.05
Sandflat	0.46 ± 0.05	0.57 ± 0.03	0.62 ± 0.07	0.52 ± 0.07	0.60 ± 0.05	0.61 ± 0.06
H′ ($\log_2$)						
Mangrove	1.77 ± 0.48	2.46 ± 0.05	2.25 ± 0.21	2.01 ± 0.27	1.92 ± 0.22	2.21 ± 0.20
Sandflat	1.55 ± 0.16	1.83 ± 0.18	2.03 ± 0.15	1.61 ± 0.17	2.10 ± 0.19	2.15 ± 0.20
Molokai						
Biomass (g WW m^{-2})						
Mangrove	0.82 ± 0.21	1.97 ± 0.51	4.38 ± 1.56	7.76 ± 6.37	2.43 ± 0.55	2.63 ± 1.73
Sandflat	1.56 ± 0.35	3.60 ± 1.01	7.33 ± 4.01	1.97 ± 0.22	2.02 ± 0.50	2.25 ± 0.40
S						
Mangrove	12.3 ± 0.9	16.0 ± 1.5	14.3 ± 1.8	11.0 ± 1.5	11.7 ± 0.7	11.0 ± 2.5
Sandflat	10.0 ± 2.5	9.7 ± 3.2	10.0 ± 2.5	11.0 ± 1.5	10.7 ± 2.2	10.3 ± 1.5
d						
Mangrove	2.57 ± 0.21	2.90 ± 0.26	2.85 ± 0.48	2.67 ± 0.44	2.95 ± 0.21	2.92 ± 0.55
Sandflat	2.42 ± 0.38	2.28 ± 0.59	2.68 ± 0.53	2.64 ± 0.28	2.61 ± 0.54	2.63 ± 0.34
J′						
Mangrove	0.66 ± 0.01	0.69 ± 0.02	0.71 ± 0.11	0.75 ± 0.10	0.86 ± 0.06	0.86 ± 0.04
Sandflat	0.80 ± 0.04	0.77 ± 0.08	0.89 ± 0.02	0.81 ± 0.01	0.79 ± 0.06	0.85 ± 0.07
H′ ($\log_2$)						
Mangrove	2.39 ± 0.06	2.77 ± 0.15	2.74 ± 0.54	2.61 ± 0.49	3.03 ± 0.15	2.89 ± 0.14
Sandflat	2.56 ± 0.15	2.28 ± 0.22	2.90 ± 0.36	2.77 ± 0.13	2.63 ± 0.25	2.81 ± 0.16

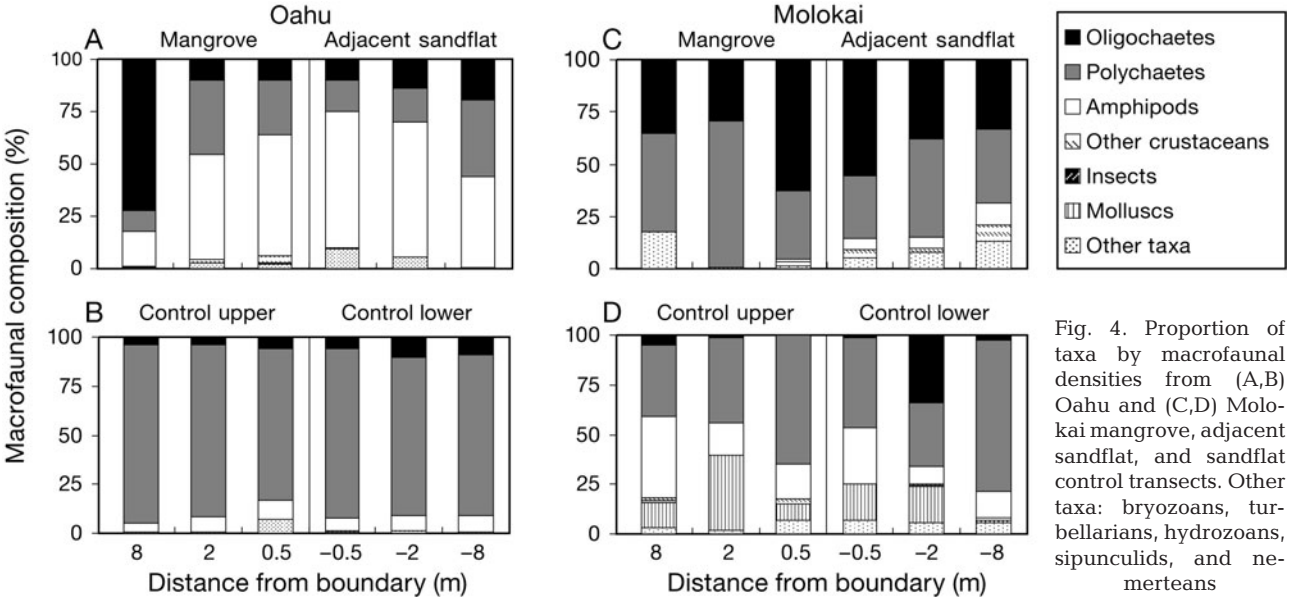

Fig. 4. Proportion of taxa by macrofaunal densities from (A,B) Oahu and (C,D) Molokai mangrove, adjacent sandflat, and sandflat control transects. Other taxa: bryozoans, turbellarians, hydrozoans, sipunculids, and nemerteans

Table 3. Top 10 taxa, in rank order, as determined from densities and similarity percentages analysis found in mangroves, adjacent sandflats, and control sandflat sediments on Oahu and Molokai. Taxa in **bold** are those found exclusively in mangrove sediments. Underlined taxa are those found only in island-specific mangrove and adjacent sandflat cores. Shaded taxa are cryptogenic/introduced species

Mangrove transect location	Distance from boundary (m)					
	8	2	0.5	−0.5	−2	−8
Oahu	*Ainudrilus* spp.	*Corophium insidiosum*	*Corophium insidiosum*	*Corophium insidiosum*	*Corophium insidiosum*	*Corophium insidiosum*
	Marionina coatesae	*Potamilla* sp. 1	*Potamilla* sp. 1	*Neomicrodeutopus* cf. *makena*	*Neomicrodeutopus* cf. *makena*	*Ainudrilus* spp.
	Neomicrodeutopus cf. *makena*	*Neomicrodeutopus* cf. *makena*	*Ainudrilus* spp.	*Ainudrilus* spp.	*Capitella capitata*	*Capitella capitata*
	Potamilla sp. 1	*Ainudrilus* spp.	*Neomicrodeutopus* cf. *makena*	*Potamilla* sp. 1	*Ainudrilus* spp.	*Neomicrodeutopus* cf. *makena*
	Capitella capitata	*Capitella capitata*	*Capitella capitata*	*Exogone* sp. E	*Malacoceros* sp. 1	*Exogone* sp. E
	Phallodrilinae sp.	***Marionina coatesae***	*Malacoceros* sp. 1	*Malacoceros* sp. 1	*Sphaerosyllis* cf. *centroamericana*	*Potamilla* sp. 1
	Corophium insidiosum	Hydrozoa	Hydrozoa	*Capitella capitata*	*Exogone* sp. E	*Marphysa corallina*
	Nemertean	*Potamilla* sp. 2	*Marphysa corallina*	*Sphaerosyllis* cf. *centroamericana*	*Potamilla* sp. 1	*Sphaerosyllis* cf. *centroamericana*
	Hydrozoa	*Anatanais insularis*	*Sphaerosyllis* cf. *centroamericana*	Polychaete larva	Hydrozoa	*Typosyllis cornuta*
	Potamilla sp. 2	*Sphaerosyllis* cf. *centroamericana*	*Anatanais insularis*	Bryozoa	Bryozoa	Insect sp. d
Molokai						
	Pseudopolydora corallicola	*Potamilla* sp. 1	*Tectidrilus* cf. *bori*	*Thalassodrilides* cf. *gurwitschi*	*Armandia intermedia*	*Thalassodrilides* cf. *gurwitschi*
	Thalassodrilides cf. *gurwitschi*	*Thalassodrilides* cf. *gurwitschi*	*Thalassodrilides* cf. *gurwitschi*	*Armandia intermedia*	*Thalassodrilides* cf. *gurwitschi*	*Apseudes* n. sp. *moniker*
	***Polydora* sp. 1**	***Monticellina* sp. 2**	*Armandia intermedia*	*Neomicrodeutopus* cf. *makena*	*Tectidrilus* cf. *bori*	Flatworm
	Sipunculid	*Exogone* sp. E	*Potamilla* sp. 1	*Apseudes* n. sp. *moniker*	*Malacoceros* sp. 1	*Armandia intermedia*
	Enchytraeidae sp. 2	***Monticellina* sp. 3**	*Myriochele* sp. 1	*Capitella capitata*	*Potamilla* sp. 1	*Neomicrodeutopus* cf. *makena*
	Amphiglena mediterranea	*Potamilla* sp. 4	*Myriochele oculata*	*Malacoceros* sp. 1	*Typosyllis cornuta*	*Malacoceros* sp. 1
	Typosyllis cornuta	***Carazziella* cf. *reishi***	*Potamilla* sp. 4	*Tectidrilus* cf. *bori*	*Neomicrodeutopus* cf. *makena*	Sipunculid
	Carazziella* cf. *reishi	*Tectidrilus* cf. *bori*	*Malacoceros* sp. 1	Flatworm	*Capitella capitata*	*Potamilla* sp. 1
	Capitella capitata	***Pseudopolydora corallicola***	*Apseudes* n. sp. *moniker*	*Smithsonidrilus capricornae*	Nemertean	*Capitella capitata*
	***Paraonella* sp. A**	*Capitella capitata*	*Exogone* sp. E	Nemertean	*Pionosyllis spinesetosa*	*Eriopisella sechellensis upolu*

Table 3 (continued)

Control transect location	Distance along transect (m)					
	8	2	0.5	–0.5	–2	–8
Oahu						
	Potamilla sp. 1	*Potamilla* sp. 1	*Potamilla* sp. 1	*Potamilla* sp. 1	*Potamilla* sp. 1	*Potamilla* sp. 1
	Potamilla sp. 2	*Potamilla* sp. 2	*Potamilla* sp. 2	*Ainudrilus* spp.	*Capitella capitata*	*Capitella capitata*
	Capitella capitata	*Neomicrodeutopus* cf. *makena*	*Neomicrodeutopus* cf. *makena*	*Neomicrodeutopus*	*Potamilla* sp. 2 cf. *makena*	*Ainudrilus* spp.
	Neomicrodeutopus cf. *makena*	*Capitella capitata*	*Ainudrilus* spp.	*Potamilla* sp. 2	*Ainudrilus* spp.	*Potamilla* sp. 2
	Ainudrilus spp.	*Ainudrilus* spp.	*Capitella capitata*	*Capitella capitata*	*Neomicrodeutopus* cf. *makena*	*Neomicrodeutopus* cf. *makena*
	Nemertean	*Exogone* sp. E	*Exogone* sp. E	Nemertean	Nemertean	*Exogone* sp. E
	Exogone sp. E	*Malacoceros* sp. 1	Nemertean	*Exogone* sp. E	*Exogone* sp. E	*Malacoceros* sp. 1
	Lysidice sp. 1	Nemertean	*Malacoceros* sp. 1	*Malacoceros* sp. 1	*Armandia intermedia*	*Armandia intermedia*
	Malacoceros sp. 1	Hydrozoa	*Sphaerosyllis* cf. *centroamericana*	*Lysidice* sp. 1	*Malacoceros* sp. 1	*Marphysa corallina*
	Mediomastus sp. 1	*Marphysa corallina*	Bryozoa	*Sphaerosyllis* cf. *centroamericana*	*Mediomastus* sp. 1	Nemertean
Molokai						
	Malacoceros sp. 1	*Malacoceros* sp. 1	*Malacoceros* sp. 1	*Malacoceros* sp. 1	*Malacoceros* sp. 1	*Corophium insidiosum*
	Corophium insidiosum	*Typosyllis cornuta*	*Corophium insidiosum*	*Corophium insidiosum*	*Exogone* sp. E	*Typosyllis cornuta*
	Typosyllis cornuta	*Neomicrodeutopus* cf. *makena*	*Neomicrodeutopus* cf. *makena*	Nemertean	*Corophium insidiosum*	*Neomicrodeutopus* cf. *makena*
	Smithsonidrilus capricornae	*Corophium insidiosum*	*Exogone* sp. E	*Typosyllis cornuta*	*Smithsonidrilus capricornae*	Malacoceros sp. 1
	Exogone longicornis	*Exogone longicornis*	*Spiochaetopterus* cf. *costarum*	*Neomicrodeutopus* cf. *makena*	*Thalassodrilides* cf. *gurwitschi*	Nemertean
	Neomicrodeutopus cf. *makena*	*Potamilla* sp. 1	*Exogone longicornis*	*Typosyllis* cf. *variegata*	*Neomicrodeutopus* cf. *makena*	*Exogone* sp. E
	Gastropod sp. 1	*Smithsonidrilus capricornae*	*Typosyllis cornuta*	Gastropod sp. 1	*Potamilla* sp. 1	*Potamilla* sp. 1
	Scyphoproctus djiboutiensis	Nemertean	Gastropod sp. 1	*Exogone* sp. E	*Potamilla* sp. 4	*Potamilla* sp. 4
	Decamastus sp. 2	Gastropod sp. 1	*Potamilla* sp. 1	*Exogone longicornis*	Gastropod sp. 1	*Sabellidae* sp. B
	Thalassodrilides cf. *gurwitschi*	*Scyphoproctus djiboutiensis*	*Decamastus* sp. 2	*Potamilla* sp. 1	Nemertean	*Decamastus* sp. 2

dora corallicola); these taxa were found in higher densities in mangrove transects. In contrast, higher densities of amphipods (*Corophium insidiosum*, *Neomicrodeutopus* cf. *makena*), Gastropod sp. 1, and *Malacoceros* sp. 1 were found in sandflat controls. Lastly, mangrove infaunal communities were significantly different on Oahu from Molokai (R = 0.944, p = 0.002, SIMPER dissimilarity = 87%). The top 7 species responsible for ~50% of the mangrove community differences included *Corophium insidiosum*, *Neomicrodeutopus* cf. *makena*, *Ainudrilus* spp., *Potamilla* sp. 1, *Capitella capitata* found in Oahu mangrove transects versus *Thalassodrilides* cf. *gurwitschi* and *Tectidrilus* cf. *bori* found in Molokai mangrove transects.

Taxonomic richness (S) per sediment core was highest overall within Molokai mangrove communities (ANOVA, $F_{3,71} = 17.39$, $p < 0.001$; Table 2). Taxonomic richness (S) in mangrove transects was higher than control sandflats at the same tidal elevations on Oahu (2, 0.5, and −0.5 m, Wilcoxon, $\chi^2 = 6.0$, p = 0.043). In addition, diversity (d), Shannon-Wiener index (H'), and evenness (J') were higher in both mangrove and sandflat transects in Molokai compared to Oahu (ANOVA, $F_{3,71} = 18.983$, p = 0.004; Table 2).

Of the 89 macrofaunal taxa found in the mangrove, adjacent sandflat, and control sandflat habitats in the present study, 29 taxa were exclusive to Molokai mangrove transects (including mangrove and adjacent sandflat habitats) and 13 were exclusive to Oahu mangrove transects. Oligochaetes and polychaetes dominated the species found exclusively along mangrove transects (>10% contribution), including *Marionina coatesae*, Enchytraeidae sp. 2, *Tectidrilus* cf. *bori*, and *Pseudopolydora corallicola* (Table S5 in the supplement). Furthermore, 8 taxa were found only inside the Oahu mangrove habitat proper (i.e. at mangrove transect distances of 0.5 to 8 m) and 16 taxa were found exclusively inside the Molokai mangrove habitat (Table S5). Thus it appears that the Hawaiian mangroves harbor a specific fauna, with limited species overlap with adjacent sandflat and control sandflat transects.

Trophic modes and introduction status

Mangrove infaunal communities on both islands had significantly higher densities and percentages of subsurface deposit feeders than sandflat controls (ANOVA, $F_{3,17} = 15.447$, $p < 0.001$; Fig. S1, Table S1 in the supplement). In particular, subsurface deposit feeders, primarily tubificid and enchytraeid oligochaetes, dominated Oahu mangrove sediments ($F_{5,17} = 6.94$, p = 0.003 at 8 m). In contrast, Oahu sandflat controls were dominated by surface feeders (which include surface-deposit feeders and suspension feeders) (71 to 80%, Wilcoxon, $\chi^2 = 245.0$, p = 0.005; Fig. S1). Subsurface deposit feeders were a dominant group throughout Molokai mangrove transects, with the highest densities located at 0.5 m inside the mangrove habitat ($\chi^2 = 6.0$, p = 0.050).

Lastly, mangrove transects had greater densities of cryptogenic and introduced species than sandflat controls (Wilcoxon, Oahu: $\chi^2 = 238.0$, p = 0.003; Molokai: $\chi^2 = 216.5$, $p < 0.001$; Fig. 5). These fauna were often among the community dominants in mangrove transects (Table 3), attaining the highest densities near the mangrove forest boundary (Fig. 5); densities were significantly higher at 2 m inside mangrove forests than in adjacent sandflat sediments on Oahu ($\chi^2 = 6.0$, p = 0.050). While there was a trend toward higher densities of both native and introduced fauna inside Molokai mangroves, there were no significant differences between mangrove forests and adjacent sandflat sediments. Overall, mangroves had a higher proportion of cryptogenic and introduced species relative to sandflat controls (Oahu: $\chi^2 = 211.0$, $p < 0.001$; Molokai: ANOVA, $F_{11,35} = 2.353$, p = 0.039). In addition, densities of native fauna were lower in Oahu mangroves relative to sandflat controls ($\chi^2 = 193.0$, $p < 0.001$).

DISCUSSION

Invasive plant influence on sediments and fauna

Mangrove invasion into previously non-vegetated Hawaiian sandflats has changed habitat properties by increasing above- and belowground plant biomass, porewater salinity, sediment organic carbon content, the availability of hard substrate for encrusting organisms, and decreasing sediment grain size. All of the parameters responsible for the differences are functions of mangrove presence. Thus the results of the present study are consistent with our first hypothesis, that mangrove invasion significantly alters the physical and chemical environment of non-vegetated tidal flats by increasing belowground plant biomass, decreasing sediment grain size, and increasing porewater salinities and sediment organic carbon content. We observed that porewater salinity was highest both in the mangrove sediments and adjacent sandflats, indicating that mangrove influence on environmental parameters may extend beyond the mangrove forest boundary into adjacent non-vegetated sandflats. Organic carbon and nitrogen content vary among native mangrove forests; our results fall within ranges reported from *Rhizophora apiculata* mangrove stands in Thailand (Alongi et al. 2001), but were lower compared to native mangroves in Micronesia (Gleason & Ewel 2002) and Puerto Rico (Demopoulos 2004). Sedi-

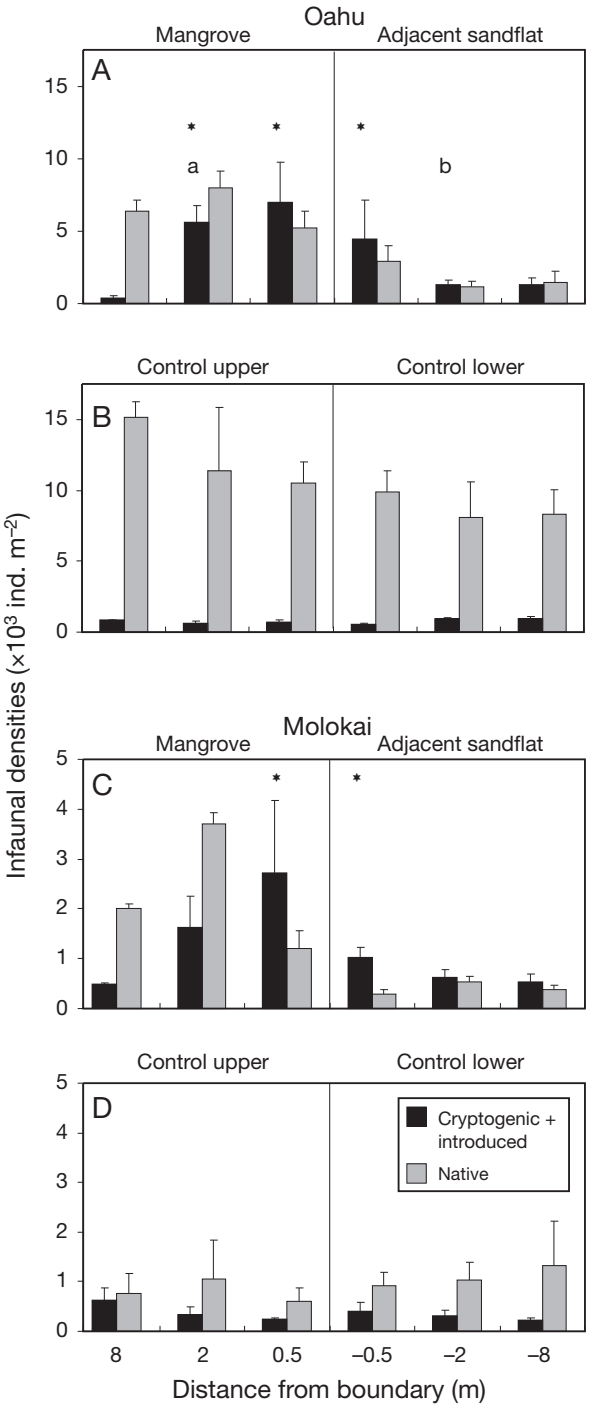

Fig. 5. Densities of sediment macrofauna classified into 2 categories: cryptogenic/introduced, and native from mangrove, adjacent sandflat and sandflat control transects on (A,B) Oahu and (C,D) Molokai. Lowercase letters indicate significant differences (ANOVA, $p < 0.05$) between distance pairs from the mangrove fringe, i.e. between 2 and –2 m and between 0.5 and –0.5 m along the mangrove transect. *Significant differences in the densities of cryptogenic and introduced species between mangrove and control sandflat transect samples at the same tidal elevations (ANOVA or Wilcoxon, $p < 0.05$)

ment particle size in native *Rhizophora* forests varies from fine-grained sediments (75 to 87% silt/clay) in *R. apiculata* stands in Thailand and *R. mangle* stands in Puerto Rico (Alongi et al. 2001, A. W. J. Demopoulos unpubl. data) to sandy sediments (85%) found in Kenyan forests (Schrijvers et al. 1995), a range comparable to our results. Sediment particle size in 2 other mangrove forests in Pearl Harbor, Hawaii, were composed of primarily fine grained sediments whereas sandflat sediments in Paiko Lagoon, Hawaii, were mostly sand, indicating that mangrove sediments in Hawaii are generally composed of fine-grained sediments. Where native *R. mangle* thrives in other parts of the world, it creates deep peat layers centuries old (Cohen & Spackman 1968); thus changes in the belowground root environment in Hawaii have the potential to persist over the long term (>100 yr).

Mangroves provided new substrate for a variety of epifaunal and infaunal species in Hawaii. More epifauna (both root- and non-root-associated) were observed along mangrove transects than in sandflat control transects. Enhanced densities of infauna were also found in mangrove sediments relative to adjacent sandflats. Changes in infaunal composition in invaded mangroves involved a distinct shift towards oligochaetes in the interior of mangroves and dominance by polychaetes on the adjacent sandflats. Along Oahu mangrove transects, the seaward increase in surface feeders (including suspension and deposit feeders), particularly sabellid polychaetes, may result from increased water flow in the absence of root structures, promoting suspension feeding (e.g. LaBarbera 1984). However, sabellids were abundant in both mangrove and control transects, suggesting that these taxa are well distributed in the Oahu intertidal zone. In contrast, mangrove transects on Molokai were dominated by subsurface deposit feeders, primarily oligochaetes and capitellid polychaetes, indicating that there likely were differences among Hawaiian mangrove habitats in overall community structure. These differences may be a function of between-island differences in species pools available to colonize the mangroves, or mangrove habitat age.

Among studies using similar sampling techniques, infaunal densities in native *Rhizophora mangle* forests ranged from 32 000 to 57 000 ind. m^{-2} in Puerto Rico and 22 591 to 52 964 ind. m^{-2} in Florida (Sheridan 1997, Demopoulos 2004) versus 39 000 to 108 000 ind. m^{-2} in exotic mangroves in Hawaii (present study). Tanaid crustaceans and annelids (capitellid polychaetes and oligochaetes) were typically the dominant taxa found in native mangroves (Sheridan 1997, Demopoulos 2004). In Hawaii, mangrove infauna were also dominated by capitellid polychaetes and oligochaetes (e.g. enchytraeids and tubificids), with

small proportions of insect larvae and nemerteans (Demopoulos 2004, Demopoulos et al. 2007). Infaunal trophic groups found in native mangrove forests were dominated by surface-deposit feeders and suspension feeders, with few carnivores (Wells 1984, Sheridan 1997, Demopoulos et al. 2007); in contrast, at some mangrove locations, infaunal groups in introduced mangroves on Hawaii were dominated by subsurface deposit feeders. Mangrove infaunal diversity in Hawaii was similar to native mangrove forests (Table S6 in the supplement) (Kumar 1995, Sheridan 1997, Morrisey et al. 2003, Ellis et al. 2004), although it should be noted that diversity levels in native mangroves span an extremely broad range. The pattern of enhanced infaunal diversity with greater distance into the mangrove forest in Hawaii has also been observed in native mangroves. Hart & Chindah (1998) observed a landscape gradient in infaunal diversity, with values increasing from the low to high intertidal zone. They attributed this pattern to decreasing exposure of the benthos to predators as a result of increased protection from mangrove roots. Frith (1977) found enhanced species richness in the *Rhizophora* zone relative to adjacent mudflats, and credited these patterns to increased shade, substrate moisture, attachment points, and abundance of organic detritus in the forest, all functioning to provide a favorable habitat for colonizing benthos. In other words, mangroves may increase the availability of microhabitats and food resources for infaunal benthos, facilitating enhanced diversity and infaunal densities.

Mangrove infaunal diversity in Hawaii was enhanced by the presence of oligochaetes. Oligochaetes are often the numerically dominant infaunal macrobenthic taxon in native mangrove sediments; they are also important functionally, contributing substantially to the remineralization of organic material (Erseus 1999) and to the production of biomass for consumption by higher trophic levels, including crustaceans and fish (Giere & Pfannkuche 1982). Oligochaetes in the present study included genera and species similar to those found in native mangrove forests in Australia and Belize, e.g. Phallodrilinae sp., *Thalassodrilides* cf. *gurwitschi*, *Marionina coatesae*, *Tectidrilus* cf. *bori*, *Smithsonidrilus capricornae*, and *Ainudrilus* spp. These taxa were associated with different environmental conditions, e.g. with fully marine environments (e.g. Phallodrilinae sp.), low salinities (*Ainudrilus* spp.), and/or organically enriched sediments (*Thalassodrilides gurwitschi*, *S. capricornae*, and *Tectidrilus bori*) (Erseus 2002). *Tectidrilus* cf. *bori* and *Thalassodrilides* cf. *gurwitschi* were both associated with mangrove and sandflat sediments on Molokai, where the sediments were typically enriched in organic carbon relative to Oahu sediments. Enchytraeid oligochaetes were found exclusively in mangrove sediments in Hawaii, which possibly reflects their plant-associated environmental preferences (Healy & Walters 1994), as they are often associated with *Spartina* salt marsh sediments (Levin et al. 2006).

Chapman & Tolhurst (2004) found that the most distinct macrofaunal groups residing in native mangrove sediments were oligochaetes, polychaetes, gastropods, amphipods, and insect larvae; oligochaetes in particular were important in distinguishing habitat-associated assemblages. Structures associated with mangrove trees (roots, leaf litter) were often the most important determinants of benthic assemblages. Plant-associated changes in infaunal communities also have been observed in temperate wetlands. For example, higher macrobenthic densities and species richness were associated with native *Spartina alterniflora* stands relative to unvegetated wetlands (Lana & Guiss 1991, Netto & Lana 1999); densities of dominant polychaetes in these habitats were found to be positively correlated with live belowground biomass (Lana & Guiss 1992). Roots and rhizomes from seagrasses have also been found to protect infauna from predators, possibly leading to enhanced infaunal abundance (Posey 1988, Posey et al. 1993). Introduced mangroves may provide a refuge for fauna by offering protection from abiotic disturbance (e.g. desiccation) and physical barriers to some predators (e.g. birds and juvenile fish) (cf. Sasekumar 1974, Sheridan 1997). Therefore, enhanced species richness and densities in introduced mangrove habitats in Hawaii relative to non-vegetated adjacent sandflats agreed well with existing data demonstrating the effects of vegetation on marine macrobenthos (e.g. Bertness et al. 2000).

It is interesting to note that the Hawaiian *Rhizophora mangle* habitat lacked sesarmid and ocypodid crabs, which can be major seed predators, detrital processers, and bioturbation agents in native mangroves (e.g. Cannicci et al. 2008). There appear to be no species filling these functional roles in Hawaiian mangroves (Demopoulos 2004, Demopoulos et al. 2007), suggesting that mangrove recruitment, litter dynamics, bioturbation, and porewater processes in Hawaiian mangroves may be substantially different than in native mangrove stands.

Facilitation of other invasive species

The enhanced abundance and species richness of introduced species in Hawaiian mangroves may have been the result of specific functions of the new habitat. Plant invasions have been associated with invasive hot spots (enhanced densities of introduced species) as a

consequence of increased provision of structure for encrusting species and release from predation pressure (Grosholz et al. 2009). For example, densities of introduced clams were 2-10 times higher in meadows of an invasive *Spartina* hybrid than on adjacent open mudflats. Clams utilized the *Spartina* plant as structure for attachment and as a refuge from predation by bat rays (Grosholz et al. 2009). In the present study, introduced encrusting epifauna, e.g. the barnacles *Chthamalus proteus* and *Balanus* spp. (Table S3), were found only on mangrove roots. These opportunistic species require hard surfaces and can be abundant on other hard substrates available in the Hawaiian coastal zone (Zabin 2002). In addition, the poor nutritional quality of mangrove detritus has been implicated as a factor in perpetuating the dominance of pioneering infaunal assemblages in mangrove sediments (Alongi & Christoffersen 1992). Thus the introduction of mangrove detritus may facilitate the persistence of opportunistic introduced and cryptogenic fauna with broad environmental tolerances (e.g. capitellids, oligochaetes). If introduced mangroves continue to facilitate introduced species in Hawaii (and other regions), this may lead to an invasional 'meltdown' (Simberloff & Von Holle 1999), accelerating the success of additional invasive species. However, it remains unclear whether these invasive species in turn facilitate mangrove success, a prerequisite for true invasional meltdown (Simberloff 2006).

Consequences of mangrove invasion

The ability of vascular plants to influence the structure and function of wetlands and enhance habitat complexity and heterogeneity is well documented (Lana & Guiss 1991, Leonard & Luther 1995, Levin & Talley 2000). While the present study was limited to examination of 4 sites, 2 mangrove and 2 non-mangrove controls, it represents the first study to document the impact of introduced mangroves on benthic communities in tropical–subtropical environments.

As climate and land-use patterns change worldwide, mangrove distributions are very likely to broaden. Mangrove invasion of new habitats is a particularly likely consequence of global warming because tropical and subtropical climate zones will expand (IPCC 2007). In addition, altered land-use patterns may create new habitats suitable for mangroves by changing coastal erosion and runoff to form new intertidal flats (Field 1995). For example, mangroves have spread by ~50% in last 45 yr in New Zealand, expanding into previously non-vegetated intertidal flats formed by increased estuarine sedimentation resulting from deforestation (Woodroffe 1982, Young & Harvey 1996). This mangrove expansion has resulted in the loss of sandflats (Ellis et al. 2004). The ecological effects and public perception of mangrove habitat expansion in New Zealand have been varied; mangroves may increase fisheries production and diversity and help to prevent coastal erosion, but, as in Hawaii, they interfere with recreational and commercial use of the shore and displace other habitats (e.g. mud and sandflats) that have significant ecological value (Morrisey et al. 2003). As mangrove habitats expand due to climate warming and increased coastal sedimentation, we may expect to observe similar changes in benthic ecosystem structure and function to those documented here for Hawaii, including facilitation of species invasions.

CONCLUSIONS

Rhizophora mangle habitats in Hawaii support a dense sediment macrofaunal community primarily composed of annelids and amphipods. There are significant community differences within and among mangrove stands in Hawaii, likely as a consequence of differences in sediment organic carbon content, salinity ranges, predation refuges, hard substrate availability, and grain-size distributions. Mangroves enhance macrofaunal densities and diversity relative to adjacent sandflats by providing new niches and harboring introduced species. The dominance of cryptogenic and introduced species in Hawaiian mangrove sediments indicates that invasive mangroves facilitate the persistence and spread of introduced species, which may ultimately impact the ~500 estuarine and marine endemic species in Hawaii. Facilitation of exotic species and especially the reduction of available habitat for native species (e.g. waterbirds) by invasive mangroves are likely to become significant problems if subtropical regions and associated new mangrove habitats expand due to global warming (IPCC 2007).

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