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Impacts of exotic mangrove forests and mangrove deforestation on carbon remineralization and ecosystem functioning in marine sediments

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Abstract

To evaluate how mangrove invasion and removal can modify benthic carbon cycling processes and ecosystem functioning, we used stable-isotopically labelled algae as a deliberate tracer to quantify benthic respiration and C-flow through macrofauna and bacteria in sediments collected from (1) an invasive mangrove forest, (2) deforested mangrove sites 2 and 6 years after removal of above-sediment mangrove biomass, and (3) two mangrove-free, control sites in the Hawaiian coastal zone. Sediment oxygen consumption (SOC) rates were significantly greater in the mangrove and mangrove removal site experiments than in controls and were significantly correlated with total benthic (macrofauna and bacteria) biomass and sedimentary mangrove biomass (SMB). Bacteria dominated short-term C-processing of added microalgal-C and benthic biomass in sediments from the invasive mangrove forest habitat. In contrast, macrofauna were the most important agents in the short-term processing of microalgal-C in sediments from the mangrove removal and control sites. Mean faunal abundance and short term C-uptake rates in sediments from both removal sites were significantly higher than in control cores, which collectively suggest that community structure and short-term C-cycling dynamics in habitats where mangroves have been cleared can remain fundamentally different from un-invaded mudflat sediments for at least 6-yrs following above-sediment mangrove removal. In summary, invasion by mangroves can lead to large shifts in benthic ecosystem function, with sediment metabolism, benthic community structure and short-term C-remineralization dynamics being affected for years following invader removal.

1 Introduction

Marine vascular plants can influence a variety of above- and below-sediment physical and chemical characteristics, and consequently can alter the species composition and trophic structure of benthic communities (Talley and Levin, 1999; Levin et al., 2006;

Alongi, 2008). Thus, vascular plants can play a large role in structuring the flow of organic material and energy in coastal habitats (Wardle et al., 2004). Mangroves are among the most widespread marine vascular plants, occupying $\sim 1.6 \times 10^5$ km^2 along sub-tropical and tropical coastlines (Alongi, 2002, 2008), where they play important ecosystem roles, serving as nursery grounds for commercially important fishes and invertebrates (Manson et al., 2005), and as nesting habitats for a variety of birds (Nagelkerken et al., 2008). Mangroves also act as major ecosystem engineers by reducing water flow and trapping sediments, which can lead to enhanced densities of deposit feeding fauna (Demopoulos, 2004; Demopoulos and Smith, 2010), as well as limiting coastal erosion, and providing a buffer to tropical storms and tsunamis (Environmental Justice Foundation report, 2006). They also effectively sequester nutrients (Middelburg et al., 1996; Bouillon et al., 2008), and may enhance water quality in surrounding habitats by reducing eutrophication and turbidity (Valiela and Cole, 2002; Victor et al., 2004).

Despite suitable seawater temperatures (>20°C), the geographic isolation of the Hawaiian Archipelago excluded mangroves from the Hawaiian Islands until 1902, when the red mangrove, *Rhizophora mangle*, was introduced from Florida to Moloka'i to stabilize coastal erosion from pastures and sugarcane fields (Chimner et al., 2006). Mangroves have now invaded large portions of the intertidal and high subtidal zone along the island of O'ahu, and in 2001, the total area of mangroves on O'ahu was 1500 km^2 (Chimner et al., 2006).

Recent studies have examined the effects of marine vascular plant invasions on coastal habitats, in particular in salt-marshes (Talley and Levin, 1999; Levin et al., 2006). It is now known that invasive marine vascular plants can cause local species extinctions (Grosholz, 2002) and habitat modification (Bromberg-Gedan et al., 2009). In Hawaii, the establishment of *R. mangle* has dramatically altered macrofaunal species and food-web structure, facilitating greater dominance by sub-surface deposit feeders, and creating new niches for other exotic species in mangrove sediments (Demopoulos 2004, Demopoulos et al., 2007; Demopoulos and Smith, 2010). However, the im-

pacts of *R. mangle* invasion on benthic ecosystem functioning, in particular, how mangroves modify sediment metabolism and C-remineralization processes in the Hawaiian coastal zone, remain essentially unexplored. *Rhizophora mangle* detritus is rich in tannins, which can be toxic to benthic detritivores, interfering with digestive enzymes
5   (Mahadevan and Muthukumar, 1980; Neilson et al., 1986; Alongi, 1987; Sessegolo and Lana, 1991). Therefore, we postulate that mangrove invasion will favor microbial C-remineralization processes by limiting macrofaunal consumption and assimilation of detrital carbon (Alongi, 1987; Boto et al., 1989; Tietjen and Alongi, 1990; Robertson et al., 1992).
10   Because invasive species can considerably damage natural and managed ecosystems, strategies have been developed to control, contain and/or eradicate invasive species. However, eradication or removal of invasive species alone may not allow ecosystems to rapidly or even completely recover original ecosystem function because invaders can substantially alter physical, chemical and biological conditions (Zavaleta
15   et al., 2001). In Hawaii, the success of *R. mangle* has created a suite of environmental problems (e.g. clogging of streams and fish ponds, invasion of bird sanctuaries), leading to numerous removal projects in the coastal zone. Typical mangrove clearing practices in Hawaii include the removal of the above-sediment mangrove biomass, but leaving intact the prop roots and the root-fiber mat within the sediment (Sweet-
20   man personal observations). Mangrove roots and fiber-mats are also rich in tannins and bind sediments, which may hamper faunal movement and impede bioturbation. Few data are available concerning benthic ecosystem functioning in deforested, native mangrove forests worldwide (Sjöling et al., 2005), and we know of no data on the effects of the removal strategy employed in Hawaii on benthic ecosystem functioning
25   and recovery. However, we postulate that benthic C-cycling processes may be dominated by microbes, and that sediment ecosystem function will be altered, long after mangrove removal if the toxic, nutrient trapping, root-fiber mat is not removed along with the emergent mangrove structures.
      In recent years, tracer experiments with stable isotopes have proved extremely pow-

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erful in quantifying benthic ecosystem functioning in a variety of marine environments (Middelburg et al., 2000; Moodley et al., 2000; Evrard et al., 2005; van Oevelen et al., 2006). In short, an isotopically labelled substrate (e.g. ^{13}C-labelled algae) is deposited over an enclosed area of seafloor and the uptake of labelled elements tracked into sediment-dwelling organisms and abiotic components (e.g. dissolved inorganic carbon), making it possible to quantify the uptake of specific elements into specific organisms and thus, identify the pathways through which certain elements cycle. In this case-study, we used stable-isotopically labelled algae as a deliberate tracer to explore benthic ecosystem functioning in sediments from (1) an invasive mangrove forest, (2) mangrove removal sites 2- and 6-yrs after removal of above-sediment mangrove biomass, and (3) two mangrove-free, mudflat control sites. We evaluated the effects of intact mangroves, as well as sediment root-fiber complexes remaining after mangrove removal, on respiration and C-flow though the sediment-dwelling macrofauna and bacteria to test the following hypotheses: (1) biogeochemical cycling in mangrove sediments favors bacterial pathways, yielding lower macrofaunal uptake of labile organic matter than in adjacent mudflats. (2) Due to the persistence of a dense root-fiber mat, bacterial metabolism is enhanced, and macrofaunal uptake of organic matter reduced, in sediments for years following above-sediment mangrove removal.

2 Methods

2.1 Study sites

Ex-situ experiments were carried out on sediment cores collected from 5 sites on the island of O'ahu, Hawaii (Fig. 1) between January and May of 2008. Three sites were located in the high subtidal zone of Pearl Harbor (PH) and were all sampled in January 2008 (water temperature: ~23–27 °C). The mangrove site (PHM) was located 8-m inside a healthy *R. mangle* mangrove forest in Pouhala Marsh, Pearl Harbor. The 2-yr post-removal site (PHR) was located at the fringe of a former mangrove forest in the

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Pearl Harbor National Wildlife Refuge. Most living above-sediment mangrove biomass was removed from the PHR site in 2006. The third Pearl Harbor site was a mangrove-free control (PHC) site located on a mudflat at the southern end of Neal S. Blaisdell Park, approximately 60-m away from the nearest mangrove stand. The remaining sites were located in the Kaneohe Bay (KB) low intertidal zone and were sampled at the beginning of May 2008 (Water temperature: ~27–28 °C), with the fourth site located several meters into a former *R. mangle* stand (KBR) in Kahaluu, Kaneohe Bay. The fifth site was a mangrove-free mudflat control site (KBC) located approximately 60-m away from the nearest mangrove stand (Fig. 1). Sediment characteristics are shown in Table 1. Tidal range at all sites was approximately 0.4-m. Because of logistical constraints imposed by the Pearl Harbor Naval Base and the labor-intensive nature of these experiments, we were forced to study a single mangrove site in Pearl Harbor. Only single 2-yr and 6-yr removal sites were available on O'ahu, so this investigation constitutes a case study of the various habitat types.

2.2 Experimental design

At each sampling site, four replicate, 15-cm deep sediment cores were collected in 19-cm (i.d.) clear, acrylic benthic chambers at random locations along a 15-m long transect running parallel to the water's edge, so that substantial habitat heterogeneity along the shoreline was incorporated into the design. Mangrove leaf litter was only found on top of sediments from the PHM site and was not removed from sediment cores. Sub-tidal sediments from all Pearl Harbor sites were collected from approximately 15-cm water depth at low tide, and those collected at the PHM site were sampled between mangrove prop roots at a distance of approximately 0.5-m from individual emergent roots. Cores from Kaneohe Bay were collected along a 15-m long transect line at an identical tidal elevation at low tide, ensuring that all cores were subjected to the same degree of air exposure. Immediately after collection, all cored sediments were covered with 25-cm of top water and transported to Waikiki Aquarium where they were placed in a temperature controlled water bath (24 °C). Sediments were allowed to settle, and

conditions in each chamber allowed to equilibrate for 24-h prior to the start of the experiments. Pilot studies revealed that 24-h was sufficient time to allow settlement of sediments re-suspended during chamber transport.

A non-axenic clone of the green alga *Chlorella* spp. (Chlorophyta), initially sampled off the coast of Hawaii, was used as a food source in our experiments. Phytoplankton was cultured for 3 weeks at 24 °C under a 16: 8-h light: dark cycle in artificial seawater modified with F/2 algal culture medium (Grasshoff et al., 1999), and labelled by replacing 25% of ^{12}C bicarbonate in the culture medium with NaH^{13}CO$_3$. For harvest, inocula were concentrated by centrifugation (404×g, 5 min), washed 5 times in a iso-tonic solution to remove excess labelled bicarbonate, and freeze dried. Algae samples possessed a ^{13}C-content, δ^{13}C-signature, and molar C:N ratio of 23.40±0.20 atom % (SE, $n = 4$), 26 330±303‰ (SE, $n = 4$) and 6.45±0.20 (SE, $n = 4$), respectively.

To start the experiments, ^{13}C-labelled *Chlorella* spp. were injected into three of the four chambers ($T = 0$-h) and stirrers mounted 5-cm beneath the chamber lids were activated to homogeneously distribute the algae over the enclosed sediment surface. Approximately 10 min after the algae were injected; stirrers were switched off for 1-h to allow the labelled algae to sink. Stirrers were then turned on and the chamber waters gently mixed (without creating sediment resuspension) at 3-rpm for the remainder of the experiments. Pilot studies revealed that stirring at 3-rpm maintained a sufficiently thin diffusive sub-layer (<1-mm) to ensure that O$_2$ flux into the sediments within each chamber was not diffusion limited. To avoid contaminating the control chamber (used for background isotopic signatures) with labelled algae or labelled dissolved inorganic carbon (DIC), the control chamber was hydraulically (but not thermally) isolated from the water bath with an acrylic chamber.

2.3 Chamber sampling

Water samples used to calculate fluxes of oxygen (sediment O$_2$ consumption) and dissolved inorganic ^{13}carbon (DI^{13}C) were extracted with a 140-ml syringe from each chamber at 12-h intervals throughout the duration of each 48-h study, through stop-

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cock valves fixed within the chamber lids. Simultaneously, 140-ml of replacement water from a freshly filled filtered seawater reservoir (maintained at 24 °C) was added to each chamber through a second stop-cock mounted downstream of the extraction valve. Two 60-ml samples of chamber water were immediately transferred into gas-tight glass B.O.D. bottles via a 10-cm tube attached to the syringe nozzle, and fixed for dissolved O_2 Winkler analysis. This was followed by a 2-ml water sample, which was passed through a 0.25-μm sterile, cellulose acetate filter into gas tight 4-ml borosilicate glass vials (Labco, UK) and fixed with 5-μl of 6% $HgCl_2$ for DIC and ^{13}C isotope-ratio mass-spectrometry (IRMS) analyses. Reservoir water that was used as a replacement was also sampled and fixed for O_2 and DIC analyses thereby allowing concentrations and flux rates through time to be corrected for dilution effects. After sampling for O_2 and DIC and prior to the start of the next incubation, chamber waters were re-oxygenated. Bubbles were then removed from beneath each chamber lid, lids were replaced, new samples for O_2 and DIC taken and the incubations continued. Sediment O_2 consumption rates were calculated from the linear decrease in corrected O_2 concentrations (down to $150\,\mu\mathrm{mol\,l^{-1}}$ or 70% saturation) through time.

At the end of each 48-h experiment, the chambers were removed from the water bath and immediately processed for sedimentary mangrove biomass (SMB), macro-fauna and bacterial phospholipid derived fatty acid (PLFA) analyses. Three 6.5-cm (i.d.) coring tubes were inserted into sediment (one each for SMB, macrofauna and PLFA), removed and the sample sectioned into 0–2 and 2–5-cm sediment slices using an extruder. Samples for SMB and PLFA samples were transferred to 50-ml Corning Vials ® and pre–washed (methanol: dichloromethane in a 1:1 ratio) brown glass bottles, respectively, and frozen at −20 °C until analysis. Macrofaunal samples were fixed whole with 4% buffered formaldehyde seawater.

2.4 Analysis

To measure SMB, frozen sediment sub-core samples were thawed, sieved with fresh-water on nested 250-μm and 1-mm mesh sieves, the mangrove leaf litter, roots and

fibrous material picked out at 150× magnification under a dissecting microscope and then dried at 35 °C for 4-days. Dried material was weighed on an electronic balance. As a result of a positive, highly significant correlation between SMB and sediment particulate organic carbon (POC) ($r = 0.967$, $P = 0.007$, $n = 5$) SMB has been used as a readily measured first order proxy for sediment POC content in this study.

Frozen sediment samples for bacterial analysis were freeze dried (with no oil used for sealing) and subsequently ground with a mortar and pestle. Stones were removed using a 500-µm mesh sieve, and sediment was ground-up again. Lipids were extracted from approximately 3-g of dried sediment by a Bligh and Dyer extraction procedure (Middelburg et al., 2000), in which the lipids were sequentially isolated by rinsing on a silicic acid column with chloroform, acetone and methanol. The lipid extract was then derivatized to volatile fatty acid methyl esters (FAME) and measured by gas chromatography isotopic ratio mass spectrometry (GC-IRMS) for PLFA concentration and δ^{13}C-signatures (Middelburg et al., 2000). The C-isotopic ratios were corrected for the one methyl group inserted during derivatization. Bacterial biomass was measured by GC-IRMS, and calculated as PLFA (aiC$_{17:0}$, iC$_{17:0}$, aiC$_{15:0}$, iC$_{14:0}$, 10 *Methyl*-C$_{16:0}$, see Boschker and Middelburg, 2002) concentration (µmol) ml^{-1} sediment/($a \times b$), where a is the average PLFA concentration in bacteria of 0.056 g C PLFA g^{-1} biomass (Brinch-Iversen and King, 1990), and b is the average fraction-specific bacterial PLFA encountered in sediment dominated by bacteria (0.16; calculated after Rajendran et al., 1993). The prefixes "i" and "ai" refer to "*iso*" and "*antiso*", respectively.

Faunal samples fixed in formaldehyde were gently sieved on a 500-µm mesh sieve in cool, filtered seawater in the lab and macrofauna picked out and identified under a dissecting microscope. Organisms were identified to major taxon, with polychaetes and crustaceans identified to the lowest taxonomic level possible. Separate picking utensils were used for unlabelled and labelled samples to avoid contamination with stable isotopes. Single organisms were washed of attached organic debris in cooled, filtered seawater, placed in tin cups and dried at 35–40 °C for 4-d. Calcareous shelled organisms were decalcified in double boated silver caps using the methods of Sweetman

et al. (2009). In order to obtain sufficient biomass for isotope measurements, some individual organisms were combined.

The isotopic ratios (^{13}C/^{12}C) and DIC concentration of the chamber water samples were measured against a lithium carbonate standard (calibrated against NIST 8545) using a PDZ Europa 20-20 IRMS, coupled with a Poroplot-Q GC column (15-m×0.53-mm ID, 25°C, 3 ml min^{-1}) at UC Davis, after acidification with 1-ml of 85% phosphoric acid. The isotopic measurements and biomass of macrofaunal organisms were measured using both Europa Integra (enriched isotopes) and Hydra 20/20 (natural isotopes) isotope ratio mass spectrometers at UC Davis, USA. The total amount of DI^{13}C produced from the added algal tracer (mmol ^{13}C m^{-2}) was calculated as the product of excess ^{13}C (E) (expressed as atom % ^{13}C) and the total amount of DIC, and subsequently converted to mg ^{13}C m^{-2}. E is the difference between the labelled fraction F of a sample and the background sampled from the un-amended control chamber:

$$E = F_{sample} - F_{background} \tag{1}$$

where

$$F = {}^{13}\text{C}/({}^{13}\text{C} + {}^{12}\text{C}) = R/(R+1) \tag{2}$$

and

$$R = (\delta^{13}\text{C}/1000 + 1) \times R_{VPDB} \tag{3}$$

where $R_{VPDB} = 0.0112372$.

Uptake of ^{13}C after 48-h by macrofauna (mg ^{13}C m^{-2}) was calculated as the product of the excess ^{13}C and C-content in the animal (expressed as unit weight). If "background" samples of certain taxa were unavailable in the control chamber for calculating ^{13}C-uptake, E was calculated using background F-values from closely related organisms or from fauna within the same feeding guild. Polychaete feeding modes were determined from Fauchald and Jumars (1979). For bacteria, total uptake (mg ^{13}C m^{-2})

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of [13]C (*U*) after 48-h was calculated according to Moodley et al. (2000) from label incorporation into bacterial fatty acids ($aiC_{17:0}$, $iC_{17:0}$, $aiC_{15:0}$, $iC_{14:0}$, 10 *Methyl*-$C_{16:0}$, Boschker and Middelburg, 2002) as:

$$U_{bact} = \Sigma_{bact\ fatty\ acids}/(a \times b) \qquad (4)$$

To calculate the daily production rate of DIC ($mg\,C\,m^{-2}\,d^{-1}$) from the added algal tracer, the total amount of $DI^{13}C$ produced ($mg\,^{13}C\,m^{-2}$) was divided by 2, and adjusted to account for the fractional abundance of ^{13}C in the added algae as:

$$DIC\ produced\ d^{-1}{}^1 = DI^{13}C\ produced\ d^{-1}/fractional\ abundance\ of\ ^{13}C\ in\ algae \qquad (5)$$

Total C-uptake per day ($mg\,C\,m^{-2}\,d^{-1}$) by fauna and bacteria was calculated from faunal and bacterial ^{13}C-uptake data in the same way. Approximately 1.8 g algal-C m^{-2} was added to each experimental chamber except to those collected at the KBC site, where ~1.6 g algal-C m^{-2} was added. These small quantities of algal-C contributed between 0.2–2% to the C-standing stock in the top 5-cm of sediment (85–929 $g\,C\,m^{-2}$, based on data in Table 1). Nevertheless, daily DIC production[1] and C-uptakes rates by fauna and bacteria have been normalised by the amount of algal-C added (i.e. $mg\,g\,C^{-1}\,m^{-2}\,d^{-1}$).

2.5 Statistics

Because of seasonal differences in temperature when the Pearl Harbor and Kaneohe Bay sites were sampled, as well as potential artefacts from dissimilarities in tidal elevation affecting comparisons between locations, differences among variables between Pearl Harbor sites were analysed separately from those in Kaneohe Bay using a one-way ANOVA test followed by a Tukey post-hoc test. Differences in variables between the KBR and KBC sites were analysed by parametric t-tests. Prior to statistical analysis,

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[1]DIC produced d^{-1} refers to only the DIC derived from the added microalgal-C.

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data were checked for normality and heteroscedasticity. A square-root transformation was applied, when necessary, to obtain homogeneity of variances. Correlations among variables were analysed by Pearson Product Moment correlations, after initially checking for linearity and bi-variate normality of correlation data and applying a square root transform, if necessary (Zar, 1999). An α-level of 0.05 was chosen as the criterion for statistical significance. All data was analysed using Sigma-Stat (Version 3.5, Systat) software.

3   Results

3.1   Sedimentary mangrove biomass

Leaf material was only found at the sediment surface in cores collected from the PHM site. SMB was significantly lower (by 60%) in sediment cores from the PHR compared to the PHM site ($P = 0.003$, Fig. 2a). This equates to a SMB loss rate of ~30% yr^{-1} assuming that the SMB in the original mangrove stand at the PHR location averaged 3550 g dw m^{-2} as found by Demopoulos and Smith (2010) (Fig. 2a). SMB in sediment cores from the KBR site was reduced by approximately 70% after 6-yr (decomposition rate of ~12% yr^{-1}) assuming SMB in the original mangrove forest at the KBR site was approximately 2000 g dw m^{-2} as found by Demopoulos (2004). Mean SMB increased with sediment depth in cores from all sites (Fig. 2b). No SMB was found in sediment cores from either the PHC or KBC sampling locations.

3.2   Benthic biotic structure

Macrofaunal abundance and biomass from Pearl Harbor were significantly different between sites ($P = 0.009$ and $P = 0.012$, respectively), with greater abundance (205 024±47 428 m^{-2}, SE, $n = 3$) and biomass (3391±646 mg C m^{-2}, SE, $n = 3$) in sediment cores from the PHR site compared to the PHM and PHC locations (Fig. 3a and

c, Table 2). Mean macrofaunal abundance and biomass in sediment collected from the PHR and PHC sites was higher in the top 2-cm of sediment compared to the bottom sediment layer (Fig. 3b and d). Bacterial biomass was significantly higher ($P = 0.007$) in sediment cores from the PHM site ($17\,317 \pm 1092\,\mathrm{mg\,C\,m^{-2}}$) compared to the other Pearl Harbor locations (Fig. 3e). Bacterial biomass was higher in surficial sediments in cores from both the PHM and PHR sites (Fig. 3f). In Kaneohe Bay, faunal abundance estimates were significantly higher ($P = 0.008$, Fig. 4a) in sediments from the KBR ($47\,414 \pm 3931\,\mathrm{m^{-2}}$, SE, $n = 3$) compared to the KBC site ($22\,301 \pm 3306\,\mathrm{m^{-2}}$, SE, $n = 3$), but despite higher mean faunal biomass being found in sediment cores from the KBR site (Fig. 4c, Table 2), no significant difference in faunal biomass between the two sites could be detected ($P = 0.146$). Mean faunal densities in sediments collected from the KBR and KBC sites, as well as faunal biomass in cores from the KBR site, decreased with sediment depth (Fig. 4b and d). The same pattern was found for bacterial biomass, which was higher in surficial sediments in cores collected from both Kaneohe Bay sites (Fig. 4f). However, no significant difference in total bacterial biomass could be detected between these two sites ($P = 0.116$, Fig. 4e).

3.3 Macrofauna community structure

Sub-surface deposit feeding tubificid oligochaetes dominated macrofaunal abundance (67%) and biomass (80%) in cores collected at the PHM location, whereas surface feeding spionid polychaetes were more dominant in terms of abundance (34%) and biomass (34%) in sediments from the PHR site (Table 2). Harpacticoid copepods were the most abundant taxon in sediment cores from the PHC site (30%), but spionid polychaetes accounted for the major part of the biomass (62%). Surface-feeding corophiids completely dominated the amphipod taxa in sediment samples from the KBR site and contributed most to abundance (60%) and biomass (80%) in cores collected from this site, but surface feeding sabellid polychaetes were more important in terms of abundance (39%) in cores recovered from the KBC site (Table 2). Spionid polychaetes (31%) as well as unidentified taxa (30%) contributed more to faunal biomass in sedi-

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ments sampled at the KBC site (Table 2).

3.4 Sediment oxygen consumption (SOC)

SOC in algae-amended cores was significantly different between sites in Pearl Harbor ($P < 0.001$), with greater SOC rates measured using sediments from the PHM and PHR sites compared to the PHC site (Fig. 3g). Significantly higher SOC rates were also found in the PHM experiments compared to the PHR study (Fig. 3g). In the Kaneohe Bay experiments, SOC was greater in the KBR experiments compared to the Kaneohe Bay control ($P = 0.005$, Fig. 4g). SOC was strongly correlated with both total benthic (macrofauna and bacteria) biomass ($r = 0.855$, $P < 0.001$, $n = 13$, Fig. 5) as well as SMB ($r = 0.901$, $P < 0.0001$, $n = 13$, Fig. 6).

3.5 DIC production and C-uptake from added algae

Between 75 and 90% of the algal-C that was processed was found in the DIC pool in all experiments (Table 3). Daily production of DIC from added algal-C was significantly different between Pearl Harbor sites ($P = 0.007$), with production being significantly lower in the PHC experiments compared to the other Pearl Harbor studies (Fig. 7a). No significant difference in the daily amount of DIC produced from algal-C could be detected between the KBR and KBC experiments ($P = 0.270$, Fig. 8a). The macrofauna in both removal and both control site experiments took up approximately 1.5–3 times as much algal-C as the bacteria (Table 3). These patterns contrasted with the benthic response observed in the PHM experiments, where bacteria C-uptake rates were approximately 16 times greater than for the macrofauna (Table 3). Short-term C-uptake rates by macrofauna were significantly different between Pearl Harbor sites ($P < 0.001$, Fig. 7b), with significantly higher faunal C-uptake rates measured in the PHR compared to the PHM and PHC experiments. Mean faunal C-uptake rates were also significantly higher in experiments using sediment cores recovered from the PHC versus the PHM site (Fig. 7b), and in the KBR compared to the KBC experiments

($P = 0.003$, Fig. 8b). Mean rates of uptake of algal-C by macrofauna was highest in the top-most sediment layer in the PHR, PHC, KBR and KBC experiments (Figs. 7c and 8c). Surface-feeding spionid polychaetes and corophiid amphipods in sediments from the PHR and KBR sites took up more microalgal-C in 48-h than any other taxon found in this study (Table 4), and together with surface feeding cirratulid and sabellid polychaetes, were responsible for the majority of microalgal-C-uptake after 48-h in sediments from the removal and control habitats (Table 4). Mean C-uptake rates by sedimentary bacteria within both control site experiments were approximately 40–50% of those found in sediments collected from the PHM and both removal habitats (Figs. 7d and 8d, Table 3), yet mean bacterial C-uptake rates were not significantly different between the Pearl Harbor ($P = 0.242$) or Kaneohe Bay studies ($P = 0.149$). Mean bacterial C-uptake rates decreased with sediment depth in cores in all Pearl Harbor (Fig. 7e) and Kaneohe Bay studies (Fig. 8e).

4 Discussion

Numerous studies have shown that invasive marsh grass and mangroves can modify essential habitat properties (e.g. porewater salinity, organic C-content, detrital food-supply), benthic biodiversity, and trophic structure through alterations in habitat complexity by the production of above and below-ground biomass (Demopoulos, 2004; Neira et al., 2005; Levin et al., 2006; Demopoulos et al., 2007; Demopoulos and Smith, 2010). But to the best of our knowledge, this is the first study to address how an invasive vascular plant can modify sediment metabolism, as well as examine changes to benthic ecosystem processes as a function of the removal of above-sediment invasive mangrove biomass. In the invasive mangrove sediments sampled in this case study, macrofaunal biomasses were reduced relative to microbial biomass, the macrofaunal community was dominated by sub-surface feeding tubificid oligochaetes, and C-uptake of labile carbon was dominated by bacteria. Thus, in agreement with our hypothesis (1), biogeochemical cycling in the mangrove sediments favored bacterial pathways,

yielding lower macrofaunal uptake of labile organic matter than in the control experiments.

In contrast to hypothesis (2), bacterial C-uptake and bacterial biomass were not significantly enhanced in sediments from mangrove removal sites compared to controls, disproving the microbial portion of our hypothesis (2). Nonetheless, SMB persisted in sediments from mangrove removal sites for at least 6-yrs, and ecosystem functioning in the removal site experiments differed significantly from the controls by exhibiting higher SOC rates, higher macrofaunal C-uptake rates, and higher macrofaunal abundances. Thus, major aspects of ecosystem function and structure in sediments from the mangrove removal sites differed substantially from those from the control sites 2–6 yrs after above-sediment mangrove removal.

SOC provides a good measure of depth integrated community metabolism (Middelburg et al., 2005). In our study, we added a small quantity of labile organic matter (*Chlorella* spp. algae) to each experimental chamber, which represented between 0.2–2% of the C-stock in the first 5-cm of sediment. Nevertheless, production of DIC from the added phytodetritus accounted for between 10.53 ± 1.56 (range, $n = 2$) to 11.10 ± 0.24 (SE, $n = 3$) mmol C m^{-2} d^{-1} in the mangrove and removal site experiments and 7.60 ± 0.70 (SE, $n = 3$) to 12.16 ± 0.25 (SE, $n = 3$) mmol C m^{-2} d^{-1} in the controls. Therefore, assuming a respiratory quotient between DIC and O_2 of 1 (Middelburg et al., 2005), the transfer of algal-C into respired DIC corresponded to approximately 10 to 16% of the SOC in the mangrove and removal site experiments compared to 17 to 30% in the PHC and KBC site studies. These results highlight the very labile nature of the added algal C-source and suggest that the measured SOC values may be higher than background values without algal addition. Nevertheless, SOC rates measured in the PHM experiments were quite similar to those found in previous mangrove studies (Nedwell et al., 1994; Middelburg et al., 1996; Alongi et al., 2000; Alongi, 2008), and overall rates were strongly correlated with total benthic biomass, which is consistent with other studies (e.g., Bolam et al., 2002). This strong correlation suggests that the significantly elevated bacterial biomass in sediment cores from the PHM site, in addition to the

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large macrofaunal biomasses found in sediments from both removal sites, played a major role in stimulating sediment O_2 demand in the mangrove and removal site experiments. In addition, sediment O_2 consumption was strongly correlated with SMB. We hypothesize that the presence of leaf litter and root-fiber material in sediments from the mangrove and removal habitats promoted sediment community metabolism, most likely because the release of DOC and DON from SMB provided microbial substrates (Boto et al., 1989; Alongi et al., 1989; Alongi and Sasekumar, 1992; Robertson et al., 1992; Alongi, 2008). Because of the high heterogeneity of mangrove habitats (Kristensen, 2007), and the fact that sediments were recovered from only a relatively small area at each site (i.e. along a 15-m long transect), we hesitate to generalize the results of our case study to a wide geographic area. However, if the SOC results from this study are representative of other removal sites in Hawaii, the presence of SMB and the apparent enhancement of SOC in the removal site experiments (relative to the controls) after 6-yrs suggests that restoration of native sediment ecosystem function following mangrove clearing could require many years in Hawaii. Because root-fiber mats in native stands of the mangrove *R. mangle* in Florida and central America show similar decomposition rates (ranging from ~17 to 60% per year, McKee et al., 2007; Poret et al., 2007; Alongi, 2008) to those estimated here for Hawaii (~12–30% loss yr^{-1}), we hypothesize that sediment ecosystem function may be impacted for years following above-sediment mangrove removal even in native *R. mangle* stands.

With the exception of mangroves trees, bacteria dominate biomass and are the primary players in terms of energy-flow in native mangrove ecosystems (Alongi, 2002), deriving energy from autochthonous and allochthonous particulate and dissolved organic material (Bouillon et al., 2002), such as tannins, sugars and ligninocelluloses (Benner and Hodson, 1985; Boto et al., 1989; Alongi et al., 1989; Alongi, 2008). Our findings that the bacteria accounted for approximately 24-fold greater benthic biomass and 16-fold greater short-term C-uptake rates than the macrofauna in sediments from the invasive mangrove habitat are consistent with the bacterial dominance documented for sediments within native mangrove forests (e.g. Alongi, 2002, 2008; Kristensen,

2007; Kristensen et al., 2008). Mean bacterial biomass and transfer of algal-C to bacteria was higher in the top-most sediment layers in cores collected at the PHM site and from both mangrove removal sites, even though mean SMB was higher at 2–5-cm sediment depth in all sites. Upward diffusion of DOC from sub-surface root material can stimulate bacterial growth at the sediment surface (Boto et al., 1989; Kristensen and Alongi, 2006) and may have contributed to the elevated bacterial biomasses and C-uptake rates in surficial sediment layers in the mangrove and removal site experiments. The especially high bacterial biomass and activity in surface sediments of cores from the PHM site may also have been stimulated by the mangrove leaves at the sediment surface, which are known to be capable of hosting abundant bacterial populations (Mfilinge et al., 2003).

Sediments within low energy mangrove forests are often organically enriched compared to non-mangrove habitats as a result of the deposition of plant litter and the trapping of allochthonous material in emergent vegetation (Bosire et al., 2003; Kristensen, 2007). In our study, high organic loading was indicated in sediments from the PHM site by (1) the high sediment POC content found in the un-amended control (∼8% POC, Table 1) and (2) the positive correlation between SMB and POC (see methods section) combined with large amounts of SMB within sediments from the PHM site (Fig. 2a). Organic loading in sediments from the PHR was intermediate (∼3% POC, Table 1, Fig. 2a), while sediment organic concentrations in cores from the PHC site were relatively low (∼0.5% POC, Table 1). Macrofaunal abundance and biomass in the PHM sediments were relatively low (compared to cores from the PHR site) and dominated by few potentially opportunistic taxa (oligochaetes and capitellids) suggesting sediment-community disturbance from high organic loading (Pearson and Rosenberg, 1979; Weston, 1990; Nilsson and Rosenberg, 1997, 2000; Hyland et al., 2005). The relatively low macrofaunal density and biomass in the PHM experiments also could have resulted in part from large concentrations of tannins and tannin-rich mangrove biomass in the sediments negatively affecting the reproduction and growth of native Hawaiian biota poorly adapted to tannin stress (Alongi, 1987; Tietjen and Alongi, 1990;

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Demopoulos et al., 2007). The PHR sediments had elevated macrofaunal biomass, and elevated abundances of macrofauna and capitellids, combined with intermediate levels of organic enrichment compared to PHC sediments; this pattern suggests the presence of intermediate stages of recolonization and recovery from organic loading in sediments from the PHR site, which are often associated with biomass maxima (e.g. Pearson and Rosenberg, 1978; Hyland et al., 2005). The KBR sediments also showed enhanced macrofaunal abundance, capitellid abundance, SMB, and POC concentrations relative to control sediments in Kaneohe Bay, suggesting that this community was still at an intermediate stage of recovery 6-yrs after removal of above-sediment mangrove vegetation.

In the present study, macrofauna from the mangrove site were dominated by sub-surface deposit feeding tubificid oligochaetes (Ciutat et al., 2006; Giere, 2006), which agrees with previous mangrove and salt-marsh studies showing dominance by tubificids (Schrijvers et al., 1995; Levin et al., 2006). Their dominance in the community may be a function of their ability to cope with hypoxic and sulphidic conditions (Giere, 2006). However, the small, slender body size of tubificids may also allow them to easily inhabit the dense, root fiber network present in mangrove sediments (Levin et al., 1998; Demopoulos, 2004).

Faunal-mediated uptake of added C was significantly lower in sediment cores collected from the PHM site than in the other Pearl Harbor studies (Fig. 7b, Table 3), and appeared to be partly attributable to the low (relative to the PHR experiments) macrofaunal biomasses found in these cores (Bolam et al., 2002). However, faunal communities in cores from the PHM site were dominated by sub-surface feeding taxa (e.g. oligochaetes and capitellid polychaetes), and more fauna were found deeper in the sediment column ($18\,182\pm10\,205\,\mathrm{m}^{-2}$) compared to at the surface ($8538\pm7208\,\mathrm{m}^{-2}$, see Fig. 3b), which may have collectively limited the ability of the faunal community to process C. In addition, mangrove leaf litter on the surface of the PHM cores may have acted as a barrier to algal mixing during the 48-h experiments, limiting the subduction of added C to the sub-surface feeding fauna (Dobbs and Whitlach, 1982; Levin et al.,

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1997). In the PHR and PHC experiments, no leaf litter occurred atop sediments and a much higher proportion of the macrofauna belonged to surface and suspension feeding guilds (e.g. spionids, cirratulids, and sabellids, see Table 2). These factors likely explain the significantly higher C-uptake rates by macrofauna in the mangrove removal

5 and control sediments compared to the mangrove site experiments. Likewise, suspension and surface feeding macrofauna (e.g. corophiids, sabellids, see Table 2) were highly abundant and made up a major part of the biomass (e.g. corophiids, spionids, see Table 2) in sediments recovered from the Kaneohe Bay sites, and contributed heavily to the large (relative to the PHM study) faunal C-turnover rates measured here

10 (Table 4). Therefore, it appears that both habitat and macrofaunal-community structure may be important in regulating the fate of sedimented phytodetritus in invasive mangrove forests and other shallow marine ecosystems along the Hawaiian coastal zone (cf. Josefson et al., 2002; Kamp and Witte, 2005).

While surface and suspension feeding lifestyles appeared to be an important deter-

15 minant in structuring the high macrofaunal C-uptake rates in sediment cores recovered from the removal and control sites, significantly higher macrofaunal C-uptake rates were found in both removal site experiments relative to the controls, suggesting that additional factors were at play. Macrofaunal abundance and biomass were elevated in sediment cores recovered from the removal sites compared to controls, and a much

20 larger proportion of macrofaunal abundance and biomass was found in surficial sediment layers in cores from the removal habitats (see Figs. 3a to d, 4a to d). Therefore, because of the higher macrofaunal standing stock near the sediment surface, macrofauna likely had the ability to cycle through and process newly deposited organic matter more rapidly in the removal site experiments, than communities residing in sediment

25 cores recovered from the control sites, and is possibly the main factor behind the significantly different faunal C-uptake rates measured between the removal site experiments and controls.

Overall, the faunal and bacterial C-uptake results suggest that surface-living bacteria rather than deeper-dwelling macrofauna can contribute significantly more to the

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short-term cycling of labile organic matter, such as phytodetritus (Bouillon et al., 2002, 2004, 2008), in sediments from invasive mangrove forests in Hawaii. The opposite appears to be true for sediments from removal habitats and un-invaded mudflats on O'ahu, where macrofauna appeared to be more dominant players in the early diagene-
5 sis of microalgal-C. However, our data suggests that mangrove invasion and removal in Hawaii can have a major, lasting effect on faunal structure and C-cycling dynamics, and we hypothesize that in Hawaii, as well as areas where native mangrove species ranges are increasing (e.g. the New Zealand coast), ecosystem recovery following mangrove removal may involve intermediate stages in which macrofauna standing stocks and
10 contributions to short-term microalgal-C-cycling are substantially enhanced. In order to apply these results to other areas with mangroves in Hawaii, more exhaustive short- and long-term feeding studies using different types of labelled phytoplankton and man- grove detritus (Oakes et al., 2010) must now be undertaken in a diverse range of mangrove habitats (i.e. high intertidal to subtidal, areas of extreme vs. little burrowing
15 activity) to better quantify the variability in C-cycling dynamics in sediments in invasive mangrove forests and deforested habitats.

5 Conclusions

Invasive mangroves in Hawaii can significantly elevate sediment O_2 demand, and ele- vated SOC rates can persist for at least 6-yrs after above-sediment mangrove removal.
20 Short term C-processing by bacteria can become enhanced, relative to macrofauna, in sediments from intact mangrove habitats, suggesting that bacteria dominate short- term C-cycling in sediments within invasive mangrove forests in Hawaii. Bacterial dom- inance of short-term C-cycling in sediments from Hawaiian mangrove forests is similar to early diagenetic processes in native mangrove forests (Alongi, 2002, 2008; Kris-
25 tensen, 2007; Kristensen et al., 2008). In sediments from mangrove removal areas in Hawaii, macrofauna dominated short-term microalgal-C remineralization, similarly to mangrove-free mudflats. However, key benthic ecosystem properties such as macro-

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faunal abundance, short-term microalgal-C-uptake and SOC can remain significantly different in sediments from mangrove removal sites compared to controls for up to 6-yrs following above-sediment mangrove-tree removal. This case study demonstrates that invasive mangroves can have large and persistent impacts on ecosystem function in the Hawaiian coastal zone, highlighting the need for further work to determine the generality of these findings.

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Table 1. Summary of sediment characteristics (averaged over top 5-cm of sediment) from single un-amended cores collected at all 5 sites. Water content was determined by weight loss upon drying at 60 °C and total C and N were measured by CHN analysis. POC was analyzed by CHN analysis following acidification to remove inorganic C.

Site	Density (g/ml)	Water content (%)	SMB (g dw m^{-2})	Total C (%)	POC (%)	Total N (%)	C:N
PHM	1.13	38.54	1998.01	8.75	8.22	0.44	22.13
PHR	1.23	45.88	699.15	3.44	3.05	0.20	18.24
PHC	1.72	31.79	0	2.44	0.52	0.04	16.58
KBR	1.52	27.03	599.70	1.09	0.91	0.07	16.51
KBC	1.73	33.36	0	8.20	0.49	0.04	14.79

Table 2. Mean abundance (Number $m^{-2} \pm 1$ SE, $n = 3$) and biomass (mg C $m^{-2} \pm 1$ SE, $n = 3$) estimates of major macrofaunal taxa from sediment cores collected from all 5 sites. Star (*) denotes mean±range ($n = 2$). Total macrofaunal abundance (Number $m^{-2} \pm 1$ SE, $n = 3$) and biomass (mg C $m^{-2} \pm 1$ SE, $n = 3$) is also shown.

Taxon	PHM Abundance (No. m^{-2})	PHM Biomass (mg C m^{-2})	PHR Abundance (No. m^{-2})	PHR Biomass (mg C m^{-2})	PHC Abundance (No. m^{-2})	PHC Biomass (mg C m^{-2})	KBR Abundance (No. m^{-2})	KBR Biomass (mg C m^{-2})	KBC Abundance (No. m^{-2})	KBC Biomass (mg C m^{-2})
Oligochaeta							8036±2400	155±29	402±266	8±5
Enchytraeidea			3114±1480	75±33						
Tubificidae	17981±10748	572±510	2411±1595	55±40	904±460	9±3				
Polychaeta										
Cirratulidae			29 232±26 978	525±475					301±174	8±5
Chaetopteridae									201±100	28±14
Opheliidae			9242±958	71±15	904±522	35±34			1205±522	38±1*
Syllidae									201±201	4±4
Lumbrineridae									2913±559	103±28
Capitellidae	2813±2362	107±98*	5324±1282	381±86	502±502	6±6	2210±822	47±20	201±100	4±3
Eunicidae									100±100	43±43
Sabellidae			37 871±21 799	239±136	3214±1222	28±11			8538±266	96±5
Spionidae			68 911±23 656	1111±337	8237±2147	208±62	201±201	29±29	1708±402	265±65
Crustacea										
Amphipoda			4520±3175	65±53			28 529±2861	1138±143	1607±402	29±9
Decapoda			201±100	651±354						
Harpacticoida			11 853±4111	15±2	10 648±4133	13±5				
Isopoda							100±100	1±1		
Ostracoda			1005±1005	6±6			5625±2032	21±8	100±100	1±1
Tanaidacea							1607±1317	23±20		
Mollusca										
Gastropoda			100±100	10±10						
Nematoda			8538±3688	26±18	9643±3595	21±0*	301±174		502±362	1±1*
Nemertea									100±100	1±1
Unknown	5927±4375	69±62	22 702±2271	161±40	1406±438	24±13	804±659	20±18	4219±2262	266±207
Total	26 720±17 410	713±639	205 024±47 428	3391±646	35 460±10 532	337±75	47 414±3931	1435±77	22 301±3306	882±297

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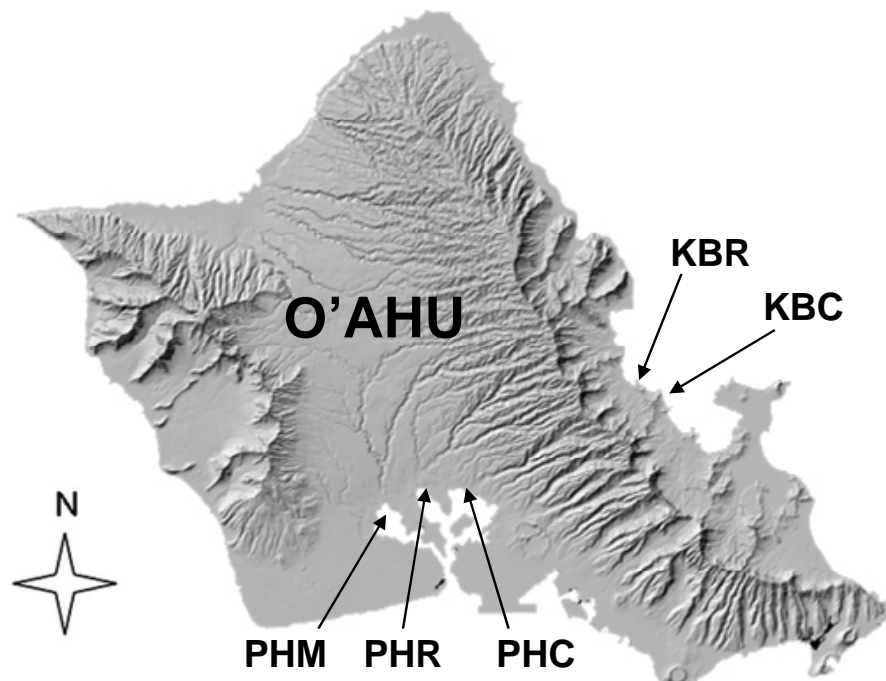
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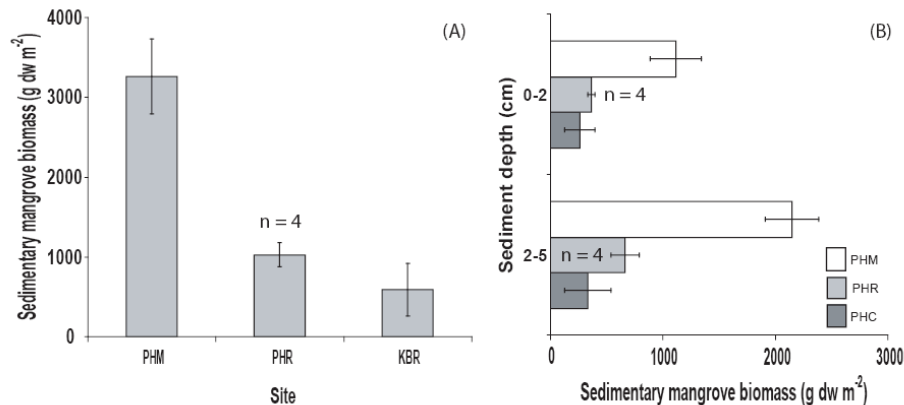**Exotic mangrove forests and mangrove deforestation**

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Table 3. Mean rate ($\text{mg g C}^{-1}\,\text{m}^{-2}\,\text{d}^{-1} \pm 1\,\text{SE}$, $n = 3$) and percentage of DIC production, faunal C-uptake and bacterial C-uptake from added algal-C in experiments from all 5 sites. Total amount of C processed d^{-1} ($\text{mg g C}^{-1}\,\text{m}^{-2}\,\text{d}^{-1} \pm 1\,\text{SE}$, $n = 3$) and the percentage of the total amount of added C which was processed is also shown. Star (*) denote mean ± range ($n = 2$).

Site	PHM		PHR		PHC		KBR		KBC	
	Rate	%	Rate	%	Rate	%	Rate	%	Rate	%
DIC	133.21±2.93	90.14±3.37*	131.83±3.88*	74.79±6.12*	91.20±8.45	87.62±1.89	126.41±18.68*	79.08±4.10*	145.91±3.01	88.79±1.48
Macrofauna	0.87±0.65	0.82±0.55*	39.70±7.12	18.83±2.57*	7.75±1.95	7.36±1.76	21.96±0.63	13.54±1.36*	12.89±1.29	7.85±0.82
Bacteria	13.59±5.09*	9.05±2.81*	13.23±4.28	6.38±3.55*	5.22±0.47	5.01±0.14	11.31±3.23*	7.37±2.74*	5.51±1.40	3.36±0.86
Total amount processed d^{-1}	146.88±10.64*		177.04±9.31*		104.18±9.79		159.06±15.37*		164.31±0.79	
% of total amount of added C processed	14.69±1.06*		17.70±0.93*		10.42±0.98		15.91±1.54*		16.43±0.08	

Table 4. Mean C-uptake rate (mg g C^{-1} m^{-2} d^{-1} ±1 SE, $n = 3$) by major macrofaunal taxa from sediments collected from all 5 sites. Star (*) denotes mean ± range ($n = 2$).

Taxon	PHM	PHR	PHC	KBR	KBC
Oligochaeta	0.71±0.59	0.12±0.05	0.09±0.07*	0.07±0.02	0.03
Polychaeta					
Cirratulidae		3.90±3.57			0.23±0.05*
Chaetopteridae					1.10±0.06*
Opheliidae		1.91±0.23	2.48±2.27*		2.73±0.69*
Syllidae					0.01
Lumbrineridae					0.15±0.07
Capitellidae	0.08±0.04	0.41±0.06	0.19	0.38±0.11	0.07±0.07*
Eunicidae					0.70
Sabellidae		5.91±3.27	0.68±0.22		4.75±0.09
Spionidae		21.98±3.29	3.96±1.45	1.69	2.44±0.64
Crustacea					
Amphipoda		0.89±0.72		20.37±1.47	1.02±0.39
Decapoda		3.39±1.09*			
Harpacticoida		0.11±0.04	0.33±0.17		
Isopoda				0.03	
Ostracoda		0.06		0.01±0.00	0.00
Tanaidacea				0.21±0.19*	
Mollusca					
Gastropoda		0.29			
Nematoda		0.11±0.10	0.28±0.25*		
Nemertea					0.07
Unknown	0.13±0.00*	2.00±0.61	0.82±0.62	0.63±0.50*	1.51±0.89

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Fig. 1. Location of the 5 sampling sites on the island of O'ahu, Hawaii.

Fig. 2. Total sedimentary mangrove biomass **(A)** and vertical distribution of sedimentary mangrove biomass **(B)** within cores from the PHM, PHR and KBR sites. Bars denote mean±1 SE ($n = 3$), unless otherwise stated.
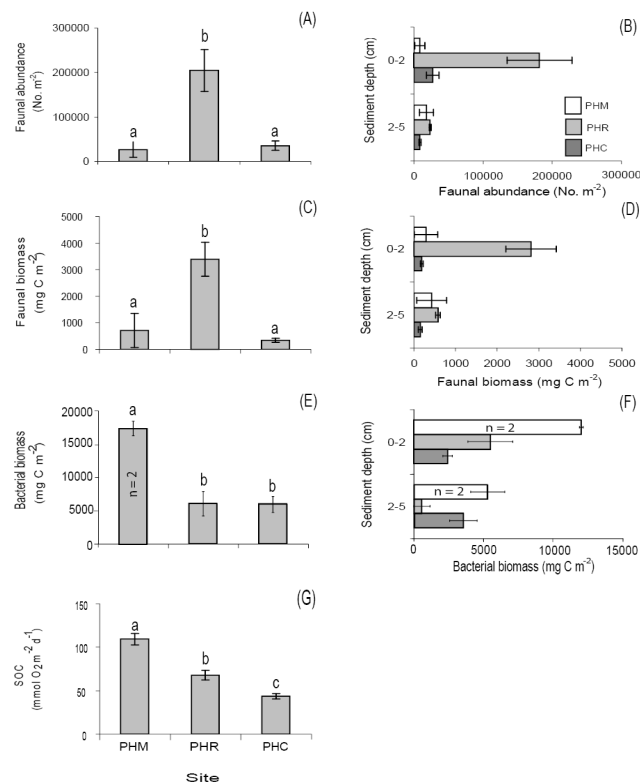
Fig. 3. Total and vertical distribution of macrofaunal abundance (**A** and **B**, respectively), biomass (**C** and **D**, respectively), and bacterial biomass (**E** and **F**, respectively) in cores from all Pearl Harbor sites. Sediment oxygen consumption rates in algae-amended cores from all Pearl Harbor sites is shown in **(G)**. Significant differences ($P < 0.05$) in parameters between sites are designated by different letters. Error bars denote ± 1 SE ($n = 3$) unless $n = 2$, where error bars denote range.
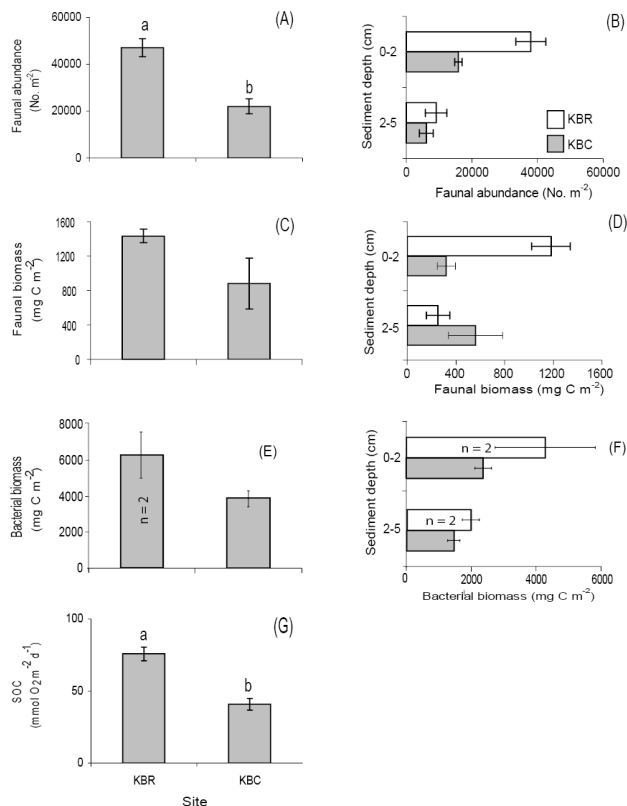
Fig. 4. Total and vertical distribution of macrofaunal abundance (**A** and **B**, respectively), biomass (**C** and **D**, respectively), and bacterial biomass (**E** and **F**, respectively) in cores from all Kaneohe Bay sites. Sediment oxygen consumption rates in algae-amended cores from all Kaneohe Bay sites is shown in **(G)**. Significant differences ($P < 0.05$) in parameters between sites are designated by different letters. Error bars denote ± 1 SE ($n = 3$) unless $n = 2$, where error bars denote range.

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Fig. 5. Relationship between SOC ($mmol\,O_2\,m^{-2}\,d^{-1}$) and total benthic (macrofauna and bacteria) biomass ($mg\,C\,m^{-2}$).
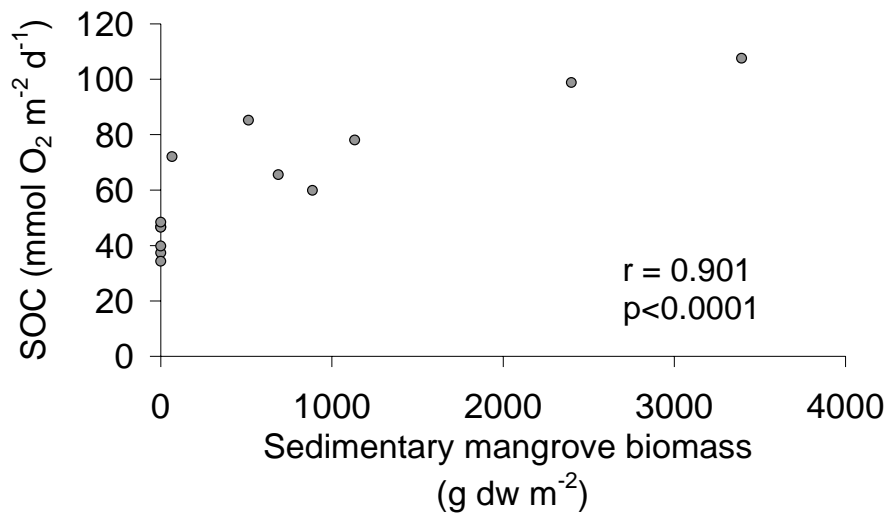
Fig. 6. Relationship between SOC ($mmol\,O_2\,m^{-2}\,d^{-1}$) and sedimentary mangrove biomass ($g\,dw\,m^{-2}$).
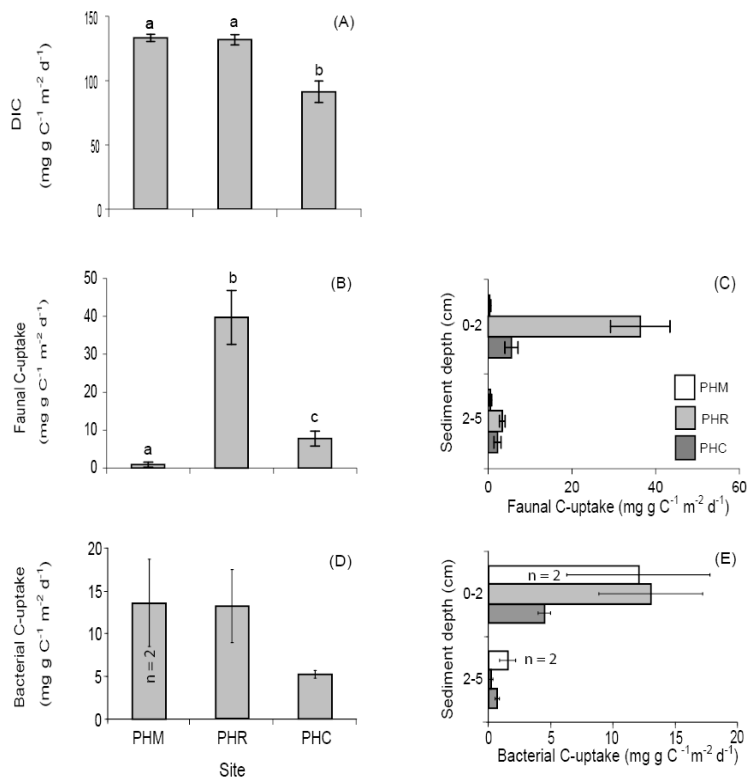
Fig. 7. Daily production of DIC **(A)** from added algal-C in cores collected from all Pearl Harbor sites. Total and vertical distribution of macrofaunal C-uptake (**B** and **C**, respectively) and bacterial C-uptake (**D** and **E**, respectively) in cores from all Pearl Harbor sites are also shown. Significant differences ($P < 0.05$) in parameters between sites are designated by different letters. Error bars denote ± 1 SE ($n = 3$) unless $n = 2$, where error bars denote range.

Fig. 8. Daily production of DIC **(A)** from added algal-C in cores collected from all Kaneohe Bay sites. Total and vertical distribution of macrofaunal C-uptake (**B** and **C**, respectively) and bacterial C-uptake (**D** and **E**, respectively) in cores from all Kaneohe Bay sites are also shown. Significant differences ($P < 0.05$) in parameters between sites are designated by different letters. Error bars denote ± 1 SE ($n = 3$) unless $n = 2$, where error bars denote range.

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