INVASIVE MANGROVE REMOVAL AND RECOVERY: FOOD WEB EFFECTS
ACROSS A CHRONOSEQUENCE

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By
Margaret C. Siple

Thesis Committee:

Megan Donahue, Chairperson
Craig Smith
Florence Thomas

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DEDICATION

This work is dedicated to Christine Whitney, who has always enriched my life and supported my career.

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ABSTRACT

Red mangrove (*Rhizophora mangle*) was introduced to Hawai‘i in 1902 and has since overgrown many coastal areas in Hawai‘i, transforming nearshore sandy habitat into heavily vegetated areas with low water velocity, high sedimentation rates, and anoxic sediments. Mangrove forests provide habitat for exotic species, including burrowing predators, which can exert top-down effects on benthic communities. Removal of mangrove overstory is a popular management technique; here we use infauna community structure, crab catch data, and a cage experiment performed over a chronosequence of removals from 2007-2010 to show that overstory removal causes gradual changes in community composition, that community shifts are concurrent with a slow decomposition of sedimentary mangrove biomass ($k = 5.6 \times 10^{-4} \pm 0.9 \times 10^{-4} \text{ d}^{-1}$), and that burrowing predators do not have significant effects on the infaunal community where *R. mangle* is intact or where it has been removed. Changes over time after removal include an increase in total infaunal abundance, a decrease in sub-surface deposit feeders, and an increase in suspension-feeding worms. Burrowing crab densities are uniform across mangrove and removal sites, and do not affect infaunal communities as they do in native mangroves. These results show that recovery from invasion and removal occurs gradually and is not governed by top-down effects.

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INTRODUCTION

Red mangrove (*Rhizophora mangle*) was introduced to Moloka'i in 1902 and to He'eia Marsh on O'ahu in 1922 to control runoff from upstream agriculture (McCaughey 1917). While other species of mangrove have been introduced to Hawai'i, *R. mangle* is the most successful, occupying coastal habitats throughout the main Hawaiian islands, including historical estuarine fishpond sites developed for aquaculture by native Hawaiians as early as 1000 C.E. (Allen 1992; Allen 1998; Kirch 2007). In their native range, mangroves are ecosystem engineers, strongly modifying their environment and providing important ecosystem services, including protecting of the shoreline from heavy storm surges, acting as a sink for heavy metal pollutants (Clark et al. 1998; Harbison 1986), stabilizing sediments (Posey 1987), subsidizing coastal habitats through litterfall (Twilley et al. 1986), and serving as nursery grounds for some fisheries (Mumby et al. 2004; Robertson and Duke 1987). In their introduced range, these potential ecosystem services must be weighed against impacts on native ecosystems: In Hawai'i, mangroves create habitats dramatically distinct from that of the few native coastal macrophytes (Allen 1998).

Hawaiian mangrove sediments host a higher diversity of infauna (>500 μm) than adjacent sandflats, despite lower porewater oxygen (O_2) concentrations in mangrove sediments (Demopoulos and Smith 2010). However, this higher diversity includes many alien species, which are more abundant in mangroves than in adjacent sandflats at the same tidal height (Demopoulos and Smith 2010). The difference in diversity and relative abundance of exotics may be a result of enhanced productivity due to litterfall subsidy or increased microhabitat heterogeneity (bottom-up effects). It may also be due to trophic effects from changes in habitat use by mobile predators (top-down effects). *R. mangle* produces more propagules and contributes more litterfall in Hawai'i than in its native range (Cox and Allen 1999; Demopoulos 2004), potentially because of lower rates of predation on flowers and developing fruits (Allen 1998). Despite *R. mangle*'s extensive contribution of litterfall subsidies to coastal marshes in Hawai'i (Cox and Allen 1999), a comparison of *R. mangle* food webs in Hawai'i and a site in its native range (Puerto

Rico) demonstrates that in Hawai‘i, much of this productivity is not consumed by benthic invertebrates (Demopoulos et al. 2007). Mangrove detrital inputs are high in tannins and relatively low in nutritional value (Robertson et al. 1992), and native communities in invaded areas may be unable to use mangrove detritus efficiently (Demopoulos and Smith 2010); instead, stable isotope evidence indicates that *R. mangle* primarily subsidizes bacterial foodwebs (Demopoulos et al. 2007). The high detrital output and undigested mangrove leaf detritus may increase sediment anoxia and negatively impact infaunal assemblages (Demopoulos 2004).

Removal has been a popular tool for the control of alien pest species in Hawai‘i (e.g., Scowcroft and Conrad 1992; Stone et al. 1992), including *R. mangle* (Chimner et al. 2006; Rauzon and Drigot 2002). The most common method of mangrove removal is to cut the prop roots below the high tide mark, flooding the roots with saltwater, haul away the overstory, and leave the flooded prop roots to decompose. While this method is favored because it does not require bulldozing and reduces the potential for dramatic resuspension of organic material and fine sediment following root removal, the time course of recovery following removal is not well resolved. Extensive removal has only been employed at a few locations on O‘ahu (Kāne‘ohe Bay and Pearl Harbor), making long-term recovery difficult to measure.

After removal, substantial mangrove biomass remains in and above the sediment. Decomposition occurs slowly, even in the presence of increased nutrient concentrations (Alongi 2009). Mangroves cope with short periods of anoxia by photosynthesizing above water and transporting gas directly into the submerged roots. Some of this O₂ diffuses out of the roots and into the surrounding sediment (Alongi 2009). Disruption of gas transport via overstory removal may result in more anoxic sediments following removal: Fine roots that normally provide O₂ to associated aerobic bacteria die and decompose, causing soil anoxia and a shift in dominance to anaerobic bacteria (Alongi 2009). Usually, aerobic respiration and anaerobic sulfate reduction are the main decomposition pathways in mangrove sediments, with slow anaerobic processes governing much of the metabolism that occurs below the first few millimeters (Alongi 2009). Mangrove roots decompose more slowly than other mangrove material (Middleton and McKee 2001), so the below-ground community is likely to sustain the longest-term impacts.

A study on mangrove deforestation in a native mangrove forest showed a community shift as well as higher fish abundance in areas where some overstory had been removed (*Sonneratia alba* and *Rhizophora mucronata* mixed forest; Huxham et al. 2004). Only one study to date has examined post-removal community dynamics in a system where mangrove is invasive by comparing two sites: a two-year removal in Pearl Harbor and a six-year removal in Kāneʻohe Bay (Sweetman et al. 2010). The roots of deforested mangrove remain above the sediment surface for years, and changes in bacterial and macrofaunal carbon consumption in invaded sediments persisted even six years after mangrove removal (Sweetman et al. 2010). Removal increased total carbon (C)-uptake, decreased overall organic loading, and enhanced macrofaunal abundance in mangrove sediments compared to living mangrove (Sweetman et al. 2010). Sweetman et al. (2010) found that while macrofauna dominated short-term C processing in sediments of an existing mangrove forest and sediments from a two-year removal site (in Pearl Harbor), bacteria dominate C processing six years following removal (in Kāneʻohe Bay). This shift in carbon processing structure is likely to influence decomposition rates. In the same study, Sweetman et al. (2010) found that infaunal communities differed between mangrove and removal sites: sub-surface deposit feeders (mostly tubificid oligochaetes) dominated macrofaunal abundance and biomass in mangroves, whereas suspension feeding spionid polychaetes were dominant in abundance and biomass at both removal sites.

Changes in infaunal community structure may be due to changes in sediment chemistry (decreased O₂ penetration depth, high sulfide concentrations), changes in the lability of organic matter (decreased sedimentary mangrove biomass, decay of tannins produced by mangrove materials), or top-down effects of a changing predator community. In mangroves, the physiochemical and biological processes that control infaunal abundance and community composition are interdependent: Biogeochemistry is strongly influenced by burrowing organisms, which change soil texture and porosity, redistribute water, and introduce O₂ into the sediments (Alongi 2009). In native mangroves, 0.3 to 3% of water volume moving through a mangrove forest moves through burrows (Alongi 2009). Following 5-10 mm of oxidized surface sediment, mangrove soils are either sub- or anoxic. Deeper in the sediment, buildup of free sulfides is

prevented by O₂ translocation to roots, and, at least where mangroves are native, by active mixing by bioturbators such as sesarimid and grapsid crabs, and small fish (Alongi 2009). In Belizean mangrove forests, the processes that speed decomposition usually also involve consumption of leaf material by epifauna (Middleton and McKee 2001). Burrows can enhance bacterial activity and algal production in mangrove sediments, altering nutrient availability (Mchenga et al. 2007). Because they can influence physicochemical processes in mangrove sediments in addition to preying on infauna, burrowing predators constitute an important link between top-down and bottom-up forcing mechanisms for mangrove infauna.

Mangrove-associated predators may exert trophic effects on infaunal assemblages that are within the “grazing shadow” of mangrove forest. While mangroves have been characterized as nursery habitat for many species (Laegdsgaard and Johnson 2001; Macia et al. 2003), vegetation can attract predators by providing habitat for benthic invertebrates (Nagelkerken and van der Velde 2004; Sheaves and Molony 2000). Smaller fish forage more frequently in mangrove than on adjacent mudflats (Laegdsgaard and Johnson 2001) and zoobenthivores are attracted to mangrove mainly for food (Verweij et al. 2006). Therefore, despite the popular notion that mangroves are primarily used as refugia from larger predators (e.g., Parrish 1989), infauna in mangrove habitats may experience enhanced predation (Huxham et al. 2004). Some zoobenthivores forage actively in native mangrove, and predation rates on shrimp among mangrove prop roots can be as high as on sand flats (Primavera 1997). Predation rates on invertebrates in mangroves can depend on the feeding strategy of the predator (Primavera 1997) or the size of the prey (Acosta and Butler 1997). Experimental exclusion of predatory crabs in native mangrove forests in Thailand led to higher species diversity, richness and biomass in the benthic infaunal community (Kon et al. 2009).

In Hawai‘i, the complex structure created by *R. mangle* provides habitat for alien predators that forage on infaunal communities. These predators include opportunistic portunid crabs such as Samoan crab (*Scylla serrata*) and the blue pincher crab (*Thalamita crenata*) (Demopoulos et al. 2008; Demopoulos and Smith 2010). Epifaunal assemblages (including predators) are more diverse in mangroves than adjacent sandflats (Demopoulos and Smith 2010), and many crab and fish species present in Hawaiian

mangroves are known to feed on infauna (e.g., Cannicci et al. 1996; Hernaman et al. 2009). In Hawai‘i, it is unclear whether the higher diversity found in mangrove infauna may be due to decreased predation pressure by mangrove-associated predators. Currently, only one unpublished study has examined communities of mobile epifauna in Hawaiian mangroves (Nakahara 2007): in this study, mangroves on Moloka‘i supported higher overall abundances and higher species richness among macrofauna (> 5 mm) than uninvaded sandflats. Mangroves also hosted higher abundances of introduced mantis shrimp (*Gonodactylaceus falcatus*), mollies (*Poecilia* sp.) and Samoan crab (*Scylla serrata*) than sandflats. The study also found smaller portunid crabs (*T. crenata* and *Portunus sanguinolentus*) inside mangroves than outside, suggesting that juveniles of these species use mangroves as habitat. *S. serrata* and *T. crenata* forage actively in mangrove habitats (Cannicci et al. 1996; Hill 1979) and are likely to influence benthic community structure through predation and burrowing. Habitat utilization by predatory and burrowing epifauna may shift with mangrove removal, thereby changing predation and bioturbation rates in removal areas.

Taking advantage of ongoing mangrove removal in He‘eia fishpond, this paper investigates the time course of shifts in community structure following removal and evaluates the effects of mangrove-associated burrowing predators in mangrove and mangrove removal areas. In this thesis, I evaluated three questions: 1) How does mangrove removal affect infaunal and epifaunal communities? 2) What is the rate of mangrove decomposition and related community shifts? 3) Do burrowing predators modify infaunal community composition in existing or removed mangroves?

METHODS

Study Site

This study took place at Loko I‘a o He‘eia, an 88-acre fishpond located in Kāne‘ohe Bay, O‘ahu (21°26’10.74” N, 157°48’28.05” W). He‘eia fishpond is a shallow reef flat surrounded by a permeable rock wall, which was surrounded by mangrove as recently as 2005. It is subject to freshwater input containing a significant amount of land-

derived nutrients from He'eia Stream and the rock wall allows exchange between pond and ocean water, which is tidally dominated (Young 2011) (Figure 1). The pond is shallow (average depth 0.413 m; 4 m maximum depth) with a soft bottom dominated by muddy sediments near stream inputs and sand/coral rubble near the seawall (Vasconcellos 2007).

After mangroves were introduced to He'eia in 1922, they formed a continuous stand around the mouth of He'eia stream. In the 1960's, *R. mangle* expanded past the stream to grow along the wall and was still colonizing the fishpond wall as recently as 1991 (Chimner et al. 2006). By the time removal began in 2005, invasive mangrove (predominantly *R. mangle*) had overgrown the entire sea wall of the pond. Since removal began in 2005, 50-75 m sections of mangrove have been removed each summer, beginning at the south end of the pond (Figure 1). The non-profit group that manages the fishpond, Paepae o He'eia (POH) removed another 75-m section of mangrove beginning in early 2011. The sequential nature of this removal provides an opportunity to study a chronosequence of mangrove removal from 2007 – 2011. Sampling sites were chosen at the center of each removal section, for a total of eight sites along the chronosequence: Two sites with fresh mangrove and six sites with mangroves removed between 2007 and summer 2011 (Table 1).

Physical Data

Salinity, pH, dissolved oxygen (DO), chlorophyll a concentration, and temperature at each site were provided by an ongoing monitoring project on the physical oceanography of the fishpond (McCoy 2011). These parameters were measured monthly using a pre-calibrated portable YSI® 6660. Measurements were taken midway between high and low tide and averaged over the bottom 25 cm of the water column at each monitoring site. Because monitoring sites were not located exactly at sampling sites used in this project, physical environmental variables for mangrove sampling sites were taken from proximal monitoring locations (Table 1). Data collected monthly between 4/28/11 and 8/25/11 were used to determine how much environmental conditions fluctuated between the beginning and end of the study. Physical variables measured over the course of the

experiment were compared among sites using non-parametric analysis of variance (Kruskal-Wallis tests).

Grain size

Cores used for grain size and were taken at the same sites in 2012, sectioned at 5 cm as before, and frozen until analysis. In the lab, core subsamples were sieved through 2 mm, 500 μm , and 53 μm meshes. Sediment fractions retained on each sieve were dried at 60°C for 2-5 days, weighed, and percent rubble ($> 2 \text{ mm}$), sand ($53 \mu\text{m} < x < 2 \text{ mm}$) and silt/clay ($< 53 \mu\text{m}$) calculated.

Decomposition Rate

Cores for sedimentary mangrove biomass (SMB) were collected in May 2012. SMB was measured from 5-cm sections (6.5 cm inner diameter) of mangrove rhizome. Roots, bark and leaf material were rinsed with fresh water on a 250 μm sieve, picked out under a dissecting microscope at 60x magnification, and dried at 60°C to constant weight (1-3 days) before weighing. A smaller set of cores was taken in 2011 but was not used for this analysis.

To estimate decomposition rate for submerged sedimentary mangrove biomass following removal, mangrove biomass from cores along the chronosequence was fit to an exponential decay model: $SMB = ae^{b \times DSR}$. The decay constant, b , was calculated in a linear regression of the natural logarithm of mangrove dry mass, SMB , on time elapsed since removal (DSR), as in previous root decomposition studies (Poret et al. 2007; Twilley et al. 1997).

Chronosequence

Infaunal cores (6.5 cm i.d.) were taken between May 10th – 16th, 2011. Sampling times for infauna and crabs are given in Table 2. These cores also provided the initial time point for the experiment described below. Cores were sectioned at 5 cm, sieved with a 500 μm mesh size, preserved in 10% formalin with Rose Bengal dye (0.05 g/L), rinsed gently with flowing tap water, then sorted in the lab to the lowest taxon possible under 60x magnification and stored in ethanol.

To analyze the infaunal community cores, total abundance, richness (S), normalized taxon richness ($d = (S-1)/\ln N$; N = number of individuals in one core), Shannon-Weiner diversity (H' ; log base e), and Shannon evenness ($e^{H'}/S$) were determined for all cores and compared along the chronosequence using generalized linear models (GLMs).

Prior to multivariate analysis, taxa containing fewer than 15 total individuals (across all cores) were removed from the dataset. All abundances are given as number of individuals per square meter, in order to allow comparison with other studies.

Taxa were assigned to trophic, domicile, and feeding guilds according to Barnes (1980), Fauchald and Jumars (1979), and Sheridan (1997). Since macrofauna were not identified to the species level in this study, taxa were assigned to a guild only if *all the species* in that taxon were classified as belonging to that guild in the literature and in a previous study in Hawaiian mangroves performed near the study site (Demopoulos 2004). Taxa containing species with different classifications for feeding or domicile guild or mobility were analyzed as “mixed” groups (Table 3). For example, tubificid oligochaetes are sometimes classified as subsurface feeders, while enchytraeid oligochaetes consume detritus—this has led to oligochaetes being classified as surface deposit feeders (Sheridan 1997) or sub-surface deposit feeders (e.g. Sacco et al. 1994). Here, we classify oligochaetes as omnivorous (Barnes 1980; Demopoulos 2004). Amphipod taxa found previously in Kāneʻohe Bay include members of multiple feeding groups: the genus *Corophium* spp. are considered suspension feeders, though other amphipods are surface deposit feeders (e.g. *Neomicrodeutopus* sp.) or omnivorous (e.g. *Eropisa* spp. and *Eriopisella* spp.) (Demopoulos 2004). Here, because amphipods were not identified below the order level, they are referred to as a mixed group.

For taxa and trophic guilds that showed distinguishable patterns across the chronosequence, relationships between mangrove removal age and abundance were determined by linear regressions on $\log(x+1)$ -transformed abundances.

Caging Experiment

Using a caging experiment, I tested the effect of burrowers and predators on the infaunal community and the time course of trophic shifts. Burrowing predators were excluded using wire mesh exclosures ($36 \times 36 \times 30$ cm, 1.27 cm mesh) with aluminum flashing below the sediment surface to prevent burrowers from digging underneath the cage. Each set of exclosures included a full predator exclusion cage; a cage control with 26×26 cm openings on each side; and a demarcated open control with no cage. Three to four replicates of each exclosure type were placed at 5 sites around the perimeter of the fishpond: two sites at the edge of mangrove that remained intact throughout the study, one site where mangrove was removed during the present study, and two sites where mangrove was removed 1-2 years prior to the present study (Figure 1). Three replicates of each treatment were deployed at the most northern and the most southern sites (M2 and R07, respectively) and four replicates were deployed at each of the other three sites.

Infaunal cores were taken in May (10th – 16th) and September (September 24th – 29th) of 2011, which corresponds to 1 month before and 3 months after mangrove was removed around site R11 on June 16th – 18th, 2011. Initial cores were taken the day after exclosures were set out, so no treatment effects were expected in the first set of cores. Cores were processed as described in the chronosequence section.

Statistical analyses were performed in R (Team 2012) and Primer-E® software (Clarke 1993). To test for changes in infaunal community composition across sites, treatments and over the course of the experiment, I used permutational analysis of variance (PERMANOVA; Anderson 2001a) based on modified Gower similarity with log (base 2) transformation (Anderson et al. 2006). In this study, community richness is relatively low, but abundance varies significantly between sampling sites, and differences in total abundance can be obscured when commonly employed dissimilarity measures are used (Clarke et al. 2006). Here, modified Gower similarity with log transformation counts a twofold change in abundance as equivalent to a species-addition in the community (Anderson et al. 2006). Permutation tests allow comparisons in an ANOVA-style framework but without the stringent distributional requirements of traditional ANOVA. Additionally, PERMANOVA is a powerful tool for analyzing both uni- and

multivariate community measures, so it was used here for univariate tests instead of conventional non-parametric univariate tests (Anderson 2001a; McArdle and Anderson 2001). To visualize community differences identified by multivariate tests, I used non-metric multidimensional scaling (MDS) plots.

To analyze the effect of predator exclusion at experimental sites (M2, M1, R11, R10, R09), I analyzed the abundance of all taxonomic groups in two different ways using PERMANOVA. First, using both September and May cores and secondly, using data from September cores only. The model formula used for the first PERMANOVA was:

$$\text{Infauna} \sim \text{Site} + \text{CageTrt} + \text{Month} + \text{Site}*\text{CageTrt} + \text{Site}*\text{Month} + \text{CageTrt}*\text{Month} + \text{Block}(\text{Site}*\text{CageTrt}) + \text{Site}*\text{CageTrt}*\text{Month}$$

Since the experimental design involved repeated measures (cores taken in each cage at each time point), cages were treated as blocks. The $\text{Block}(\text{Site}*\text{CageTrt})*\text{Month}$ term is excluded because there is only a single sample per cage at each time point. The residual error term therefore represents the variation within a cage treatment at each site. The model structure for the second analysis was:

$$\text{Infauna} \sim \text{Site} + \text{CageTrt} + \text{Site}*\text{CageTrt}$$

This model was applied to September core data.

Significant multivariate patterns were examined further with univariate PERMANOVA tests on the five dominant taxonomic groups (Oligochaeta, Amphipoda, Sabellidae, Opheliidae, and Nematoda) using Euclidean distance matrices and 3999 permutations (Anderson 2001b). This analysis is identical to an ANOVA structure but allows for non-normality: It produces the same sum of squares and F-ratios but uses permutations to obtain p-values (Anderson 2005).

Predator Community

To quantify burrowing predators at each site, two trapping methods were employed: For large (>12 cm carapace width) crabs, large (~1 m diameter), equally baited crab traps were set at each of the five experimental sites, left overnight and checked the following morning. Large traps were set 3-4 times per sampling period. For smaller crabs that tend to forage during the day (*Thalamita crenata*, *Podophthalmus vigil*, *Portunus sanguinolentus*; < 12 cm carapace width), crab nets were used to survey during the day for three or more consecutive days. All traps were baited with skin and bones from two milkfish ('awa; *Chanos chanos*) per trap (~ 1 kg total). Crabs caught in all traps were identified, sexed, and measured for carapace length and width. Biomass was calculated from carapace width using available species- and sex-specific parameters for the equation $W = aL^b$ (Langer 1952), where W is total weight and L is carapace width (Mohapatra et al. 2010; Roongrati and Iaitim 1994; Songrak et al. 2010; Sukumaran and Neelakantan 1997). Conversion factors for each species are given in Table 7. *Scylla serrata* was removed from statistical comparisons unless otherwise noted, because of its low catch rate (seven individuals captured across the course of the experiment).

To test for differences in the predator community between sites and over the course of the experiment, crab biomass and carapace width was analyzed using Kruskal-Wallis tests, because neither biomass nor carapace width were normally distributed. Crab species density was approximated using catch per unit trapping effort (CPUE; number caught per trap per day). CPUE was compared among sites for each time point using Kruskal-Wallis tests.

RESULTS

Physical Environment

The pond contains a natural gradient from fresh, turbid, productive water on the west side near the existing mangroves to more saline, less turbid waters on the east side near the sea wall. All the study sites are along the east side and are similar in mean temperature, salinity, DO, pH, turbidity and chlorophyll a concentration in the bottom 25 cm of the water column (Figure 2; Kruskal Wallis tests; df = 6, p = 0.981, 0.217, 0.979, 0.966,

0.217, 0.597 respectively). There are no systematic differences in salinity, temperature, DO, pH, or chlorophyll a concentration across the chronosequence (Figure 2).

Grain sizes are given in Table 4 and proportions of sand and silt/clay are shown in Figure 3. There are no systematic differences in grain size composition along the chronosequence.

Mangrove Decomposition Rate

Sedimentary mangrove biomass over the chronosequence is shown in Figure 4. The decay constant was calculated from an exponential fit for loss of sedimentary mangrove biomass ($SMB \sim a \times e^{b \times DSR}$) with days since removal was $b = 5.6 \times 10^{-4} \pm 0.9 \times 10^{-4} \text{ d}^{-1}$, with an intercept of $1691 \pm 107 \text{ g dw m}^{-2}$. The incomplete set of cores collected in 2011 is shown in Figure S1.

Whole-Community Patterns Across Removal Chronosequence

The only community measure that showed a consistent pattern across the chronosequence was total macrofaunal abundance, which increased with time since removal doubling every 946 days ($R^2_{\text{adj}} = 0.159$, $F = 15.9$, $p < 0.001$, Table 6, Figure 5). Taxon richness, normalized taxon richness, Shannon diversity, and Shannon evenness did not show distinct patterns over the chronosequence (Figure S2). Abundances of individual taxa by site and by days since removal are shown in Figures S3-S6. An MDS of chronosequence sites reveals no distinctive separation among sites (Figure 6).

Trophic, Domicile and Mobility Guilds Across Chronosequence

Trophic guilds across the chronosequence are shown in Figure 7. The abundance of suspension feeders doubled in 630 days ($R^2_{\text{adj}} = 0.257$, $F = 28.3$, $p < 0.001$; Figure 8), and the abundance of omnivores doubled in 835 days ($R^2_{\text{adj}} = 0.109$, $F = 10.7$, $p = 0.001$; Figure 8). The abundance of trophic groups over time since removal are shown in Figure S7, and there were no clear patterns in domicile or mobility groupings over the chronosequence (Figures S8 & S9).

Cage Effects

Total abundance, normalized richness, Shannon diversity, Simpson diversity, evenness, and Shannon evenness at all sites and treatments in September are shown in Figure S10. The infaunal community changed with site and season but not with treatment (PERMANOVA Time: $F_{[1,39]} = 3.45$, $p = 0.004$; Site: $F_{[4,39]} = 6.17$, $p < 0.001$; Treatment: $F_{[2,39]} = 1.06$, $df = 2$, $p = 0.379$), and differences between sites changed over season (Site $\times$ Time: $F_{[4,39]} = 3.60$, $p < 0.001$, Figure S11). Pair-wise tests revealed changes over time at Mangrove sites (M1, $t = 2.59$, $p = 0.002$; and M2, $t = 2.52$, $p = 0.013$) and the two-year removal site (R09, $t = 1.84$, $p = 0.043$). Site-specific differences were most marked in sabellid polychaetes (Site: $F_{[4,39]} = 3.49$, $p = 0.012$), opheliid polychaetes ($F_{[4,39]} = 7.30$, $p < 0.001$), amphipods ($F_{[4,39]} = 3.5328$, $p = 0.013$), and oligochaetes ($F_{[4,39]} = 9.89$, $p < 0.001$). Oligochaetes changed in abundance differently across sites (Site $\times$ Time: $F_{[4,39]} = 2.76$, $p = 0.043$), with a decrease occurring at mangrove (M2; $t = 5.94$, $p = 0.001$) and an increase at the most recent removal (R11; $t = 2.43$, $p = 0.037$) sites over the course of the experiment. Opheliids changed differently across sites as well (Site $\times$ Time interaction; $F_{[4,39]} = 4.37$, $p = 0.005$), with decreases at mangrove (M2; $t = 2.78$, $p = 0.036$) and increases at one-year removal (R10; $t = 3.15$, $p = 0.014$) sites. Seasonal changes in amphipod abundance also differed between sites (Site $\times$ Time: $F_{[4,39]} = 5.16$, $p < 0.001$), decreasing at both mangrove sites and the most recent removal (R11), and increasing at the two-year removal (R09). An analysis of the September data alone revealed the same patterns as the repeated-measures PERMANOVA (Figure S12).

Although the MDS plot of all experimental removal and mangrove sites in May shows no distinguishable community shifts over time following removal (Figure 11), mangrove communities are dissimilar from removal sites (SIMPER analysis; 61.28% dissimilarity between pooled intact mangrove and pooled removal; Table 5). MDS plots of September data show differences between removal sites and mangrove sites, with a recent removal (R11; in orange) grouping more closely with removal than with mangrove sites (Figure 12).

Crabs were similar in community composition, density and biomass across all study sites, and this homogeneity was consistent throughout the experiment. Total crab catch per unit effort (CPUE, individuals caught trap⁻¹ day⁻¹) was similar across all

experimental sites for both May and September (May $\chi^2 = 2.92$, $p = 0.712$, $df = 5$; September $\chi^2 = 2.39$, $p = 0.792$, $df = 5$; Figure 13). Mean individual crab biomass was also similar across sites ($\chi^2 = 0.250$, $p = 0.992$, $df = 4$; September $\chi^2 = 0.670$, $p = 0.954$, $df = 4$), as was biomass caught per day (May $\chi^2 = 5.16$, $p = 0.270$, $df = 4$; September $\chi^2 = 9.48$, $p = 0.050$, $df = 4$; Figure 14). The crab community consisted of Samoan crab (*Scylla serrata*), the blue pincher crab (*Thalamita crenata*), and two endemic Hawaiian species of swimming crab—the long-eyed swimming crab (*Podophthalmus vigil*), and the blood-spotted swimming crab (*Portunus sanguinolentus*). The dominant crab species was *T. crenata*. *P. vigil* were rare, and only found in September. Carapace widths for each species are given in Table S1 and shown in Figure S13.

DISCUSSION

Invasive species eradication can have dramatic effects on invaded ecosystems, and post-removal assessments have been recommended as a way to develop effective eradication strategies (Zavaleta et al. 2001). Alien species that are structurally complex ecosystem engineers can have widespread effects on invaded ecosystems such that eradication causes dramatic perturbations (Crooks 2002). Additionally, habitat quality shifts caused by invasions may persist following eradication; so additional site restoration is often necessary even after removal (Zavaleta et al. 2001). Invasion of nearshore sandy habitat in Hawai‘i by mangrove changes both megafaunal and infaunal community composition (Demopoulos et al. 2007; Demopoulos and Smith 2010; Nakahara 2007; Sweetman et al. 2010). Even six years after removal, fine root mass persists and benthic assemblages remain distinct from those of uninvaded sandy habitats (Sweetman et al. 2010). Shifts in community composition following removal can co-occur with changes in food web structure (Demopoulos et al. 2007) and carbon processing (Sweetman et al. 2010). This study shows that changes in community composition occur gradually after an initial rapid transformation from living to decomposing mangrove. The slow rate of root decomposition and the paucity of deep burrowing predators in Hawai‘i suggest that a return to pre-invasion conditions may take tens of years.

Mangrove and removal areas host distinct infaunal communities

There are distinct differences in community composition, including differences in total abundance (Figure 5), between mangrove and removal sites (Figure 6, 11 & 12), and many of these differences are consistent with previous studies on O‘ahu. Consistent with previous studies, I found higher abundances at removal sites than mangroves; however, total abundances differed between this study and previous work. Total abundances found at the northernmost mangrove site in this study are similar to those found by Sweetman et al. (2010) in Pearl Harbor (M2 in this study; $21,885 \pm 2,682 \text{ ind m}^{-2}$, compared to $21,597 \pm 12,731$), but other mangrove sites in this study (M1 and R11, in May) had substantially lower total abundances than those found for other mangrove forests on O‘ahu. Though a consistent increase in total infaunal abundance with increasing removal age was found here, total abundances here were more similar to a six-year removal in Kāne‘ohe Bay than a two-year removal in Pearl Harbor, suggesting that total abundances may be dependent on location. Differences between the total abundances found here and in previous work may indicate that removal response varies spatially within the main Hawaiian Islands.

Patterns in total abundance found between bare and mangrove sediments in Hawai‘i agree with abundance patterns in native mangroves. In studies comparing mud flats to mangrove habitats in *R. mangle*’s native range, mangroves host a higher infaunal density than adjacent mudflats (Sheridan 1997). The same pattern is found in Hawai‘i on Moloka‘i: densities are higher in mangroves than on adjacent sandflats at the same tidal height (Demopoulos and Smith 2010). The pattern is different for mudflats where mangrove overstory has been removed. Sweetman et al. found higher abundances (about an 8-fold increase) in a new removal (2 years old) than in an intact mangrove forest at the same location. Here, abundances increased 1.5-fold in the first two years following removal (Table 6).

Relative differences in community composition in this study are comparable to previous work. The overall differences between bare and removal sites were due primarily to oligochaetes and amphipods (Table 5), which were dominant at every site,

regardless of removal status. Relative abundances of less dominant groups were similar to those found by Sweetman et al.: The mangrove community was dominated primarily by oligochaetes (41% of abundance) and amphipods (34%), and secondarily by sub-surface deposit feeders (21%). The maximum abundance of sub-surface deposit feeders decreased as mangrove removals aged (Figure 9 & 10). Removal and pre-invasion areas in Kāneʻohe Bay have shown a higher abundance of suspension and surface-feeding macrofauna (e.g., corophiids, sabellids, and spionids) in previous studies, ostensibly because of a lack of leaf litter deposits at the surface (Sweetman et al. 2010). Sweetman et al. (2010) also found sub-surface deposit feeders to be numerically dominant at intact mangrove sites. This pattern has been attributed to decreased particle size, high sedimentation, and high levels of organic enrichment in mangroves as opposed to sand or mud flats (Ellis et al. 2004), and is consistent with previous studies of native and invasive mangrove forests (Demopoulos and Smith 2010).

Other trophic guilds show consistent patterns in abundance across mangrove and removal areas: Suspension feeders had the highest relative abundances at removal sites, with abundances increasing with removal age (Figure 8). After oligochaetes and amphipods, suspension feeding sabellid polychaetes contributed the most to % dissimilarity between all mangrove and all removal sites (22 and 19% respectively; Table 5). In Hawaiʻi, suspension feeding sabellid worms were dominant at sandy controls in a study by Sweetman et al. (2010), and sandflat communities have higher abundances of suspension and surface deposit feeders, according to previous studies (Ellis et al. 2004). Shifts in suspension feeder abundance are partly due to changes in water velocity (LaBarbera 1984), which is much lower in mangrove habitats because of prop-root structure. Lower densities of suspension feeders in native mangroves than sand or mudflats have been attributed to low flow rates and high levels of sedimentation (Ellis et al. 2004). Turbidity is actually higher at the oldest removal site than in the mangrove, but so is chlorophyll a concentration (Figure 2), so the increase in turbidity is likely to be due to more primary productivity instead of higher sedimentation rates.

Community recovery and mangrove decomposition is slow in Hawaiian mangroves

Changes in community structure were mirrored by changes in benthic habitat and remaining belowground mangrove biomass. The decay constant calculated from this chronosequence of mangrove removal ($k = 5.6 \times 10^{-4} \pm 0.9 \times 10^{-4} \text{ d}^{-1}$) is only 0.5% of the lowest rate calculated for the same species in its native range (Figure 4). In native mangrove forests, root decomposition constants have varied between $k = 1.2\text{--}1.8 \times 10^{-3} \text{ d}^{-1}$ and $2.3\text{--}2.8 \times 10^{-3} \text{ d}^{-1}$ in a mixed forest that included *R. mangle* (Poret et al. 2007). Roots of native *R. mangle* in Belize have decay constants of 0.108 and 0.092 d^{-1} (Middleton and McKee 2001). In Hawai'i, cores taken from six-year (Pearl Harbor) and two-year (Kāne'ohe Bay) removals estimated a daily mass loss between $3\text{--}7 \times 10^{-4} \text{ d}^{-1}$ for mangrove roots in Hawai'i (Sweetman et al. 2010), but these were made only with two time points (existing mangrove and 2 year removal at one site, and existing mangrove and 6 year removal at another). Previous studies have found no significant effect of mangrove species on root decomposition, finding instead that root size, tidal height, and nutrient concentrations are more important in determining decay rates (Middleton and McKee 2001; Poret et al. 2007). Since this constant was calculated using mangrove roots from the edge of the fine root mat in decomposing mangrove, where roots are constantly submerged, and mangrove roots with less water movement and less frequent tidal inundation decompose more slowly (Poret et al. 2007), this decomposition rate is likely to be an overestimate of the overall rate for mangrove roots in Hawai'i. Loss of mangrove biomass may be slow because its decomposition is primarily bacterial: Hawaiian mangroves lack coevolved macrofauna, which are responsible for much of the leaf and root decomposition in native mangroves (e.g., (Nordhaus and Wolff 2007). Macrofauna in Hawai'i do not consume mangrove-derived carbon (Demopoulos et al. 2007), and bacteria dominate short-term C processing in six-year removals (Sweetman et al. 2010). The rate at which mangrove organic matter decomposes is highly dependent on the presence of mangrove-consuming macrofauna, and rates are much lower where bacteria are solely responsible for organic carbon consumption (Kristensen et al. 2008; Middleton and McKee 2001). Mangrove decomposition state is affected by the macrofaunal and bacterial communities present, but the decomposition state of the mangrove in turn

affects faunal densities: previous work indicates that meiofaunal densities are higher on more decomposed *R. mangle* leaves, and laboratory experiments have shown that larger detritivores prefer conditioned (decomposed or excreted by crabs) mangrove material to fresh mangrove detritus (Giddins et al. 1986; Lee 1989; Torres-Pratts and Schizas 2007). Because of the important role of macrofauna in processing of mangrove-derived carbon, it is both expected that the faunal community will change with removal and important to evaluate the temporal community response in order to assess the recovery of the benthic habitat.

This study shows that infaunal density increased gradually after removal, with older sites containing higher abundances of infauna than more recent removals (Figure 5). The four-year removal in this study had abundances very similar to a six-year removal in Kāneʻohe Bay sampled by Sweetman et al. (42,154 ind m⁻² at site R07; 46,610 ind m⁻² at KBR). This suggests either that the density stabilized after four years, or that different recovery times can be expected for different sites within the main Hawaiian Islands. There may also be environmental differences between sites that are driving infaunal abundance more than time since removal.

The rate of change in community composition was more dramatic at first, followed by a slow change over time. In the first year following removal, macrofaunal abundance increased, then decreased again and slowly increased between one and four years after removal (Table 6). This increase in abundance was accompanied by a decrease in sub-surface deposit feeders, which persisted over time (Figure S7). A rapid shift to “post-removal” conditions is also apparent from the MDS plot of all sites in September (Figure 12): The removal site, which had only been removed 3 months before the collection of September cores, already appeared similar to the 2-4 year removal sites. Rapid initial shifts in community structure and total abundance agree with differences in short- vs. long-term changes in C-processing in removal sites found by Sweetman et al. (2010).

Macrofaunal community structure of benthic environments has been used in the past to characterize ecosystem health (Brown et al. 2000; Kremen 1992). If suspension feeder abundance is an indicator of lower sedimentation rates and a return to high-flow, unvegetated habitat, the long-term increase in suspension feeders following removal may

be evidence of recovery in the benthic community. At the four-year removal site in this study, sabellids were still at about half the abundance of sandy controls in Kāneʻohe Bay surveyed by Sweetman et al., suggesting that they were still in the process of returning to a pre-invasion state.

The abundance of omnivores, composed primarily of oligochaetes, increased in abundance with time since removal. In a previous food web study in Hawaiian mangroves, tubificid oligochaetes had stable isotope values matching a diet of mangrove leaves (Demopoulos 2004), so it is possible that the oligochaete community is more able to process mangrove material than other taxa, and therefore responded positively to root decomposition.

Sediment chemistry at the one-year removal (R10) and intact mangrove (M1) showed distinct differences in O₂ penetration depth, with far shallower O₂ penetration depth and higher sulfide concentrations further up in the sediment column than at the mangrove sites (Mills 2012). This may have been the result of the cessation of diffusion of O₂ into the sediments by mangrove roots following overstory removal. The main source of porewater O₂ following the death of the mangrove roots at that site might be the burrows of larger bioturbators such as crabs and gobies. If burrowers are the only source of introduced dissolved O₂, their absence may reduce mixing and increase sediment anoxia.

Food web structure and function is determined by a combination of productivity and trophic structure (Leibold et al. 1997). Decomposition may make mangrove material more labile and available to consumers. When mangroves decompose, total amounts of tannins and phenolic compounds inside the tissues decrease, potentially rendering mangrove roots and leaves more bioavailable (Lin et al. 2007). An increase in microbial production would not necessarily increase macrofaunal biomass, but a decrease in predation pressure or an increase in burrowing along the chronosequence might be responsible for the observed changes in abundance.

Top-down processes do not regulate infaunal communities in Hawaiian mangroves or mangrove removals

Burrowing crabs can greatly affect infaunal community composition because they change sediment chemistry by creating burrows (Alongi 2009) and turn over mangrove litter (Nerot et al. 2009; Werry and Lee 2005). The species that create extensive burrows and facilitate mangrove litter breakdown in native mangroves are absent from Hawaiian mangroves. Instead, mangroves on O‘ahu contain a diversity of introduced species, including the molly *Poecilia* sp., introduced mantis shrimp *Gonodactylaceus falcatus* and the Samoan or mangrove crab *Scylla serrata* (Nakahara 2007). The epifaunal community at my study site was dominated by the blue swimming crab *Thalamita crenata*, *S. serrata*, and two patchily distributed native crabs, *Podophthalmus vigil* and *Portunus sanguinolentus* (Table 8). Removal did not affect abundances: before and after the cage experiment, CPUE (density and biomass) was not significantly different between any sites for any crab species, regardless of removal age (Figure 13 & 14). *S. serrata* were not restricted to mangrove habitat and were instead caught across all sites (Figure S13). The species to which much of the bioturbation in native mangroves is attributed (*Uca* spp. and members of the family Sesarmidae) are absent from Hawaiian mangroves (Demopoulos 2004; Nakahara 2007), potentially replaced by species with less extensive burrowing activities. Though there is not a lot of published data on the domicile habits of *T. crenata* and *S. serrata*, they inhabit shallow burrows (Williams 1994), and total burrow density is much lower in mangroves on O‘ahu than in several other native mangroves (Demopoulos 2004; Kristensen 2008), so they are unlikely to have the extensive impacts on sediment chemistry and infaunal densities that ocypodid and grapsid crabs do.

The non-significant treatment effect given by PERMANOVA indicates that burrowing predators did not exert top-down effects on total abundance, abundance of numerically dominant fauna, diversity, or species richness inside or outside the mangrove. Previous caging experiments have demonstrated negative effects of epifauna (snails, as well as sesarmid, grapsid, ocypodid and hermit crabs) on meiofaunal (Schrijvers et al. 1995) and macrofaunal abundance (Kon et al. 2009; Schrijvers et al. 1998). Cage treatment replicates at each site were equal or higher in this study (n = 3-4)

than in previous studies ($n = 2$, Schrijvers 1995-1998; $n = 4$, Kon et al. 2009) that found significant effects of predators on macrobenthos, so the inability of this analysis to detect a predator effect on total abundance is not due to insufficient sample size relative to previous studies. Additionally, a power analysis of $\log(x+1)$ -transformed total abundances from this study shows that a doubling of sample size would be necessary to detect a difference between cage treatments in mangrove sites at an alpha-level of 0.05. Additional cage replicates at the removal sites would not substantially increase the power. Cage experiments performed on native mangroves (*Rhizophora apiculata*) in Thailand, found higher species richness, abundance, and biomass inside mangrove forest, and many of these differences were significant in both wet and dry seasons (Kon et al. 2009). Top-down impacts on the infaunal community, though important in native mangroves, were not present here in intact mangrove or removal sites. The Site $\times$ Time interaction shows that the infaunal community at different sites changed differently over the course of the experiment. Despite the different result of seasonal effects infaunal community shifts, the result that interactions are the same across sites holds. The fact that seasonal and spatial differences were responsible for more variation than predation or burrowing demonstrates that burrowing crabs are not as important in mediating bottom-up and top-down interactions in the introduced range of mangrove as they are in native mangrove forests.

The absence of a burrowing predator effect on Hawaiian mangroves or removals may be due to differences in crab community structure. In native mangrove forests, mangrove crabs (mainly *Uca* spp. and Sesamidae spp.) are community dominants and highly active: the majority of the benthic biomass is composed of mangrove crabs, and they behave as “shredders” which cut up leaves and create more available surface area for microbes to colonize. Water flow through their burrows can be as high as 10 mm s^{-1} and replace up to 40% of the burrow volume during a tidal cycle (Hollins et al. 2009; Wolff et al. 2000). This flow is thought to be an efficient vector for transporting O_2 and nutrients into mangrove sediments. Burrowing fauna in native mangrove have a strong positive effect on meiofaunal abundances, with higher abundances near burrows than far away (Dittmann 1996). The most abundant crab found here, *T. crenata*, inhabits burrows which are not as deep or extensive as sesamid burrows (Gillikin 2000). Even if similar

processes occur in Hawaiian mangroves, burrows may be shallower and play a less important role in turnover of organic matter and other “bottom up” processes.

Post-removal assessment of this management strategy indicates that removal is returning some community characteristics to a pre-invasion state (high abundances of suspension feeding polychaetes, lower belowground mangrove biomass). The uniform distribution of burrowing crabs across sites, slow rates of change in infaunal communities, lack of top-down control on infaunal communities, and slow decomposition rate of sedimentary mangrove biomass found here suggest that changes in community structure will continue to occur slowly, and more likely as a result of bottom-up than top-down processes.

Table 1. Chronosequence sites, days between removal and infauna cores, and corresponding long-term monitoring site for physical data. Sedimentary mangrove biomass (SMB) was measured from cores taken in both 2011 and 2012. One year elapsed between the two collection points, hence the two columns of days since removal.

Site	Years between removal and the beginning of this study in May 2011	Date removed	Days since removal (2012 SMB)	Days since removal (Infauna & 2011 SMB)	Physical data site name (Ruttenberg et al. unpubl.)	Distance between physical site and site for this study (m)
M2	0 (Fresh mangrove)	Not yet removed	NA	NA	006	38
M1	0 (Fresh mangrove)	Not yet Removed	NA	NA	005*	59
R11	0 (Fresh mangrove)	6/30/2011	324	NA	005	47
R10	1	7/23/2010	666	291	004	30
R09	2	7/10/2009	1044	669	003	27
R08_Jul	2	July 2008	1404	1055	001	70
R08_Feb	3	February 2008	1555	1206	012	80
R07	4	7/5/2007	1780	1431	020	44

* 005 is on other side of the makaha.

Table 2. Sampling schedule. Dashes indicate that a site was not sampled that month. I = Infauna, C = Crabs, SMB = Sedimentary Mangrove Biomass.

Site	Cage Experiment (May to Sept)	May 2011	September 2011	May 2012
M2	X	I, C	I, C	SMB
M1	X	I, C	I, C	SMB
R11	X	I, C	I, C	SMB
R10	X	I, C	I, C	SMB
R09	X	I, C	I, C	SMB
R08_Jul	-	I, C	-	SMB
R08_Feb	-	I, C	-	SMB
R07	-	I, C	-	SMB

Table 3. Feeding and domicile groups used in this study. SF = suspension feeder, ssdf = sub-surface deposit feeder, sdf = surface deposit feeder, omni = omnivore, carni = carnivore, tdw = tube-dweller, ntdw = non-tube-dweller, b = burrowing, nb = non-burrowing, n = native, c = cryptogenic, u = unknown biogeostatus. Asterisks (*) indicate taxa not found by Demopoulos (2004). “Mixed” groups are taxa whose members belong to more than one trophic, domicile, or feeding mode.

Taxon	Trophic mode	Domicile	Mobility	Biogeostatus
Spionidae	sdf	tdw	nb	Mixed
Nereididae	carni	tdw	b	u
Syllidae	omni	ntdw	nb	Mixed
Opheliidae	ssdf	ntdw	b	c
Cossuridae*	ssdf	ntdw	b	u
Sternaspidae*	ssdf	ntdw	b	u
Sabellariidae*	SF	tdw	nb	u
Sabellidae	SF	tdw	nb	Mixed
Capitellidae	ssdf	ntdw	b	Mixed
Dorvillidae*	sdf	Unknown	b	u
Cirratulidae	sdf	ntdw	nb	u
Oligochaeta	omni	ntdw	b	Mixed
Nemertea	carni	ntdw	nb	u
Nematoda	omni	ntdw	nb	u
Platyhelminthes	carni	ntdw	b	u
Sipuncula	sdf	tdw	nb	u
Ostracoda*	omni	ntdw	b	u
Decapoda	Mixed	Mixed	Mixed	Mixed
Amphipoda	Mixed	Mixed	nb	Mixed
Isopoda	omni	ntdw	nb	Mixed
Copepoda*	Mixed	ntdw	nb	u
Tanaidacea	omni	tdw	nb	Mixed
Hydrozoa	SF	ntdw	nb	u
Anthozoa*	Mixed	Mixed	Mixed	Mixed

Table 4. Grain size measured from 2012 sediment cores. Sediment grain sizes are expressed as a percentage by weight of a sediment subsample.

Site	Date Removed	% Silt/Clay	% Sand	% Rubble
M2	Not yet removed	27.76	64.73	7.52
M1	Not yet Removed	15.99	51.75	32.26
R11	6/30/2011	14.63	75.41	9.96
R10	7/23/2010	12.87	37.01	50.12
R09	7/10/2009	46.95	53.05	0.00
R08_Jul	July 2008	51.07	48.93	0.00
R08_Feb	February 2008	39.02	60.98	0.00
R07	7/5/2007	31.66	68.04	0.29

Table 5. SIMPER results for all removal (R07, R08, R09, R10, R09) vs. all mangrove (M2, M1, R11) sites in May. Total dissimilarity = 61.28%.

Species	Avg dissimilarity	% Contribution to Dissimilarity
Oligochaeta	13.59	22.19
Amphipoda	11.84	19.33
Sabellidae	6.37	10.40
Nematoda	4.65	7.59
Opheliidae	3.75	6.12
Capitellidae	3.59	5.68
Sternaspidae	2.94	4.79
Syllidae	2.87	4.68
Cossuridae	2.68	4.38
Ostracoda	2.63	4.29
Spionidae	1.63	2.67

Table 6. Infaunal Abundance for each taxon at each site in May. Abundances for each taxon are in units of individuals m⁻², for 5 cm depth.

Site/Taxon	R07	R08_Feb	R08_Jul	R09	R10	R11	M1	M2
Spionidae	33.67 ± 33.67	2121.21 ± 1148.37	265.15 ± 165.15	0	25.25 ± 25.25	25.25 ± 25.25	25.25 ± 25.25	67.34 ± 67.34
Nereididae	0	0	0	0	0	50.51 ± 50.51	0	0
Syllidae	134.68 ± 73.38	404.04 ± 231.44	189.39 ± 79.71	808.08 ± 733.63	277.78 ± 108.48	378.79 ± 124.41	404.04 ± 218.56	0
Opheliidae	0	336.70 ± 233.88	1439.39 ± 657.33	1077.44 ± 339.22	151.52 ± 58.98	454.55 ± 352.88	505.05 ± 342.54	269.36 ± 106.47
Cossuridae	0	0	75.76 ± 75.76	168.35 ± 134.68	0	0	0	3333.33 ± 1127.07
Sternaspidae	0	0	0	33.67 ± 33.67	0	0	1515.15 ± 468.86	202.02 ± 202.02
Sabellariidae	0	0	0	0	0	0	0	0
Sabellidae	4343.43 ± 1798.43	3333.33 ± 1679.63	3484.85 ± 1931.02	2121.21 ± 968.85	252.53 ± 110.86	277.78 ± 164.54	151.52 ± 69.78	370.37 ± 110.39
Capitellidae	67.34 ± 44.54	909.09 ± 505.05	871.21 ± 609.94	168.35 ± 134.68	151.52 ± 102.15	126.26 ± 101.87	151.52 ± 102.15	1952.86 ± 529.97
Dorvillidae	33.67 ± 33.67	0	0	0	176.77 ± 58.48	25.25 ± 25.25	0	67.34 ± 44.54
Cirratulidae	0	33.67 ± 33.67	75.76 ± 75.76	0	0	25.25 ± 25.25	0	33.67 ± 33.67
Oligochaeta	19831.65 ± 4886.51	11851.85 ± 4066.03	6401.52 ± 2387.05	2727.27 ± 1367.37	16868.69 ± 6777.33	2045.45 ± 856.39	3055.56 ± 967.99	8720.54 ± 1158.07
Nemertea	0	0	0	33.67 ± 33.67	25.25 ± 25.25	0	0	0
Nematoda	538.72 ± 206.87	1178.45 ± 503.65	492.42 ± 235.68	437.71 ± 220.79	328.28 ± 168.71	1161.62 ± 505.74	631.31 ± 215.76	1010.10 ± 422.56
Platyhelminthes	0	0	0	0	0	0	0	0
Ostracoda	6868.69 ± 4915.62	2491.58 ± 164.13	0	0	0	25.25 ± 25.25	25.25 ± 25.25	33.67 ± 33.67

Decapoda	33.67 ± 33.67	33.67 ± 33.67	75.76 ± 49.59	134.68 ± 53.24	101.01 ± 68.10	25.25 ± 25.25	50.51 ± 34.05	202.02 ± 142.85
Amphipoda	10235.69 ± 4633.48	10707.07 ± 3207.37	7007.58 ± 3304.90	5185.19 ± 1310.65	2272.73 ± 1111.84	5378.79 ± 2392.50	6388.89 ± 2296.47	5488.22 ± 2446.47
Isopoda	0	0	0	0	0	0	0	0
Copepoda	0	0	75.76 ± 75.76	33.67 ± 33.67	0	176.77 ± 131.66	0	0
Tanaidacea	33.67 ± 33.67	0	303.03 ± 198.38	0	101.01 ± 77.65	126.26 ± 78.76	202.02 ± 150.75	0
Hydrozoa	0	0	0	134.68 ± 134.68	0	0	0	0
Anthozoa	0	0	0	0	0	0	0	0
Cnidarian larvae	0	0	0	0	0	0	0	0
Tunicata	0	0	0	0	0	0	0	0
Mollusca	0	33.67 ± 33.67	0	101.01 ± 71.42	25.25 ± 25.25	0	0	134.68 ± 134.68
Shannon Evenness (Hill's ratio)	0.47 ± 0.05	0.61 ± 0.04	0.60 ± 0.04	0.71 ± 0.07	0.57 ± 0.06	0.66 ± 0.05	0.62 ± 0.03	0.57 ± 0.03
Pielou Evenness (J')	0.48 ± 0.06	0.68 ± 0.03	0.68 ± 0.03	NA	0.54 ± 0.08	0.66 ± 0.06	0.66 ± 0.04	0.68 ± 0.04
Taxon richness	4.77 ± 0.46	5.44 ± 0.62	5.25 ± 0.59	5.66 ± 0.88	4.33 ± 0.59	4.75 ± 0.62	5.08 ± 0.51	6.66 ± 0.47
Shannon Diversity (e ^H)	2.11 ± 0.16	3.19 ± 0.28	3.07 ± 0.22	3.79 ± 0.60	2.28 ± 0.31	3.26 ± 0.56	3.06 ± 0.29	3.84 ± 0.36
Total	42154.88 ± 5181.00	33434.34 ± 4788.13	20757.58 ± 5606.06	13164.98 ± 3513.32	20757.58 ± 7033.93	10303.03 ± 2634.64	13106.06 ± 3126.60	21885.52 ± 2682.37

Table 7. Carapace width (c.w.) to biomass conversion factors for each species of crab surveyed. Parameters are for biomass in grams and carapace width in mm, unless otherwise noted. These parameters were based on regressions of $W = aL^b$ with $R^2 > 0.75$.

Species	Sex	a	b	Reference
<i>Scylla serrata</i>	Male	0.0000628	3.220	Mohapatra et al. 2010
	Female	0.0002114	2.924	
<i>Podophthalmus vigil</i> (c.w. in cm)	Male	0.110674	2.810366	Roongrati and Iaitim 1994
	Female	0.147515	2.735783	
<i>Thalamita crenata</i>	Male	0.0002	3.014	Songrak et al. 2010
	Female	0.0008	2.695	
<i>Portunus sanguinolentus</i>	Male	0.0000362	3.09969	Sukumaran and Neelakantan 1997
	Female	0.0000658	2.96044	

Table 8. Biomass of crabs caught at each study site during the sampling months.

Time	Site	Species	N	Biomass (g)	St dev	St error	95% CI
May	M1	<i>Scylla serrata</i>	1	1611.67	-	-	-
	M1	<i>Thalamita crenata</i>	11	36.32	13.08	3.94	8.79
	M2	<i>T. crenata</i>	13	37.33	14.70	4.08	8.88
		<i>Portunus</i>					
	R09	<i>sanguinolentus</i>	1	129.20	-	-	-
	R09	<i>T. crenata</i>	17	40.42	16.29	3.95	8.38
	R10	<i>T. crenata</i>	14	35.88	13.90	3.71	8.02
September	R11	<i>T. crenata</i>	10	42.16	15.84	5.01	11.33
	M1	<i>P. sanguinolentus</i>	1	200.09	-	-	-
	M1	<i>Podophthalmus vigil</i>	2	82.15	2.95	2.09	26.53
	M1	<i>T. crenata</i>	14	44.11	13.17	3.52	7.60
	M2	<i>P. sanguinolentus</i>	2	94.53	17.89	12.65	160.71
	M2	<i>P. vigil</i>	8	72.85	22.13	7.83	18.50
	M2	<i>S. serrata</i>	1	709.30	-	-	-
	M2	<i>T. crenata</i>	34	47.76	16.78	2.88	5.85
	R09	<i>P. vigil</i>	1	53.86	-	-	-
	R09	<i>T. crenata</i>	8	35.13	12.12	4.28	10.13
	R10	<i>P. vigil</i>	1	59.09	-	-	-
	R10	<i>S. serrata</i>	1	2527.69	-	-	-
	R10	<i>T. crenata</i>	13	39.52	21.15	5.87	12.78
					828.0		7439.6
	R11	<i>S. serrata</i>	2	899.98	4	585.51	5
	R11	<i>T. crenata</i>	18	43.52	16.64	3.92	8.28

Figure 1. Map of study sites. The red line indicates where mangrove was at the beginning of the study. *R. mangle* used to grow around the entire pond (purple line; Chimner 2006).

Figure 2. Mean (± 1 SE) temperature ($^{\circ}\text{C}$), salinity, turbidity (NTU), pH, chlorophyll a ($\mu\text{g/ml}$), and dissolved oxygen (% Sat.) at each of the study sites measured over the course of the experiment. All physical variables are averaged over the bottom 25 cm of the water column.

Figure 3. Grain size at each of the study sites, measured in 2012. Rubble weights were excluded from this figure, so this chart shows only proportional contributions of silt/clay and sand.

Figure 4. Sedimentary mangrove biomass measured in 2012 vs. days since removal. Biomass measured in previous studies is in red and blue. The line represents model predictions for the exponential decay model.

Figure 5. Log(total infaunal abundance/core + 1) vs. days since removal, with linear regression in green. The model for this regression is $\log(A + 1) = 7.32 \times 10^{-4}(DSR) + 3.491$, where A is abundance and DSR is days since removal.

Figure 6. MDS plot of all sites in May included in the chronosequence.

Figure 7. Components of infauna at each site by feeding guild. Heights of each bar represent total abundance (summed across all cores) at a site.

Figure 8. Linear regressions for suspension feeders and omnivores, with linear regression models in green. The equation for suspension feeder population growth is $\log(SF + 1) = 1.09 \times 10^{-3}(DSR) + 0.398$ and the equation for omnivore abundance is $\log(OMNI + 1) = 8.295 \times 10^{-4}(DSR) + 2.498$.

Figure 9. Total infauna at each site by domicile guild. Heights of each bar represent total abundance at a site in May (summed across all cores).

Figure 10. Total infauna at each site by mobility guild. Heights of each bar represent total abundance at a site in May (summed across all cores).

Figure 11. MDS plot showing all experimental mangrove and removal sites in May. Red sites are intact mangrove.

Figure 12. MDS plot showing all experimental mangrove and removal sites in September. Red sites are intact mangrove.

Figure 13. Crab catch per unit effort (CPUE) (± 1 SE) at each of the cage experiment sites in May and September. Average densities are higher at the removal sites but not significantly so.

Figure 14. Crab biomass (g) caught per day at each site and sampling period.

APPENDIX 1: SUPPLEMENTARY TABLE

Table S1. Mean counts and size (carapace width) for crabs collected at all sites for each sampling period.

Time point	Site	Species	N	Mean carapace width (cm)	St dev	St error	95% CI
May	R10	<i>Thalamita crenata</i>	14	5.31	0.75	0.20	0.43
	R09	<i>Portunus sanguinolentus</i>	1	13.00	-	-	-
	R09	<i>T. crenata</i>	17	5.58	0.83	0.20	0.43
	M1	<i>Scylla serrata</i>	1	20.00	-	-	-
	M1	<i>T. crenata</i>	11	5.38	0.75	0.23	0.50
	M2	<i>T. crenata</i>	14	5.35	0.84	0.22	0.49
	R11	<i>T. crenata</i>	10	5.68	0.87	0.28	0.62
September	R10	<i>Podophthalmus vigil</i>	1	8.94	-	-	-
	R10	<i>S. serrata</i>	1	23.00	-	-	-
	R10	<i>T. crenata</i>	13	5.43	1.25	0.35	0.75
	R09	<i>P. vigil</i>	1	9.04	-	-	-
	R09	<i>T. crenata</i>	8	5.36	0.77	0.27	0.64
	M1	<i>P. sanguinolentus</i>	1	14.97	-	-	-
	M1	<i>P. vigil</i>	2	10.51	0.13	0.09	1.21
	M1	<i>T. crenata</i>	14	5.79	0.71	0.19	0.41
	M2	<i>P. sanguinolentus</i>	2	12.00	0.77	0.55	6.92
	M2	<i>P. vigil</i>	8	9.92	1.27	0.45	1.06
	M2	<i>S. serrata</i>	1	15.50	-	-	-
	M2	<i>T. crenata</i>	34	5.96	0.79	0.14	0.27
	R11	<i>S. serrata</i>	2	15.77	5.28	3.73	47.39
	R11	<i>T. crenata</i>	18	5.77	0.75	0.18	0.37

APPENDIX 2: SUPPLEMENTARY FIGURES

Figure S1. SMB data from 2011 with exponential model fit for decomposition.

Figure S2. Shannon diversity, Shannon evenness, normalized taxon richness, richness, Simpson diversity, and Pielou evenness along the chronosequence in May.

Figure S3. Mean abundance of the thirteen most abundant taxa (± 1 SE) across the chronosequence, with data from May cores only.

Figure S4. Mean abundance of the thirteen most abundant taxa (± 1 SE) vs. days since overstory removal, with data from May cores only.

Figure S5. Mean abundance of the thirteen most abundant taxa (± 1 SE) across the chronosequence, with data from September cores only.

Figure S6. Mean abundance of the thirteen most abundant taxa (± 1 SE) vs. days since removal, with data from September cores only.

Figure S7. Scatter plots of abundance of feeding guilds vs. days since removal along the chronosequence.

Figure S8. Scatter plots of abundance of domicile groups vs. days since removal along the chronosequence.

Figure S9. Scatter plots of abundance of burrowers and non-burrows vs. days since removal along the chronosequence.

Figure S10. Total abundance (ind m⁻²) (± 1 SE), normalized richness, Shannon diversity, Simpson diversity, evenness, and Shannon evenness at all sites in September (after 3 months of cage treatment), including data from all cores.

Figure S11. Bar plots of abundance changes (± 1 SE) in the five most abundant species between May and September in all cage treatments at all sites. Despite decreases in total abundance at the previously removed sites, there were increases in the abundances of the overall most dominant species.

Figure S12. Abundance of the five most abundant taxa (± 1 SE) across sites and cage treatments in September.

Figure S13. Average ($\pm$ SE) carapace width of crabs caught at each site. Each box is one species (PSAN = *Portunus sanguinolentus*, PVIG = *Podophthalmus vigil*, SSCYL = *Scylla serrata*, TCREN = *Thalamita crenata*). Crabs caught in May are black columns, crabs caught in September are white. If one color is missing for a site or month, it was not caught at that location or sampling period.

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