Invasive mangrove removal and recovery: Food web effects across a chronosequence

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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. Introduced 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, and, here, we study community change over a chronosequence of mangrove removals from 2007 to 2011, investigating infaunal community structure, crab abundance, and response to predator exclusion in the presence of mangrove overstory and along the chronosequence of removals. Overstory removal results in gradual changes in community composition concurrent with slow decomposition of sedimentary mangrove biomass (k = 0.36 ± 0.06 × 10^-3 d^-1). 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, unlike in native mangroves, their effects on infaunal communities are similarly negligible in both mangrove and removal areas. These results show that recovery from invasion and removal occurs gradually and is not governed by top-down effects.

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1. Introduction

Red mangrove (Rhizophora mangle L.) was introduced to Hawai‘i in 1902 and to He‘eia Marsh on the island of 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 estuarine fishpond sites developed for aquaculture by native Hawaiians as early as 1000 C.E. (Allen, 1992, 1998; Kirch, 2007). In their native range, mangroves are ecosystem engineers, strongly modifying their environment and providing important ecosystem services, including shoreline protection, entrainment of heavy metals (Clark et al., 1998; Harbison, 1986), sediment stabilization (Posey, 1987), litterfall subsidy (Twilley et al., 1986), and nursery grounds (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 the sandflats inhabited by the few native coastal macrophytes (Allen, 1998).

Hawaiian mangrove sediments host a higher diversity and abundance of infauna than adjacent sandflats, but this higher diversity includes many alien species (Demopoulos and Smith, 2010). This difference between mangrove sediments and adjacent sandflats may result from enhanced productivity due to litterfall subsidy or increased microhabitat heterogeneity (bottom-up effects) or from trophic effects, such as changes in habitat use by mobile predators (top-down effects). Despite R. mangle’s substantial litterfall subsidy to coastal habitats in Hawai‘i (Cox and Allen, 1999), stable isotopic analysis indicates that this productivity is not consumed by benthic invertebrates but, instead, subsidizes bacterial foodwebs (Demopoulos et al., 2007). The high detrital output and undigested mangrove leaf detritus increase sediment anoxia and negatively impact native 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, and haul away the overstory, leaving the flooded roots to decompose. While this method is favored in Hawai‘i, the time course of recovery following removal is poorly resolved. The only study examining recovery dynamics after removal compared sites in two different estuaries: a two-year-old removal in Pearl Harbor and a six-year-old removal in Kāne‘ohe Bay (Sweetman et al., 2010). Sweetman et al. (2010) found that removal increased total macrofauna abundance and shifted the infaunal community from sub-surface deposit feeders (mostly tubificid oligochaetes) to suspension feeding spongiid polychaetes. Even six years after removal, flooded mangrove roots remained above the sediment surface along
with persistent changes in bacterial and macrofaunal carbon consumption (Sweetman et al., 2010).

Post-removal changes in infaunal community structure may be due to changes in sediment chemistry, changes in the lability of organic matter, or top-down effects of a changing predator community. In mangroves, the physicochemical and biological processes that control infaunal abundance and community composition are interdependent: Burrows can enhance bacterial activity and algal productivity in mangrove sediments, altering nutrient availability (Mchenga et al., 2007), and burrowers structure infaunal communities through predation (Alongi, 1989). 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. While mangroves have been characterized as refugia from predators (Macia et al., 2003) and nursery habitat for many species (Laegdsgaard and Johnson, 2001), vegetation may also attract predators by providing habitat for benthic invertebrates (Nagelkerken and van der Velde, 2004). Therefore, despite the popular notion that mangroves primarily function as refugia from larger predators (e.g., Primavera, 1997), infauna in mangrove habitats may experience enhanced predation. 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, R. mangle provides habitat for introduced crabs (Nakahara, 2007) that forage on infaunal communities (Cannicci et al., 1996; Hill, 1979) and may influence benthic community structure through predation and burrowing.

Taking advantage of ongoing mangrove removal in a native Hawaiian fishpond, this paper investigates the time course of shifts in community structure following removal and the effects of burrowing predators in mangrove and mangrove removal areas. We address 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 introduced or removed mangrove areas?

2. Methods
2.1. Study site

This study took place at Loko‘a 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 built 600–800 years ago. Mangrove was introduced to the area in 1922, and the wall was completely covered by mangrove as recently as 2005, forming a large stand that is contiguous with surrounding forest (Fig. 1). Mangrove was introduced to He‘eia in 1922 and spread to form a continuous stand around the mouth of He‘eia stream. In the 1960s, R. mangle expanded past the stream to grow along the fishpond wall (Chimner et al., 2006). Mangrove completely covered the fishpond wall by the time managers began removing 50–75 m sections of mangrove in 2006 (Fig. 1). Like most other mangrove areas in Hawai‘i, He‘eia fishpond is a modified coastline with mangrove stands less than 100 years old. This fishpond is one of several in the main Hawaiian Islands invaded by R. mangle, and the same management solution (above-ground removal) has been proposed for many of them. For this study, sampling sites were chosen at the center of each removal section, for a total of eight sites along this well-documented chronosequence: two sites with fresh mangrove and six sites with mangrove removed between 2007 and summer 2011.

The fishpond is tidally dominated, exchanging seawater through four sluice gates (mākūhā) and the permeable rock wall; it also receives freshwater input from He‘eia Stream containing sediment and land-derived nutrients (Young, 2011). Flow rates through mākūhā into the pond vary between 0.1 and 4.9 m³/s on a flood tide and flow rates out vary between 0.1 and 4.6 m³/s, with most of the exchange occurring through the two east-facing mākūhā (Fig. 1; Young, 2011). 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).

2.2. Physical environment

To test for environmental differences across sites, we used data from an ongoing monitoring project on the physical oceanography of the fishpond. Salinity, pH, dissolved oxygen (DO), chlorophyll a concentration, and temperature were measured monthly at or near our benthic sampling sites (McCoy, 2011). These parameters were taken from April to August of 2011 at midtide using a pre-calibrated YSI® 6660 and averaged over the bottom 25 cm of the water column. Data were collected monthly. Physical variables were compared between sites using Kruskal–Wallis tests.

2.3. Grain size

Cores for grain size were collected at each site in 2012, sectioned at 5 cm, and frozen until analysis. In the lab, core subsamples were sieved through 2-mm, 500-μm, and 63-μm meshes. Sediment fractions retained on each sieve were dried at 60 °C for 2–5 days, weighed, and percent rubble (≤ 2 mm), sand (63 μm ≤ x < 2 mm) and silt/clay (< 63 μm) calculated. We used a log-linear model to test for independence between grain size distribution and site.

2.4. Decomposition rate

Sedimentary mangrove biomass (SMB) was measured from the top 5 cm section of 6.5-cm (inner diameter) cores collected in December 2012. Roots, bark and leaf material were rinsed with fresh water on a 250 μm sieve, picked out under a dissecting microscope at 60 × magnification, and dried at 60 °C to constant weight (1–3 days) before weighing. Three nested models were compared for mangrove decomposition: a single exponential model, \( SBM = ae^{−bt} \), where \( t \) is days since removal (Poret et al., 2007; Twilley et al., 1997), a double exponential model, \( SBM = a(e^{−bt} + (1−c)e^{−bt}) \) which assumes that a proportion, \( (1−c) \), of the material is less labile and decomposes at rate \( b2 \) while the more labile material decomposes at rate \( b1 \) (Wieder and Lang, 1982), and an asymptotic model \( SBM = a(e^{−bt} + (1−c)) \), which assumes that a proportion, \( (1−c) \), of the material will never decompose (Wieder and Lang, 1982). Models were fit using the minpack1m package in R (Elzhov et al., 2013) for nonlinear regression and compared using likelihood ratio tests.

2.5. Chronosequence

Infaunal cores (6.5 cm i.d.) were collected May 10th–16th, 2011. This core diameter is standard for sampling small infaunal invertebrates. These cores also provided the initial time point for the exclusion experiment described below. Twelve cores were collected at sites M1, R11, R10, and R09, and 9 cores were collected at sites M2, R08 Jul and R08 Feb and R07. Cores were sectioned at 5 cm, sieved through a 500 μm mesh, and preserved in 10% formalin with Rose Bengal dye (0.05 g/L). In the lab, samples were rinsed gently with flowing tap water, then sorted under 60 × magnification and stored in ethanol.

Polychaetes were sorted to family; other organisms were sorted into the following taxonomic groups: oligochaetes, amphipods, ostracods, tanaeid amphipods, and nematodes. Taxon richness (S), normalized taxon richness \( d = \frac{(S−1)}{ln(N)} \), Shannon–Weiner diversity, and Shannon evenness were determined.
for all cores and compared along the chronosequence using general linear models. In addition, taxa were assigned to trophic, domicile, and feeding guilds according to Barnes (1980), Fauchald and Jumars (1979), and Sheridan (1997) (Supplementary Table 3). 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; see Supplementary Table 3 for guild assignments and Supplementary Table 4 for a list of species found around O’ahu). We tested for changes in the total abundance and abundance of taxa and trophic guilds over the chronosequence using linear regression on log-transformed counts to meet the homogeneity of variance assumption. Finally, we used a SIMPER analysis to compare the overall similarity of community composition between mangrove and removal sites.

2.6. Predator exclusion experiment

We tested the effect of burrowing predators on the infaunal community using a replicated exclosure experiment across the five northern sites of the chronosequence (M2, M1, R11, R10, and R09; Fig. 1). Burrowing predators were excluded using wire mesh cages (36 × 36 × 30 cm, 1.27 cm mesh) with 10 cm of aluminum flashing below the sediment surface. Each set of exclosures included a predator exclusion cage, a cage control with 26 × 26 cm openings on each side, and an open control with no cage. Three (M2 and R09) or four (M1, R11, R10) replicates of each exclosure type were randomly located within each of the five sites. An infaunal core (6 cm inner diameter) was taken from each experimental unit in May (May 10–16, 2011) and in September (Sept 24–29, 2011), corresponding to 1 month before and 3 months after mangrove removal at site R11. Infaunal cores were processed as described in the Chronosequence section.

To test for changes in infaunal community composition due to treatments and over the course of the experiment, we used permutational analysis of variance (PERMANOVA; Anderson, 2001). Within-site replication allowed us to test for an interaction between Treatment and Site, i.e., whether predator effects differed between sites. In our study system, community richness is relatively low and abundance varies substantially between sampling sites; therefore, we used the modified Gower similarity index with log base 2 so that a single species change in community richness was equivalent to a doubling.
of abundance (Anderson et al., 2006). Prior to multivariate analysis, taxa containing fewer than 15 total individuals (summed across all cores) were removed from the dataset (excluded taxa are indicated in Supplementary Table 2). We used the PERMANOVA model: Infauna - Site + CageTrt + Month + Site × CageTrt + Site × Month + CageTrt × Month + Block(Site × CageTrt) + Site × CageTrt × Month. Since the experimental design involved repeated measures (cores taken in each cage at each time point), cages were treated as blocks. The Block(Site × CageTrt) × 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. Significant multivariate patterns were examined further with univariate PERMANOVA tests. Statistical analyses were performed using the vegan package in R (R Team, 2012; Oksanen et al., 2012) and Primer-E® software (Clarke, 1993).

2.7. Predator community

To compare the density of burrowing predators across sites in May and in September, we set large traps overnight (modified commercial crab traps) for 3–4 nights and set small crab nets during the day for 3–5 days. All traps were baited with skin and bones from two millfish (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 (Mohapatra et al., 2010; Roomgrati and laitim, 1994; Songrak et al., 2010; Sukumaran and Neelakantan, 1997). Scylla serrata was removed from statistical comparisons because of its low catch rate (seven individuals captured across the course of the experiment) and large size (15–25 cm c.w.). We tested whether community composition was independent of site and month using a log-linear analysis. Crab size (individual biomass) and crab density (number of individuals caught per unit effort) and crab biomass-density (biomass of catch per unit effort) were compared across sites in each month using Kruskal–Wallis tests.

3. Results

3.1. Physical environment and grain size

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 of the study sites were along the east side and experienced similar monthly mean temperature, salinity, DO, pH, turbidity and chlorophyll a concentration over the course of the study (Kruskall–Wallis tests; df = 6, p = 0.981, 0.217, 0.979, 0.966, 0.217, and 0.597 respectively). Grain size distribution varied by site with less rubble and more silt/clay in the southern site 0.217, 0.979, 0.966, 0.217, and 0.597 respectively). Grain size distribution varied by site with less rubble and more silt/clay in the southern site.

3.2. Mangrove decomposition rate

The single exponential model of mangrove root decomposition was most parsimonious (R² = 0.37; p > 0.17 for all likelihood ratio tests). Sedimentary mangrove biomass decreased over the chronosequence with decay constant k = 0.36 ± 0.06 × 10⁻³ d⁻¹ and an intercept of 1285 ± 77 g dw m⁻², equivalent to a loss of 12.6% (Chesx = (8.4, 16.7)) per year (Fig. 2).

3.3. Community patterns across a chronosequence of mangrove removal

Total infaunal abundance increased with time since removal with a doubling time every 2.6 years (R² adj = 0.159, F = 15.9, p = 0.001; Fig. 3). Taxon richness, normalized taxon richness, Shannon diversity, and Shannon evenness did not change over the chronosequence.

The abundance of suspension feeders increased with time since removal with a doubling time of 1.7 years (R² adj = 0.257, F1,78 = 28.3, p < 0.001; Fig. 4), and the abundance of omnivores doubled in 2.3 years (R² adj = 0.109, F1,78 = 10.7. p = 0.001; Fig. 4). There were no clear patterns in domicile or mobility groupings over the chronosequence.

Overall, mangrove communities are 61.28% dissimilar from removal sites (Fig. 5), with higher abundances of oligochaetes (contributing 22.19% of the dissimilarity), amphipods (19.33%), and sabellids (10.4%) in the removal sites contributing most to the dissimilarity.

Differences in environmental variables across sites explained 25% of the variance in community composition, with the first three canonical axes of the CCA explaining 20% of the variation (permutation test: p = 0.005; Fig. 5). Sites M1 and M2 were most clearly distinct from each other. M1 was distinguished by the presence of sternaspid polychaetes and was positively associated with salinity and negatively associated with turbidity. M2 was distinguished by the presence of cossurids and was positively associated with temperature and pH. Ostracods distinguished two cores at R07.

3.4. Predator exclusion experiment

The infaunal community differed between sites and over time but not between treatments (Supplementary Fig. 1, PERMANOVA Time: F1,39 = 3.45, p = 0.004; Site: F4,39 = 6.17, p < 0.001; Treatment: F2,39 = 1.06, p = 0.379). Sites differed in the abundance of sabellid polychaetes (Site: F4,39 = 3.49, p = 0.012), amphipod polychaetes (F4,39 = 7.30, p < 0.001), amphipods (F4,39 = 3.53, p = 0.013), and oligochaetes (F4,39 = 9.89, p < 0.001). Sites also differed in the pattern of community change over time (Site × Time: F4,39 = 3.60, p < 0.001). Oligochaetes changed in abundance differently across sites (Site × Time: F4,39 = 2.76, p = 0.043): decreasing at one mangrove site (M2; t = 5.94, p = 0.015) and increasing at the 2011 removal site (R11; t = 2.43, p = 0.037). Opheliids changed differently across sites, as well (Site × Time interaction; F4,39 = 4.37, p = 0.005): decreasing at one mangrove site (M2; t = 2.78, p = 0.036) and increasing in the one-year-old removal site (R10; t = 3.15, p = 0.014). Shifts in amphipod abundance also differed between sites (Site × Time: F4,39 = 5.16, p < 0.001), decreasing at both mangrove sites (M1, W = 112, p = 0.02; M2, W = 65.5, p = 0.02).
3.5 Predator community

The crab community was similar in density, size, and community composition across sites. There was no difference in crab density (individuals caught trap−1 day−1) or crab biomass-density (biomass caught trap−1 day−1) between sites in May (density: $\chi^2_{df=4} = 2.92$, $p = 0.712$; biomass-density: $\chi^2_{df=4} = 5.16$, $p = 0.270$) or in September (density: $\chi^2_{df=4} = 2.39$, $p = 0.792$; biomass-density: $\chi^2_{df=4} = 9.48$, $p = 0.05$). Similarly, there was no difference in crab size between sites in May ($\chi^2_{df=4} = 0.250$, $p = 0.992$) or in September ($\chi^2_{df=4} = 0.670$, $p = 0.954$). Although the crab community changed between months ($\chi^2_{df=3} = 32.7$, $p = 0.001$, N = 151), the crab community was independent of site in both May ($\chi^2_{df=2} = 6.21$, $p = 0.90$, N = 68) and September ($\chi^2_{df=2} = 14.33$, $p = 0.27$, N = 83). The community consisted of Samoan crab (S. serrata, $n_{May} = 1$, $n_{Sept} = 4$), the crenate swimming crab (Thalamita crenata, $n_{May} = 66$, $n_{Sept} = 66$), and two endemic Hawaiian species of swimming crab: the long-eyed swimming crab (Podophthalmus vigil, $n_{May} = 0$, $n_{Sept} = 9$) and the blood-spotted swimming crab (Portunus sanguinolentus, $n_{May} = 1$, $n_{Sept} = 4$).

4. Discussion

4.1. Mangrove decomposition is slow in Hawaiian mangroves

Decomposition rate estimated from this chronosequence was 12.6% ($CI_{95\%} = (8.4, 16.7)$) per year after mangrove removal (Fig. 2, $k = 0.36 \pm 0.06 \times 10^{-3} d^{-1}$), which overlaps with previously reported estimates for Oahu (12–36% per year, Sweetman et al., 2010). Since decomposition data is largely unavailable for the invaded range of R. mangle in Hawai‘i, we use native mangroves as a point of comparison, and present the following results as a baseline with which to compare decomposition in other invasive stands. In native mangrove forests, root decomposition was much higher at 52% per year in Belize ($k = 1.9 \pm 0.38 \times 10^{-3} d^{-1}$) (Middleton and McKee, 2007; estimated from their Supplementary Fig. 1 using an exponential model) and 38% and 65% at two sites in the Everglades ($k = 1.3 \pm 0.48 \times 10^{-3} d^{-1}$ to $2.9 \pm 0.15 \times 10^{-3} d^{-1}$, Poret et al., 2007). This study suggests that mangrove decomposition in its introduced range in O‘ahu is much slower than in its native range and that habitat recovery following mangrove removal may take decades, as also noted by Sweetman et al. (2010).

The difference in mangrove decomposition rate between O‘ahu and the native range may be due to differences in flow conditions, methodology, effects of mangrove removal, and/or macrofaunal diversity. First, flow conditions affect decomposition rates and may be modified by the fishpond walls. However, flow rates measured within the mangrove removal area (mean current magnitude 0.06 m/s over 4 days; Ruttenberg et al. 2013) are comparable to bulk flow rates through native mangrove forests (~0.2 m/s; Furukawa et al., 1997; neither Middleton and McKee (2001) nor Poret et al. (2007) report flow rates for comparison). Second, Middleton and McKee (2001) and Poret et al. (2007) both used litter bags to experimentally measure decay rates, while this study and Sweetman et al. (2010) estimated decomposition from in situ measurements of root biomass. Litter bag experiments are likely to overestimate decomposition rates because root material is dried before burial, which causes tannins and phenols to leach out more rapidly than they would in situ, hastening microbial colonization and decomposition (Bárlocher, 1997). Third, we measured decomposition rate at mangrove removal sites, where
mangrove roots are no longer oxygenating the sediments. Sediment chemistry at the one-year removal (R10) had shallower O₂ penetration depth and higher sulfide concentrations compared to the intact mangrove site (M1) (Ruttenberg et al. 2013). Finally, 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) and can oxygenate the sediments through bioturbation.

 Decomposition rate 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). In addition, 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). However, unlike in its native range, macrofauna in Hawai‘i do not decompose mangrove-derived carbon (Demopoulos et al., 2007), and bacteria dominate short-term (2d) C processing in the leaf and root decomposition in native mangroves (e.g., Nordhaus and Wolff, 2007) and can oxygenate the sediments through bioturbation.

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 Differences in total infaunal abundance between mangrove and removal sites (Fig. 3), are similar in direction but differ in magnitude than prior studies on O‘ahu. Total abundances found at the northernmost removal sites (Fig. 3), are similar in direction but differ in magnitude than prior studies on O‘ahu. Total abundances found at the northernmost removal sites (Fig. 3), while Sweetman et al. (2010) found an 8-fold increase in the first two years following removal (Fig. 3), while Sweetman et al. (2010) found an 8-fold increase in the first two years following removal (Fig. 3), they were shifted in less dominant groups between mangrove and removal sites (Supplementary Table 1) similar to prior studies. Sites with intact mangrove were dominated by amphipods (39% of abundance), oligochaetes (29%), nematodes (6%), and sub-surface deposit feeding oscurid polychaetes (6%) while removal sites contained oligochaetes (46%), amphipods (26%), sabellid polychaetes (9%), and ostracods (6%). Sweetman et al. (2010) also found sub-surface deposit feeders to be numerically dominant at intact mangrove sites, while removal sites and pre-invasion areas in Kāne‘ohe Bay had a higher abundance of suspension and surface-feeders (e.g., corophiids, sabellids, and spionids). 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 (Demopoulos and Smith, 2010; Ellis et al., 2004) and is consistent with previous studies of native and invasive mangrove forests (Demopoulos and Smith, 2010). After oligochaetes and amphipods, suspension feeding sabellid polychaetes contributed the most to dissimilarity between mangrove and removal sites (Supplementary Table 1). Shifts in suspension feeder abundance have been attributed to changes in water velocity (LaBarbera, 1984), which is much lower in mangrove habitats because of prop-root structure, and the associated increase in sedimentation.

 4.3. Community recovery after mangrove removal

 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 (Torres-Pratts and Schizas, 2007), 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). When mangroves decompose, total amounts of tannins and phenolic compounds inside the tissues decrease, potentially rendering mangrove roots and leaves more bioavailable (Alongi, 2009). An increase in microbial production may explain the gradual increase in infaunal density after removal, with older sites containing higher abundances of infauna than more recent removals (Fig. 3).

 The increase in total abundance (Fig. 3) was accompanied by a decrease in sub-surface deposit feeders, which persisted over time. A rapid shift to “post-removal” conditions is also apparent from the MDS plot of all sites in September (Supplementary Fig. 1): The removal site (R11), which was removed just three months before the collection of September cores, already appears similar to the 2–4 year removal
sites. Rapid post-removal shifts in community structure and total infaunal abundance coincide with rapid changes in short-term C-processing found at 2-year removal sites 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 sandflat controls in Kāne‘ohe Bay surveyed by Sweetman et al. (2010), suggesting that they have not yet reached pre-invasion density.

4.4. Top-down processes do not regulate infaunal communities in Hawaiian mangrove or mangrove removal habitats

Changes in predation pressure or bioturbation rate are unlikely to account for the increase in infaunal abundance along the chronosequence: crab density, biomass, and community structure were similar across sites. The fishpond hosts a diversity of introduced predators (Nakahara, 2007), including the portunids T. crenata and S. serrata, as well as two patchily distributed native portunid crabs, P. vigil and P. sanguinolentus. The range of the most abundant species, T. crenata, was smaller than the length of each study site, so differences in abundance across sites were not due to differences in short-term aggregation. The taxa responsible for extensive bioturbation in native mangroves (Uca spp. and members of the family Sesarmidae) are absent from Hawaiian mangroves (Demopoulos, 2004), while T. crenata and S. serrata, the most abundant and largest crabs at our sites respectively, inhabit shallow burrows (Williams, 1994). Further, total burrow density is much lower in mangroves on O‘ahu than in native mangroves (Demopoulos, 2004; Kristensen, 2008) so burrowing is unlikely to have the dramatic impacts on sediment chemistry seen in native mangrove habitats.

Burrowing predators did not exert top-down control (Supplementary Fig. 1): there was no effect of predator exclusion on infaunal communities. This was a surprise, because similar experiments in native mangrove have demonstrated negative effects of epifauna (sesarmid, graspid, oocypodid and hermit crabs, as well as snails) on meiofaunal (Schriijvers et al., 1995) and macrofaunal abundance (Schriijvers et al., 1998) with similar levels of replication (n = 2, Schriijvers et al., 1995, 1998; n = 4, Kon et al., 2009). Additionally, a power analysis of log-transformed total abundances from this study shows that a doubling of sample size would be necessary to detect a difference (α = 0.05) between cage treatments in mangrove sites. Additional cage replicates at the removal sites would not substantially increase the power.

The low power calculated for this study indicates that predator effects, if present, were overwhelmed by spatial variation. Instead of strong top-down control, we found communities that differed between sites and community shifts from May to September that depended on strong top-down control, we found communities that differed between mangrove sites. Additional cage replicates at the removal sites would be useful 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 sandflat controls in Kāne‘ohe Bay surveyed by Sweetman et al. (2010), suggesting that they have not yet reached pre-invasion density.

Mangrove foodwebs in Hawai‘i function differently than mangroves in their native range. Demopoulos et al. (2007) demonstrated that mangrove-derived carbon is not taken up by macrofauna in Hawai‘i, and, in this study, we see no evidence of top-down control on infaunal communities as is seen in native mangrove (Kon et al., 2009; Schriijvers et al., 1998). Instead, we see strong evidence of habitat heterogeneity, even at the sub-meter scale.

Invasive species eradication can have dramatic effects on invaded ecosystems, and post-removal assessments have been recommended as a way to monitor the effect of eradication. This study shows that changes in community composition occur gradually after an initial rapid transformation from living to decomposing mangrove. However, the slow rate of mangrove root decomposition and the lack of deep burrowing predators in Hawai‘i suggest that a return to pre-invasion conditions may take decades without additional intervention.

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