Macrofaunal Invertebrate Communities on Hawaii's Shallow Coral-Reef Flats: Changes Associated with the Removal of an Invasive Alien Alga

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Honolulu, Hawaii
October 2011

COVER

An oblique aerial photograph of the Kuli‘ou‘ou reef flat of Maunalua Bay, O‘ahu, showing areas cleared of the alien alga *Avrainvillea amadelpha* as of June 11, 2010. Photo courtesy of The Nature Conservancy.

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Prepared for The Nature Conservancy

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Bishop Museum
Honolulu, Hawaii 96817, USA

Bishop Museum Technical Report 54

Honolulu, Hawaii
October 2011

Bishop Museum Press
1525 Bernice Street
Honolulu, Hawai‘i

ISSN 1085-455X

Contribution No. 2011-021 to the Hawaii Biological Survey

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EXECUTIVE SUMMARY

In an attempt to restore reef-flat habitat, the community organization Mālama Maunalua along with The Nature Conservancy Hawaii Chapter directed the removal of an invasive alien alga, *Avrainvillea amadelpha* or mudweed, from more than 9 hectares of the Kuli'ou'ou reef flats of Maunalua Bay, O'ahu, Hawai'i. We examined the resulting macrofaunal invertebrate community to evaluate the success of habitat restoration and to suggest how any changes to the invertebrate community might impact coral reef fishes.

The mudweed removal schedule was structured such that replicate sites with varying times since clearance (3, 6, and 9 months) were created, thus providing the opportunity for a space-for-time study design. The invertebrate communities in these cleared areas were compared to mudweed and native (seagrass, algae, and sand) habitats. We considered evidence of restoration success to be a shift away from the community composition found in mudweed, and a shift toward the community composition of one of the native reference habitats.

Mean species richness in plots cleared of mudweed was indistinguishable from any native habitat. Classification and ordination indicate these cleared plots differed from the community composition of the mudweed habitat. The same analyses suggest mudweed removal shifts communities toward those found in sand and seagrass. The dominant species in mudweed-removal plots were most similar to those found in sand. There were fewer nonindigenous species in plots cleared plots relative to the mudweed habitat. These results suggest mudweed removal was, in the short term, a successful habitat restoration technique. Whether mudweed removal is effective over the long run will require a longer-term study.

Total invertebrate abundance and, in particular, peracarid abundance declines significantly with the removal of mudweed. Because mudweed invertebrate communities appear similar to those in native algae, this decrease may result in smaller populations of fishes that feed in algae-dominated habitats. On the other hand, the abundances of invertebrates associated with mudweed-removal treatments are, in general, indistinguishable from any native habitat. From a food-availability perspective, mudweed-removal plots may be able to support fish populations similar to those found in Hawai'i's native reef-flat habitat.

INTRODUCTION

Background

Nonindigenous marine species introduced into coastal ecosystems can monopolize energy resources, reduce populations of endemic species, and be disease vectors (Coles *et al*. 2004). Macroalgae are especially worrying nonindegenous marine species because they can monopolize space, alter the physical structure of ecosystems, and change foodwebs (Schaffelke *et al*. 2006).

The green alga *Avrainvillea amadelpha*, or mudweed, is a bryopsidalean alga. Bryopsidaleans are distinguished from other algae by their unusual ability to root in sand (Peyton 2009), and when occupying sedimentary habitats, the majority of *A. amadelpha* biomass is subsurface (Smith *et al*. 2002). It is Hawai‘i’s only invasive macroalga that anchors itself both on solid reef and in sediment and, like other bryopsidaleans, is predicted to have an exceptional ability to invade a broad range of habitats (Peyton 2009). These algae are common members of the understory in seagrass meadows, are the earliest colonizers of newly opened space, and some have been implicated in the loss of seagrasses in the Mediterranean, Hawaii and the Bahamas (Peyton 2009). In Hawaii, *Avrainvillea amadelpha* is invasive and capable of forming meadows or large mounds greater than 30 m in diameter (Peyton 2009). It is suspected of displacing the native seagrass *Halophila hawaiiana* (Eldredge & Smith 2001, Smith *et al*. 2002)

Avrainvillea amadelpha, was first reported from the shallow waters of Hawaii in 1981 (Brostoff 1989). In 1985, *A. amadelpha* was collected at 10-m depth from rock and sand substrates in Maunalua Bay, O‘ahu. By 1987, the alga was collected from the bay’s intertidal zone (Brostoff 1989). In 2003, it had reached up to 100% cover in some areas, forming extensive mounds more than 30 m in diameter at the margins of *Halophila hawaiiana* meadows (Peyton 2009). Currently, *A. amadelpha* can exists in persistent shallow-water populations on tidal benches, coral reefs and seagrass meadows (Peyton 2009). It is now one of the five most-common alien algae in Hawai‘i (Smith *et al*. 2002).

Peyton (2009) reports that prior to the establishment of *A. amadelpha* (*i.e.*, late 1960s to at least 1976), long, narrow *Halophila hawaiiana* meadows were found parallel to and 8 – 100 m from the sandy beach at Kuli`ou`ou, Maunalua Bay. Conklin (2009) summarized later floral surveys of Maunalua Bay as follows: In 1973 the dominant macroscopic plants on the reef flat were *Halimeda discoidea* on sedimentary patches and *Acanthophora spicifera*, *H. discoidea*, *Sargassum* sp., and *Ulva reticulata* on solid substrate. In 1984 (just prior to the first report of *A. amadelpha* in Maunalua Bay), the seagrass, *Halophila hawaiiana*, still occurred in a series of dense patches on mudflats and sand along the shore and inside the reef.

The replacement of seagrass by *A. amadelpha* may be detrimental to the reef-flat ecosystem. Sediments may become more anoxic, species richness may decrease, and the abundance of economically valuable species may decrease (Conklin 2009).

Increased attention to invasive species and concerns about their potential impact on the native ecosystem led to several community-outreach projects focusing on large-scale removal of *Avrainvillea amadelpha* as a means of habitat restoration in Maunalua Bay. These projects focused on the manual removal of *Avrainvillea amadelpha*, with the goal of restoring seagrass beds and native algal meadows (Conklin 2009). However, removal of the alga also changes hydrodynamics at the sediment-water interface such that sediments are altered, often such that little or no sediment remains on the consolidated reef substraum (Conkin 2009).

The near-term goals of habitat restoration can generally be described as providing habitat for species likely to be found in an area by returning an ecosystem back to its former structure and/or function as suggested by historical information or the state of nearby unimpacted sites (Miller & Hobbs 2007). The usual longer-term goal of habitat restoration is to prevent additional loss of habitat (Grayson *et al*. 1999). Evidence of near-term success in restoration efforts is usually an "acceptably small" difference between the structure and/or function of the restored system and its reference system (*e.g.*, McCoy & Mushinsky 2002). Its urban location creates difficulty in evaluating the longer-term goal of preventing habitat loss. Ecosystems in urban areas are often subject to ongoing disturbances, and it can be difficult to decide whether restoration efforts have been successful in the long run (*e.g.*, Grayson *et al*. 1999).

Purpose

The purpose of this study is to evaluate the near-term effectiveness of habitat restoration efforts at Maunalua Bay. This evaluation will be accomplished by examining invertebrates sampled with cores (*i.e.*, sediment-associated communities). Our focus is on macrofauna, or organisms retained on a 500 μm sieve. Because these invertebrates are likely fish prey, we will also suggest how any mudweed-removal-associated changes in invertebrate community structure is likely to impact fishes.

We will consider the following as criteria for successful restoration:

1) The invertebrate community structure of manipulated plots differs from reference mudweed plots.
2) The invertebrate community structure of manipulated plots is similar to that of reference plots not impacted by mudweed.
3) Fewer introduced species in manipulated than in reference mudweed plots.

Evidence in favor of the first two criteria will be diversity indices, community classification, and community ordination indicating manipulated plots are dissimilar to reference mudweed plots but similar to plots not impacted by mudweed. For community ordination we would expect manipulated plots to be grouped with reference plots unimpacted by mudweed, and unmanipulated mudweed plots to be excluded from this group. Evidence in favor of the last criterion will be lower richness and abundance of introduced species in manipulated plots relative to reference mudweed plots.

METHODS

Study Area

Maunalua Bay is located on the southeast shore of the island of O‘ahu, Hawai‘i. A shallow fringing reef extends approximately 1 km from the shoreline to the reef crest and gradually drops to a broad shelf reaching depths of approximately 18 m. The reef is principally consolidated-carbonate substrate and patches of loose sediment (Conklin 2009). This reef offers sufficient protection for assemblages of seagrasses (*Halophila hawaiiana* and *H. decipiens*), native macroalgae (*Halimeda discoidea*, *Spyridia filamentosa*, *Gracilaria coronopifolia*), and monospecific stands of *Avrainvillea amadelpha*. The macrophytes are anchored in or on soft sediments, sediment-covered carbonate and exposed carbonate (Peyton 2009).

Avrainvillea amadelpha was removed from more than 9 hectares of the Kuli‘ou‘ou reef flats (21.28° N, 157.73° W) of Maunalua Bay over an approximately one-year period. The removal schedule was structured such that replicate sites with varying times since clearance (3, 6, and 9 months) were created, thus providing the opportunity for a space-for-time study design.

Sampling

Invertebrates

Invertebrate samples were collected from four reference habitats: mudweed, native algae, seagrass, and unvegetated sand. Samples were also collected from 3 mudweed-removal treatments: 3-, 6-, and 9-months post-removal.

For each habitat/treatment (except sand), eight random sampling points were selected from a benthic-habitat map. For sand, field conditions did not correspond well enough with the benthic-habitat map to allow random point selection. Samples from sand were haphazardly collected from patches located in the field. In the field, after a GPS unit indicated we had arrived at a sampling site (or after we encountered a sand patch) we used a 10.16-cm-diameter core to collect a single invertebrate sample from the nearest point with intended bottom cover. The core was inserted up to 10 cm into the substrate. Core contents were washed over a 500 µm sieve, all material retained on the sieve (including vegetation) was transferred to jars, and relaxants (ethanol and menthol) were added. When invertebrates relaxed, jar contents were fixed in formalin for 24 hr. In the laboratory, formalin was replaced with water. After 24 hr in water, samples were preserved in 70% ethanol.

Sediments

Up to 50 mm^3 of sediment was collected near invertebrate cores with a 50 cc syringe from which the needle-attachment-end was removed. These samples were transferred to plastic bags and frozen.

Sample Processing

Vegetation

All vegetation was removed from preserved invertebrate-core samples. This was damp-weighed after blotting with absorbent material. Vegetation biomass estimates are presented as total vegetation weight per core.

Invertebrates

Invertebrates recovered from preserved core samples were rough sorted into major taxonomic groups (*e.g.*, platyhelminths, polychaetes, sipunculids, hemichordates, peracarids, decapods, mollusks) and stored in vials until identified. Better-known taxa (*i.e.*, polychaetes, mollusks, and crustaceans) were identified using the following aids to identification: Bailey-Brock 1987 (polychates); Coovert 1987, DuShane 1988, Hershler 2001, Hickman & McLean 1990, Houbrick 1993, Kay 1979, Knudsen 1993, Philipps 1977, Ponder 1985, Sleurs 1987, Sleurs 1993, Sleurs & Preece 1994, Yamamoto & Tagawa 2000; and the Pittman & Fiene website www.seaslugsofhawaii.com (molluscs); Barnard 1970, Barnard 1971 (amphipods); Miller 1941, Miller & Menzies 1952 (isopods); Harrison & Ellis 1991 (sphaeromatid isopods); Miller 1940 (tanaids); Banner 1953 (alpheids); Holthius 1993 (caridean shrimp). We follow the nomenclature of the above references for polychates and molluscs, whereas the nomenclature of the Integrated Taxonomic Information System, or ITIS, (http://www.itis.gov) is used for crustaceans. The lesser-known invertebrates (*e.g.*, sipunculids, hemicordates) were identified to higher taxa only. All invertebrates were counted after identification. Abundance estimates are presented as number of individuals per core.

We used Carlton and Eldredge (2009) to compile a list of nonindigenous species. These include demonstrably introduced (exotic) species and cryptogenic species. The latter are species that cannot reliably be assigned as either native or exotic (Carlton 1996).

Sediments

Sediment samples were dried at 80º C for at least 24 hr. Dried samples were seived through the following series: 355, 246, 125, 63, and 45 µm. Sediment retained on each seive and in the bottom pan were weighed.

Data Analyses

Descriptive Indices

Common diversity indices were calculated for each habitat/treatment. These include species richness, Shannon Diversity Index (H), and Simpson's Index (D).

$$H = -\sum_{i=1}^{n} p_i \ln p_i$$

and

$$D = \sum_{i=1}^{n} p_i^2$$

where p_i equals the proportion of the total number of individuals represented by the i^{th} species in each habitat.

Univariate Analyses

Analysis of variance was used to test for differences in richness and abundance among habitats/treatments. When a difference was detected, Tukey's pairwise comparison was used to determine which groups differed.

Multivariate Analyses

Ordination was performed using principal components analysis (PCA) of a correlation matrix of species abundances. Best-subsets regression analysis was used to explore possible relationships between environmental variables and the location of invertebrate samples along principal components axes. Classification analysis was based on single (*i.e.*, minimum distance or "nearest neighbor") linkages suggested by correlation distance measures for cumulative abundance estimates for each habitat/treatment.

RESULTS

Community-Level Comparisons

A total 147 taxa were identified from 56 samples (8 in each of 7 habitats/treatments). We sampled two algal habitats: we distinguish between the using the common name, mudweed, for the invasive alga *Avrainvillea amadelpha*, and the Hawaiian name, *limu*, for native algae. Sampling coordinates and dates, along with habitat characteristics such as vegetation biomass and sediment weights are presented in Appendix I. Invertebrate identifications and abundance in each sample are provided in Appendix II. The following results are presented as abundance per core.

Values of diversity indices are presented in Table 1. In all cases, absolute values indicate lower diversity in post-mudweed-removal treatments than in the mudweed habitat as well as all native habitats not impacted by mudweed. Analysis of variance indicates a significant difference in mean species richness among habitats/treatments. Figure 1 shows the results of Tukey's pairwise comparison. The only significant difference is a decrease in species richness from the mudweed habitat (18.25±6.73 species) to the 9-month post-mudweed-removal treatment (9.13±4.73 species).

Table 1. Diversity indices for each habitat/treatment.

	Mud-weed	Limu	Grass	Sand	3 month	6 month	9 month
Richness	58	66	54	62	46	45	35
Diversity (H)	2.82	3.30	2.98	3.45	2.60	2.92	2.41
Evenness (D)	0.10	0.06	0.09	0.06	0.15	0.11	0.19

Table 2 lists the ten most-abundant taxa (the majority as species) in each habitat/treatment. All habitats/treatments share the isopod *Apseudes tropicalis*, the gammaridean amphipod *Eriopisella upolu*, and the gastropod *Cerithium zebrum*. The top-ten-species composition of the mudweed habitat appears most similar to the native limu habitat; they share seven species. The removal treatments appear similar; they share a total of five top-ten species. Of these, only the tanaid, *Leptochelia dubia*, is not shared with the mudweed habitat. On the other hand, the gammaridean amphipods *Mallacoota insignis* and *Gammarella amikai*, the alpheid shrimp *Alpheus lobidens*, and the fouling polychate *Phyllochaetopterus verrilli* are abundant in mudweed but not in any of the removal treatments. Among the removal treatments, 3-month and 9-month appear most similar. In addition to the five species shared among all removal treatments, they share the gastropod *Ittibittium parcum* between them and with all native habitats (but not mudweed). They also uniquely share the gammaridean amphipod *Tethygenia pacifica*. The 3- and 9-month treatments may be most similar to the sand habitat. All three also share the gastropod *Leptothyra rubricincta*. The 6-month removal treatment differs from the other removal treatment in the persistence of the isopod *Carpias algicola* as one of the ten most-abundant species. This isopod is also abundant in the mudweed and native algae habitats.

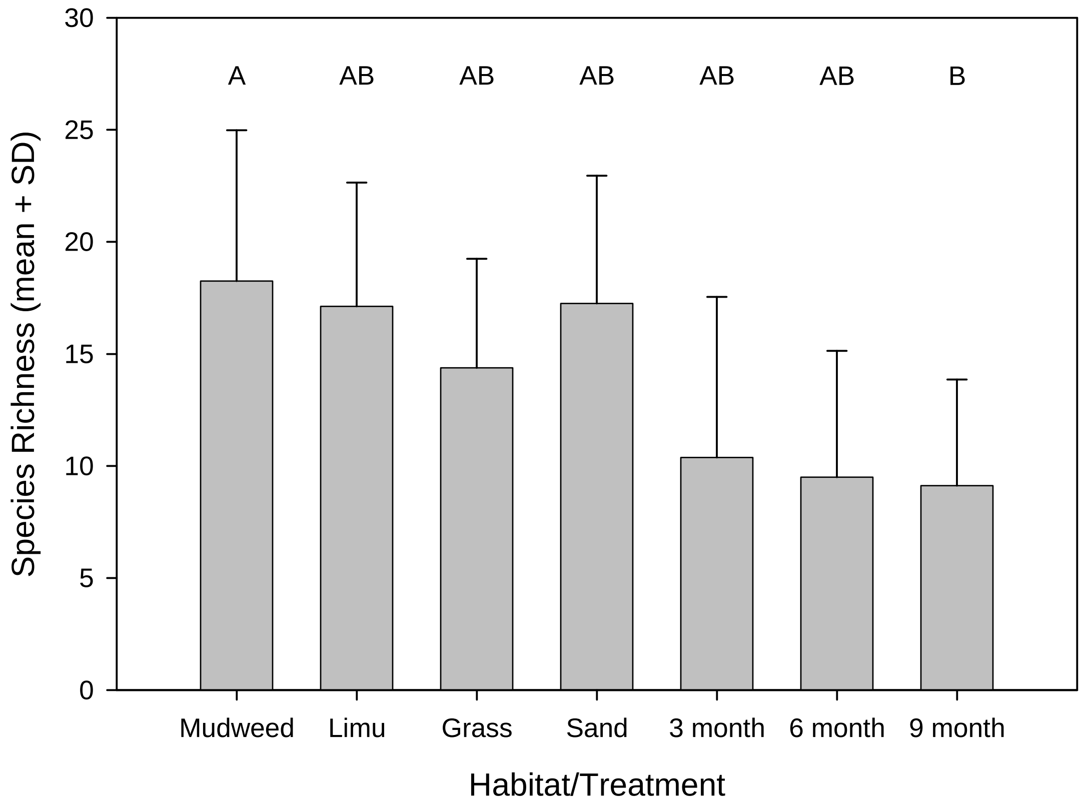

Figure 1. Mean species richness in each habitat/treatment. Treatments/habitats sharing the same letter (top) are not significantly different.

Table 3 lists the minimum subset of species required to represent at least 50% of total invertebrate abundance for each habitat/treatment. No species are shared amongst these subsets. The mudweed, native algae, and 6-month-removal treatments are dominated by peracarid crustaceans. All of them share the isopod *Apseudes tropicalis* and the gammaridean amphipod *Bemlos pualani*. The seagrass and sand habitats are dominated by a combination of peracarid crustaceans, molluscs, and polychaetes. They share the isopod *Apseudes tropicalis*, the gammaridean amphipod *Eriopisella upolu*, and the gastropod *Cerithium zebrum*. The 3- and 9-month-removal treatments are dominated by a mixture of pericarid crustaceans and molluscs. They share the gammaridean amphipod *Eriopisella upolu*, and the gastropod *Cerithium zebrum* (which are also members of the seagrass and sand subsets).

Table 2. The ten most abundant taxa in each habitat/treatment. Species names in bold font are shared among all habitats/treatments.

Mudweed	Limu	Grass	Sand	3 month	6 month	9 month
Bemlos pualani	*Mallacoota insignis*	***Apseudes tropicalis***	***Cerithium zebrum***	***Eriopisella upolu***	***Eriopisella upolu***	***Eriopisella upolu***
Apseudes tropicalis	*Bemlos pualani*	***Eriopisella upolu***	***Eriopisella upolu***	*Leptochelia dubia*	*Bemlos pualani*	***Cerithium zebrum***
Mallacoota insignis	*Ampithoe kaneohe*	*Mesochaetopterus sagittarius*	***Apseudes tropicalis***	***Cerithium zebrum***	*Leptochelia dubia*	***Apseudes tropicalis***
Eriopisella upolu	***Apseudes tropicalis***	***Cerithium zebrum***	*Tricolia variabilis*	*Ittibittium parcum*	***Apseudes tropicalis***	*Mesochaetopterus sagittarius*
Carpias algicola	*Carpias algicola*	*Phytochaetopterus verrilli*	*Phyllochaetopterus socialis*	*Leptothyra rubricincta*	***Cerithium zebrum***	*Ittibittium parcum*
Gammarella amikai	*Melita pahuwai*	SYLLIDAE 1	*Ittibittium parcum*	***Apseudes tropicalis***	*Bemlos intermedius*	*Bemlos pualani*
Alpheus lobidens	***Eriopisella upolu***	*Smaragdia bryanae*	*Smaragdia bryanae*	*Synaptocochlea concinna*	*Ampithoe kaneohe*	*Leptothyra rubricincta*
Phyllochaetopterus verrilli	***Cerithium zebrum***	SPIONIDAE 1	*Leptothyra rubricincta*	*Antisabia foliacea*	*Carpias algicola*	*Leptochelia dubia*
Cerithium zebrum	*Phyllochaetopterus verrilli*	HEMICHORDATA	*Pilumnus* sp.	*Bemlos pualani*	*Cerithium boeticum*	*Tricolia variabilis*
Mesochaetopterus sagittarius	*Ittibittium parcum*	*Ittibittium parcum*	SIPUNCULA	*Tethygeneia pacifica*	SYLLIDAE 1	*Tethygenia pacifica* *

* tied with *Pilumnus* sp., *Alpheus rapax*, Cumacea

Table 3. Minimum set of species representing at least 50% abundance.

Mudweed	Limu	Grass	Sand	3 month	6 month	9 month
Bemlos pualani *Apseudes tropicalis* *Mallacoota insignis* *Eriopisella upolu*	*Mallacoota insignis* *Bemlos pualani* *Ampithoe kaneohe* *Apseudes tropicalis* *Carpias algicola* *Melita pahuwai*	*Apseudes tropicalis* *Eriopisella upolu* *Mesochaetopterus sagittarius* *Cerithium zebrum*	*Cerithium zebrum* *Eriopisella upolu* *Apseudes tropicalis* *Tricolia variabilis* *Phyllochaetopterus socialis* *Ittibittium parcum* *Smaragdia bryanae* *Leptothyra rubricincta*	*Eriopisella upolu* *Leptochelia dubia* *Cerithium zebrum*	*Eriopisella upolu* *Bemlos pualani* *Leptochelia dubia* *Apseudes tropicalis*	*Eriopisella upolu* *Cerithium zebrum*
60.3%	54.3%	52.8%	51.3%	58.9%	54.2%	52.7%

Figure 2 shows the distribution of samples in ordination space. No well-defined groups are obvious in the scatterplot, however the mudweed and native algae samples tend toward the lower left, whereas the removal treatments tend toward the upper right.

Best-subsets regression analysis was used to attempt to identify environmental variables that may influence sample position along either ordination axis. We considered vegetation weight, latitude (a proxy for distance from shoreline and/or depth), longitude (a proxy for longshore position), total and fractional sediment weight, mean sediment size, and up to three-way-interaction terms. None of these demonstrated a useful relationship with PCA axis 1. For axis 2, only vegetation weight demonstrated a somewhat explanatory relationship. However, with an r^2 of only 0.453, vegetation weight does not appear to be a particularly strong influence on axis 2.

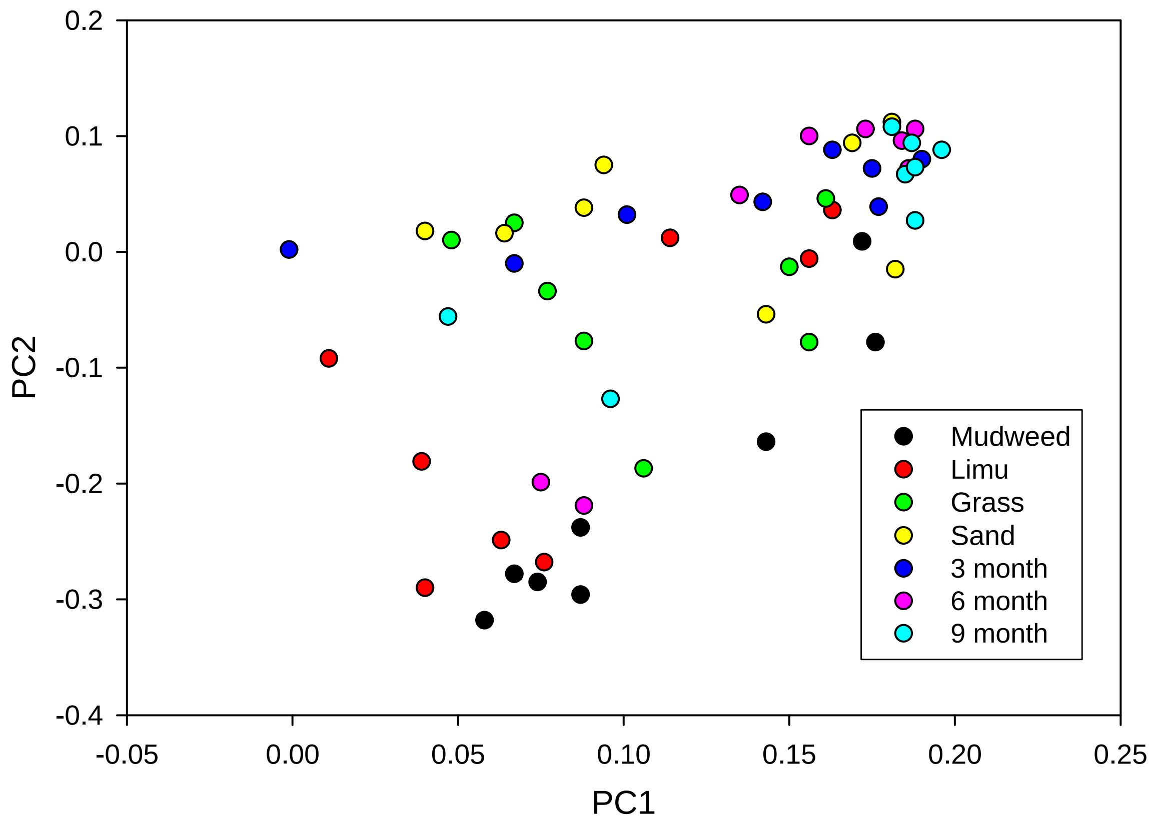

Figure 2. An ordination plot of samples based on invertebrate species abundance.

Given the lack of obvious groupings in sample-level PCA ordination, a habitat/treatment-level analysis was performed (using cumulative species abundance data). The results are shown in Figure 3; habitats/treatments are grouped similarly to the suggestions of less-formal examinations of the taxonomic composition. That is, mudweed and native algae are positioned near one another, and the removal treatments are positioned far from mudweed but in close relation to one another. The removal treatments are positioned most closely to sand habitat, suggesting their community compositions are most similar. However the removal treatments are located at the extreme right of the ordination plot, suggesting that their community composition is unique, rather than representing a transition state between two or more habitats.

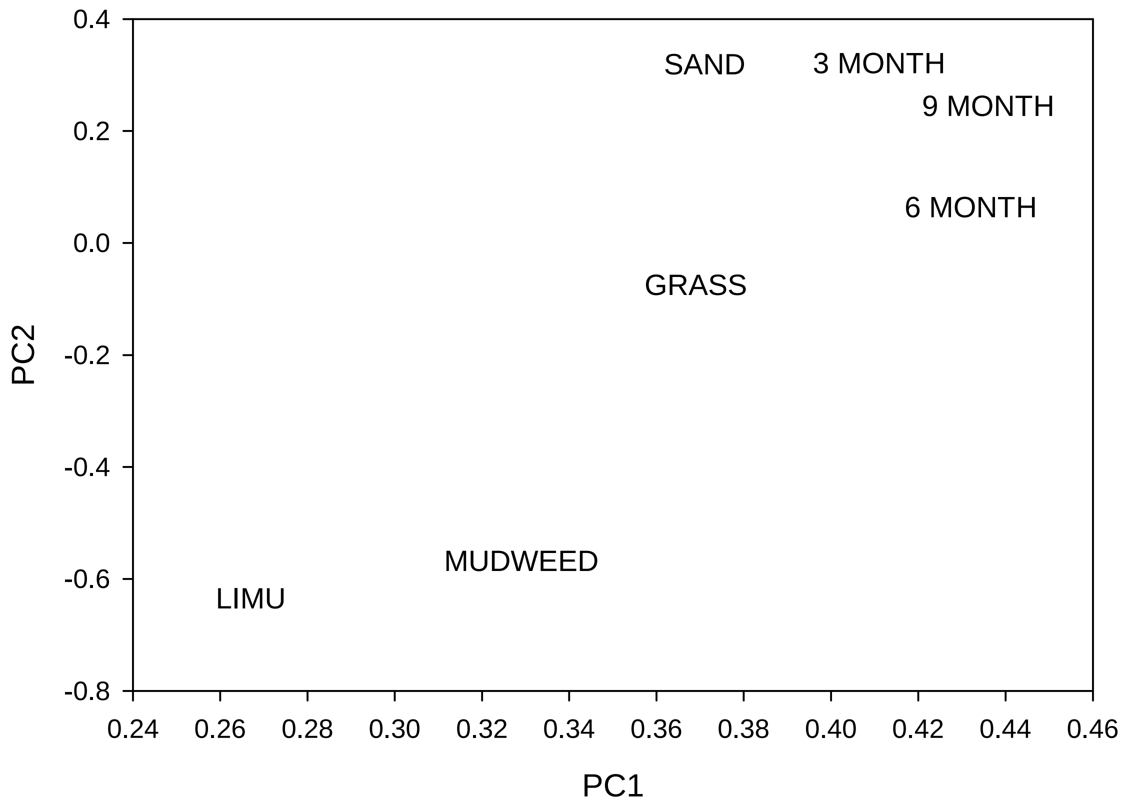

Figure 3. Habitat/treatment-level ordination analysis.

The habitat/treatment community similarities suggested by ordination analysis are supported by classification analysis. Mudweed and native algae form a group separated from all other habitats/treatments. Of all habitats/treatments, the removal treatments are most similar to one another (and therefore least similar to mudweed). The removal treatments appear most similar to the sand habitat (Figure 4).

Nonindigenous Species

A total nine nonindigenous taxa (introduced or cryptogenic) were identified during this study. Table 4 shows presence/absence for each taxon in each habitat/treatment. The seagrass habitat had the most nonindigenous species (6), followed by mudweed with five, and sand with four. The 3- and 9-month post-mudweed-removal treatments each had 3 non-indigenous species, whereas the 6-month treatment had two. The native algae habitat had the fewest non-indigenous species (1).

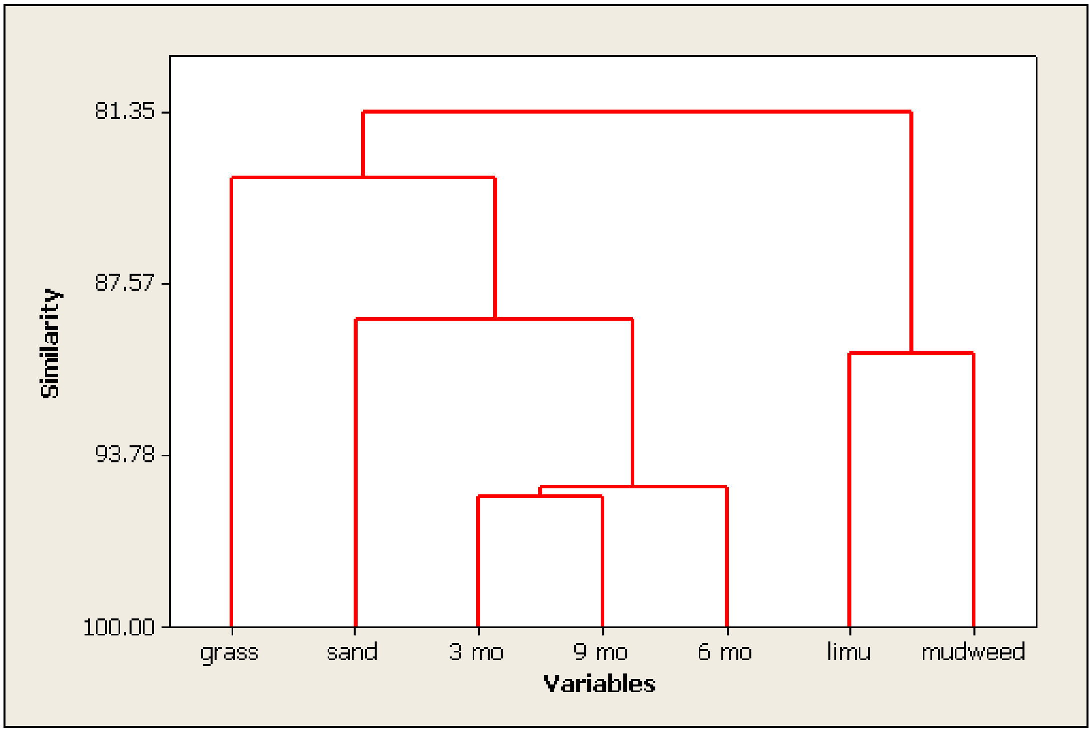

Figure 4. Cluster analysis of habitats/treatments.

Table 4. Non-indigenous species present in each habitat.

Taxon	Mud-weed	Limu	Grass	Sand	3 month	6 month	9 month
Neanthes arenaceodonta	X		X	X	X		
Neanthes succinea	X		X				
Neodexiospira foraminosa	X						
Crepidula aculeata				X			
Melanoides turberculata			X				
Erichthonius brasiliensis			X			X	
Grandidieralla makena	X		X	X	X		X
Leptochelia dubia	X	X	X	X	X	X	X
CUMACEA*							X

* Cumaceans were not identified to species, however Carlton & Eldredge (2009) report that cumaceans were unknown in Hawai‘i prior to 1996 and suggest that all cumacea are introduced.

Table 5 presents mean absolute values of non-indigenous species richness and abundance, as well as the percentage of total richness and abundance represented by non-indigenous species. Analysis of variance results indicate there is no significant difference in the mean number of non-indigenous species among habitats/treatments. For the other metrics (abundance, relative abundance, and relative species richness) results of analysis of variance did indicate a significant difference among habitats/treatments. Figures 5 – 7 show the results of Tukey's pairwise comparisons. In general, the 3-month post-mudweed-removal treatment had the highest value for all three metrics. However, the 6- and 9-month post-mudweed-removal treatments did not differ from any of the native habitats or from the mudweed control habitat.

Patterns of non-indigenous species abundance appear to be driven by the abundance of *Leptochelia dubia* (compare Figures 6 and 8). This tanaid is cryptogenic (not demonstrably indigenous or introduced), thus abundances of non-indigenous species may be grossly overestimated.

Abundances of Higher Taxa

At the gross taxonomic level, most habitats/treatments are dominated by crustaceans (primarily peracarids), as shown in Figure 9. The exception is the sand habitat, which is dominated by molluscs. The seagrass habitat, which is dominated by crustaceans, has the highest percentage of polychaete annelids. Post-mudweed-removal treatments are dominated by crustaceans and, in the 3-month and 9-month post-mudweed-removal treatments, have higher proportions of molluscs than are seen in the non-sand habitats. Table 6 presents the mean abundance of all invertebrates, and select higher taxa, by habitat/treatment. Results of analysis of variance indicate significant differences among habitats/treatments for all taxa. Figures 10 – 14 show results of Tukey's pairwise comparisons. Total invertebrate abundance and, in particular, peracarid and decapod abundances decline significantly with the removal of mudweed. However, the abundances of invertebrates associated with mudweed-removal treatments are, in general, indistinguishable from any native habitat.

Table 5. Nonindigenous species (NIS) richness and abundance in absolute and relative (to total invertebrates) values (mean ± standard deviation).

Habitat/Treatment	NIS richness	% total richness	NIS abundance	% total abundance
Mudweed	0.625 ± 0.916	2.60 ± 3.89	1.000 ± 1.604	1.03 ± 1.63
Limu	0.125 ± 0.354	1.14 ± 3.21	0.125 ± 0.354	0.74 ± 2.08
Grass	1.125 ± 0.991	8.05 ± 6.84	1.375 ± 1.188	4.65 ± 4.83
Sand	1.125 ± 0.835	6.53 ± 6.21	1.750 ± 1.389	6.79 ± 8.67
3 month	1.250 ± 0.463	19.69 ± 15.39	6.125 ± 6.151	27.09 ± 22.14
6 month	0.625 ± 0.744	5.33 ± 6.63	2.125 ± 3.137	6.68 ± 9.14
9 month	0.625 ± 0.744	6.46 ± 7.67	1.250 ± 1.581	4.98 ± 9.14

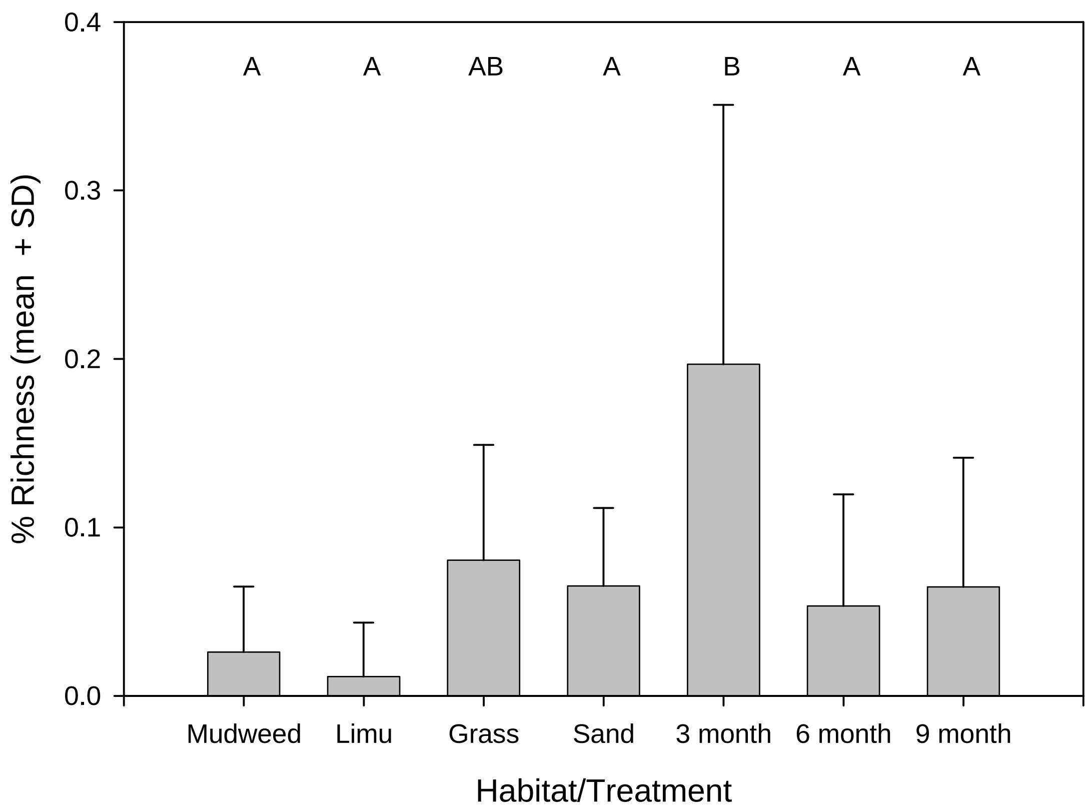

Figure 5. Mean percent species richness represented by nonindigenous species. Treatments/habitats sharing the same letter (top) are not significantly different.

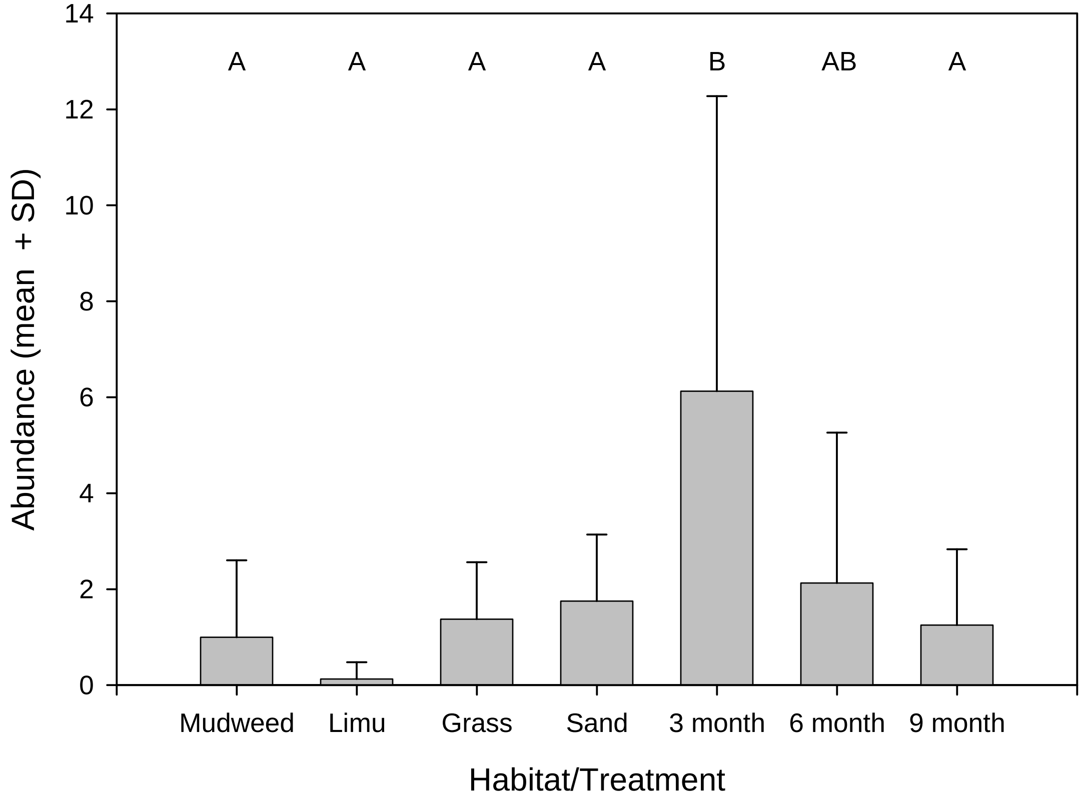

Figure 6. Mean abundance of nonindigenous species. Treatments/habitats sharing the same letter (top) are not significantly different.

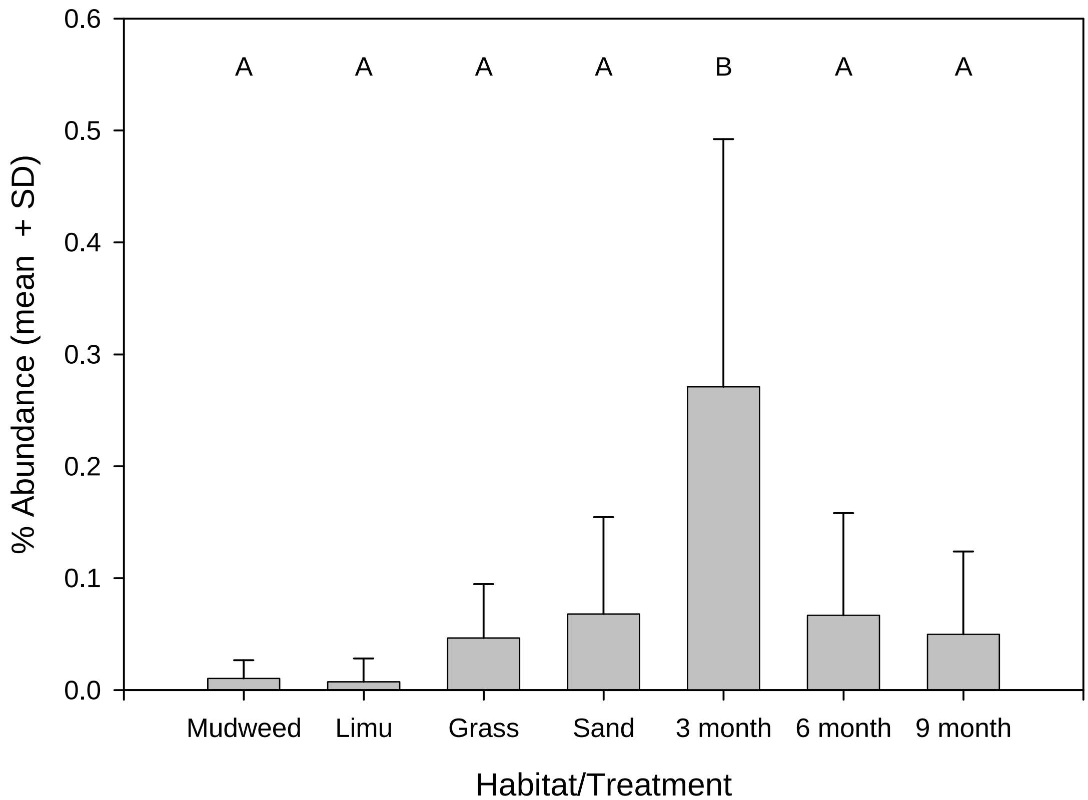

Figure 7. Mean percent abundance represented by nonindigenous species. Treatments/habitats sharing the same letter (top) are not significantly different.

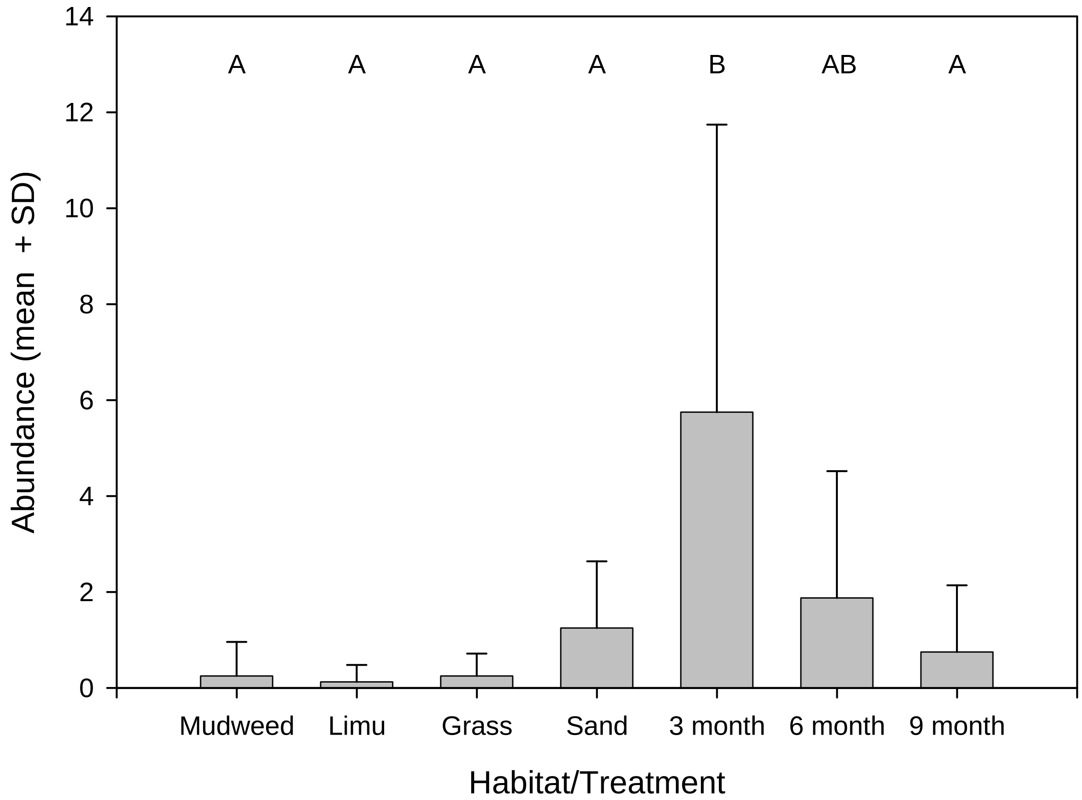

Figure 8. Mean abundance of the cryptogenic tanaid *Leptochelia dubia*. Treatments/habitats sharing the same letter (top) are not significantly different.

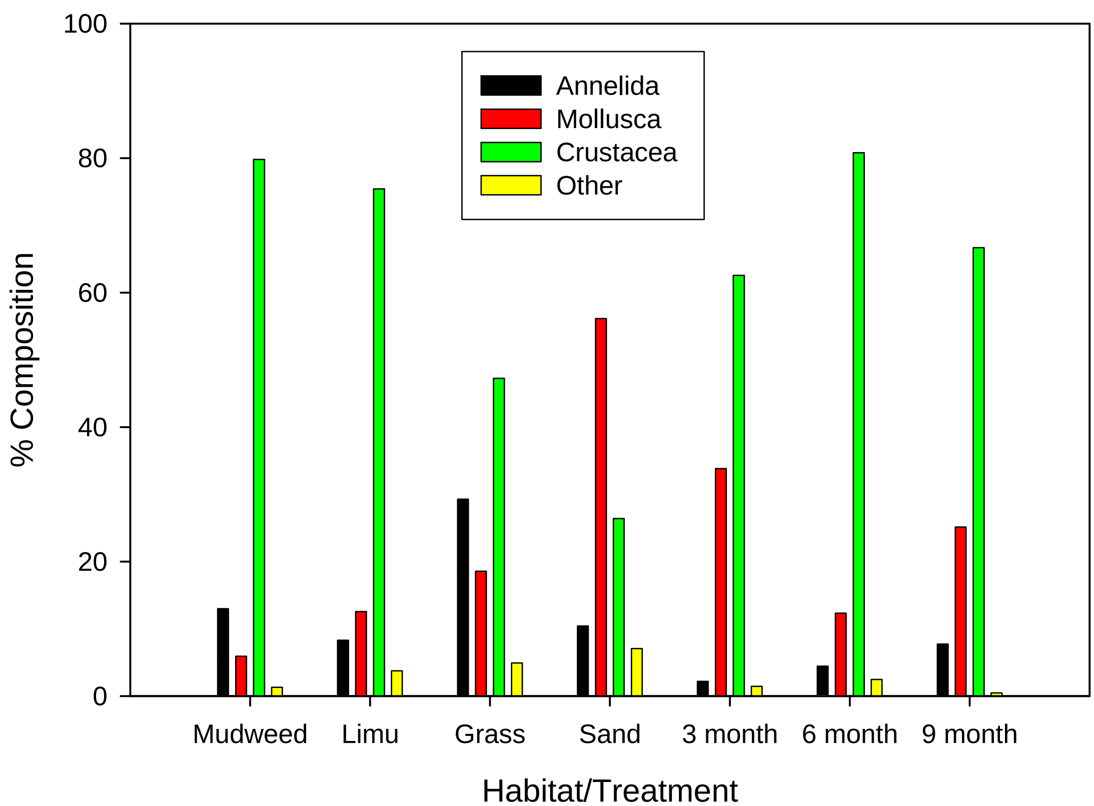

Figure 9. Gross-taxonomic-level composition of invertebrates by habitat/treatment (based on cumulative abundances).

Table 6. Abundance of all invertebrates and select higher taxa (mean ± standard deviation).

Habitat	All Invertebrates	Polychaetes	Molluscs	Peracarids	Decapods
Mudweed	86.63 ± 44.05	11.25 ± 10.91	5.13 ± 4.45	66.25 ± 45.54	2.88 ± 3.14
Limu	46.75 ± 28.78	3.88 ± 3.83	5.88 ± 3.94	33.75 ± 26.27	1.25 ± 1.58
Grass	43.13 ± 28.22	12.63 ± 10.91	8.00 ± 7.13	19.25 ± 22.40	1.00 ± 1.20
Sand	33.63 ± 15.30	3.50 ± 2.45	18.88 ± 18.80	8.00 ± 5.66	0.88 ± 0.64
3 month	34.38 ± 25.53	0.75 ± 0.89	11.63 ± 14.45	21.50 ± 16.13	0.00 ± 0.00
6 month	25.38 ± 18.75	1.13 ± 2.10	3.13 ± 5.44	19.75 ± 17.23	0.75 ± 0.46
9 month	25.88 ± 13.58	2.00 ± 2.20	6.50 ± 6.32	16.38 ± 8.85	0.88 ± 1.46

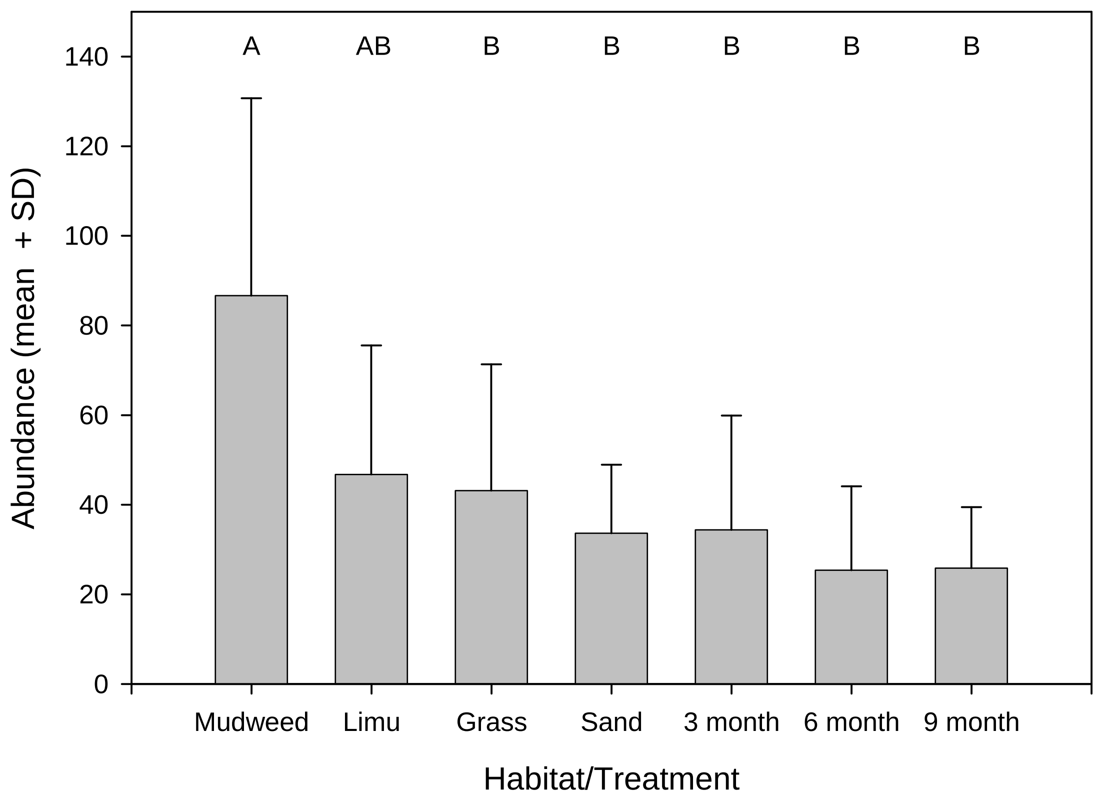

Figure 10. Mean abundance of all invertebrates. Treatments/habitats sharing the same letter (top) are not significantly different.

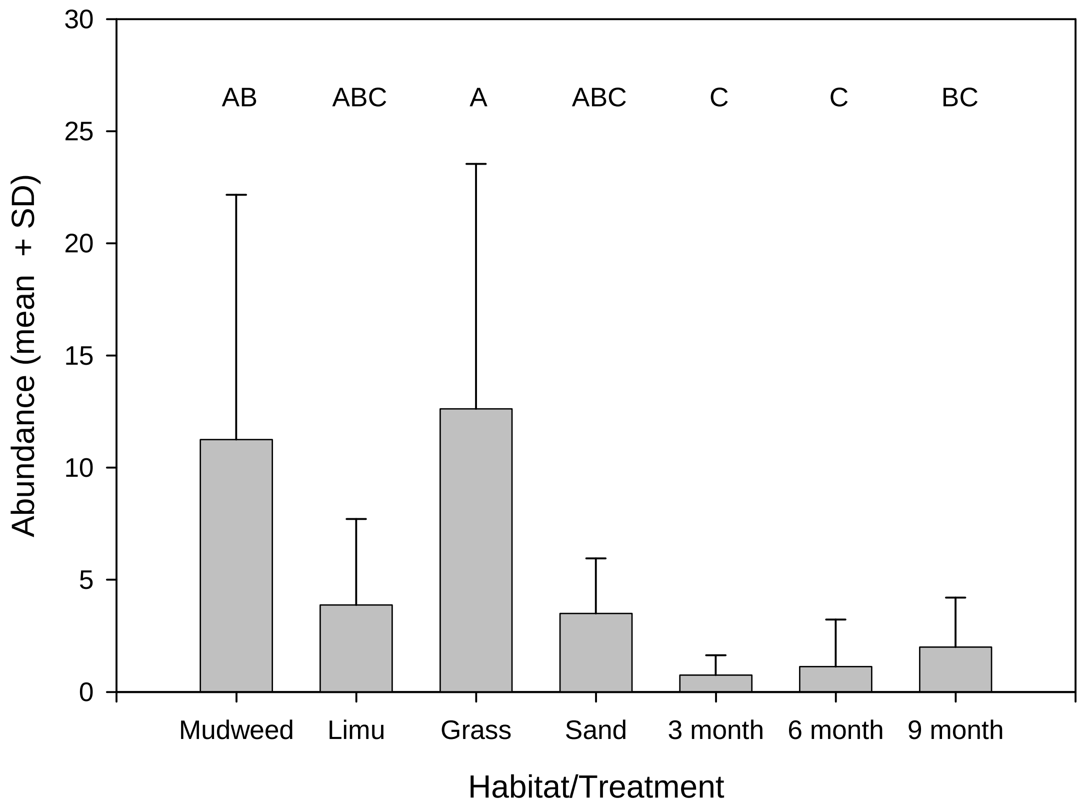

Figure 11. Mean abundance of polychaetes. Treatments/habitats sharing the same letter (top) are not significantly different.

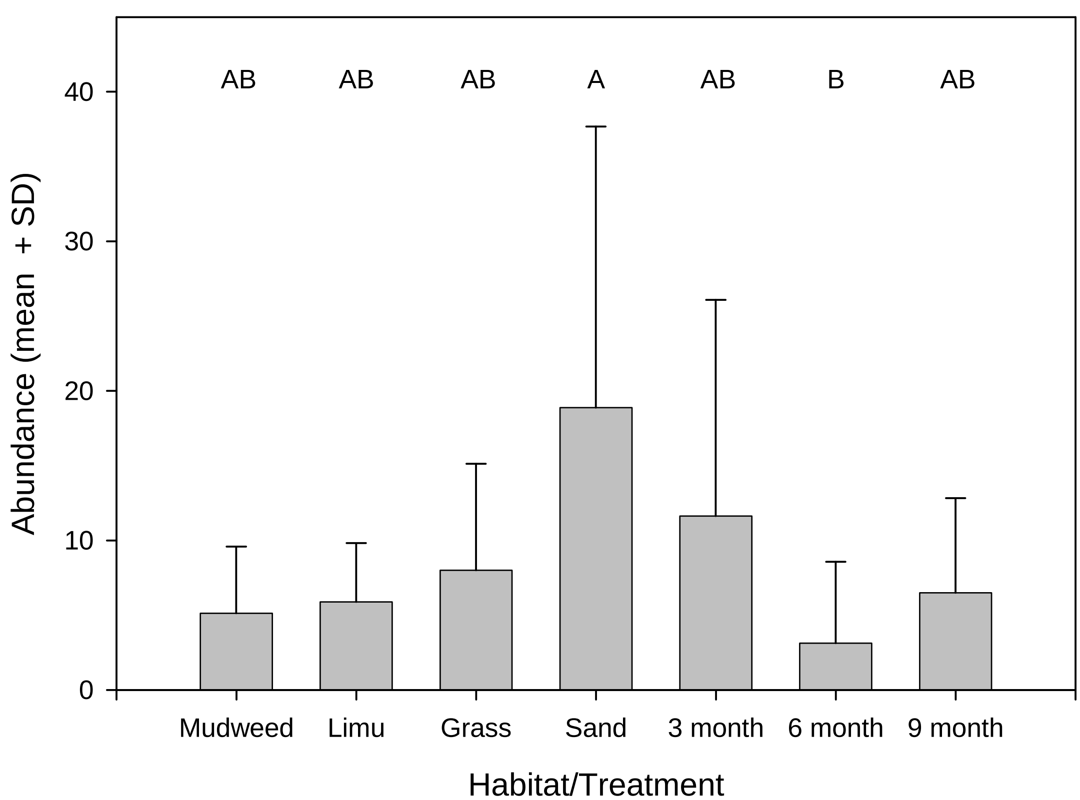

Figure 12. Mean abundance of molluscs. Treatments/habitats sharing the same letter (top) are not significantly different.

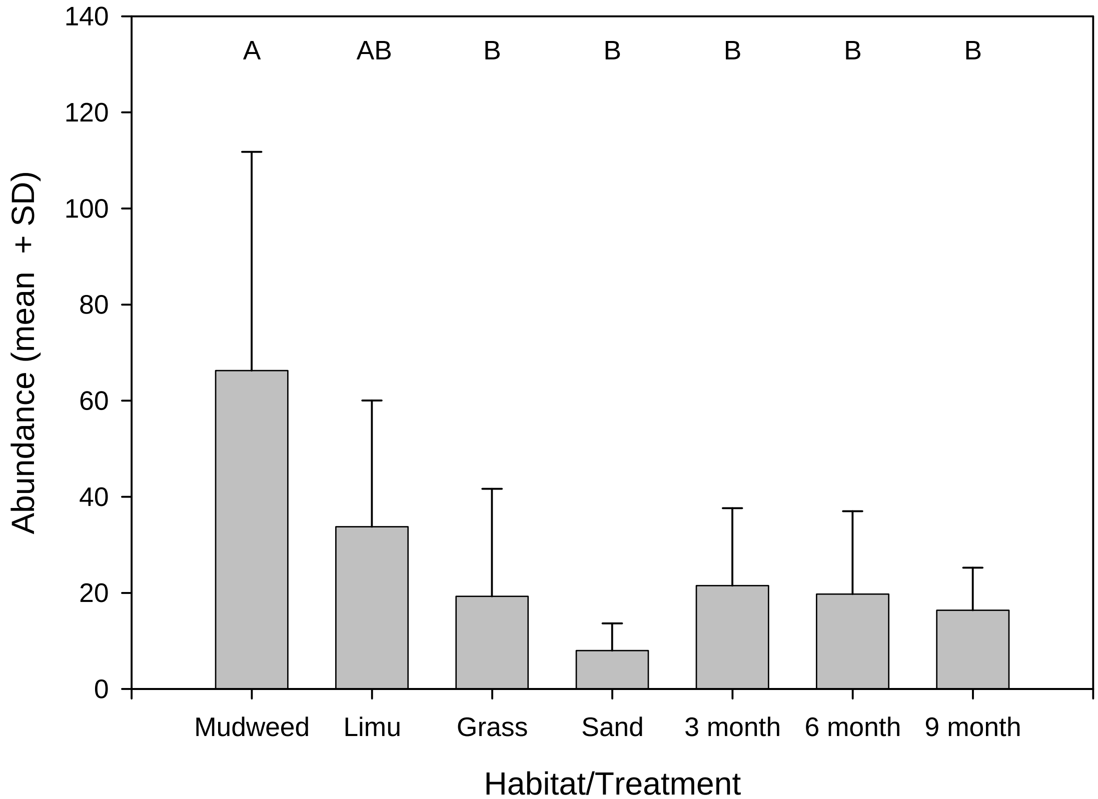

Figure 13. Mean abundance of peracarid crustaceans. Treatments/habitats sharing the same letter (top) are not significantly different.

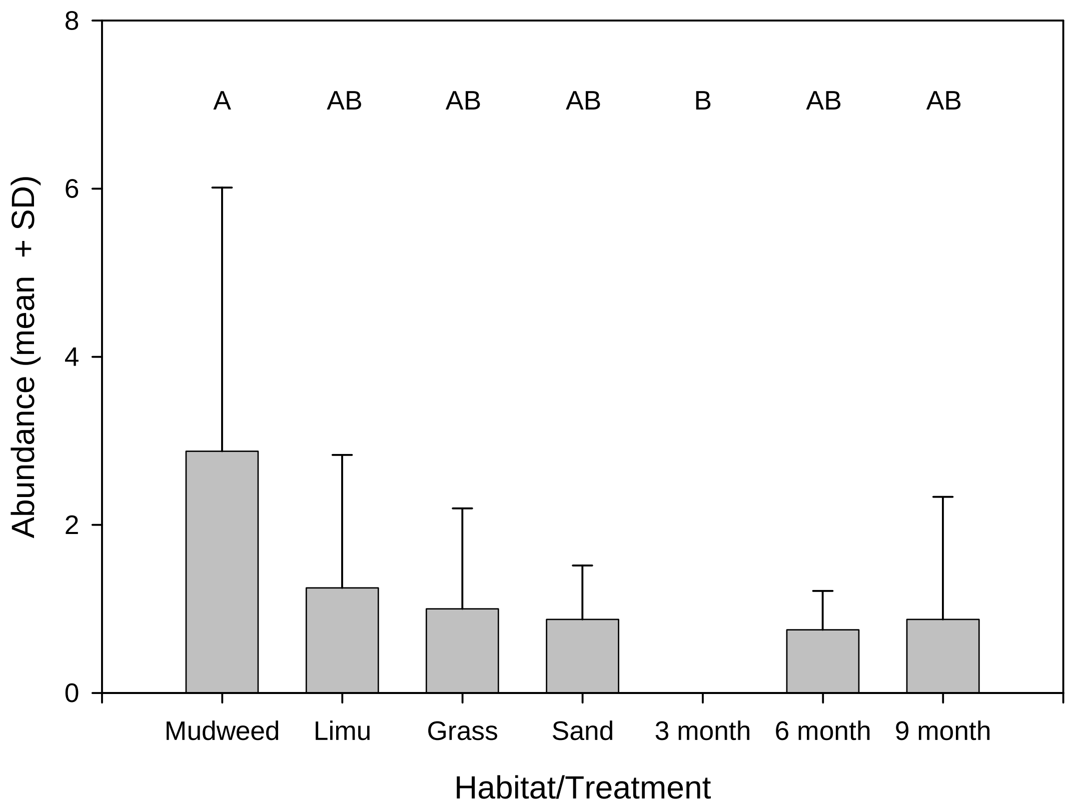

Figure 14. Mean abundance of decapod crustaceans. Treatments/habitats sharing the same letter (top) are not significantly different.

DISCUSSION

Habitat Restoration

The proximate goal of habitat restoration is to modify an area such that is resembles its pre-impacted state, and thus differs from the impacted state. Restoration activity in Maunalua Bay focused on the large-scale removal of an invasive alga, *Avrainvillea amadelpha*, or mudweed. Based on the criteria established in the introduction, it appears that this was a successful habitat restoration effort because:

1) Mean species richness where mudweed was removed is indistinguishable from any native habitat (those not impacted by mudweed; or limu, seagrass, and sand). Further, nine months after mudweed was removed, mean species richness was significantly different from areas where mudweed remained, although all indices indicate lowest diversity in the mudweed removal area (*i.e.*, mudweed removal resulted in decreased diversity, which is probably not a desired outcome).
2) Classification and ordination suggest mudweed removal shifts invertebrate communities toward those typically found in sand and seagrass habitats.
3) Importantly, classification and ordination also suggest that mudweed removal changes invertebrate community structure such that cleared plots are no longer similar to mudweed habitat.
4) A comparison of dominant species suggests invertebrate communities in mudweed-removal plots are similar to those in sand.
5) Mudweed removal resulted in a decrease in the absolute number of nonindigenous species (however when means were compared, all nonindigenous species metrics considered here increased significantly at three months, and the 6- and 9-month treatments were statistically indistinguishable from mudweed).

Overall, removing mudweed from the Kuli‘ou‘ou reef flat of Maunalua Bay, O‘ahu, Hawai‘i, resulted in invertebrate communities similar to native habitats (*i.e.*, those not impacted by mudweed). The resulting communities are most similar to those in the sand habitat.

Our assertion that habitat restoration was successful requires several qualifications. First, invertebrate communities in mudweed and native algae were similar, so a shift away from the mudweed community effectively resulted in a shift away from the native-algae state. Second, mudweed removal plots were initially colonized by a high abundance of nonindigenous species. Third, although the invertebrate communities in plots cleared of mudweed are similar to those in sand, there are also some large differences between the two. Finally, this was a relatively short-term evaluation. We do not know the ultimate fate of areas cleared of mudweed.

The mudweed invertebrate community did differ from that in native algae in absolute terms: total species richness was lower, non-indigenous-species richness was higher, and mean total invertebrate abundance was higher. However, in no case did the results of univariate statistical analysis indicate the two communities were significantly different. Further, multivariate analyses suggest the communites are quite similar.

Because of the similarity between the mudweed and native-algae invertebrate communities, desirable changes in invertebtrate community structure away from that found in mudweed also caused a, perhaps undesirable, change away from that found in native algae. As Miller & Hobbs (2007) suggest, removing exotic vegetation may be counter productive because the net effects of these species on a given system can be neutral or even beneficial. These results highlight the need for explicit goals when planning habitat restoration.

Although mudweed impacts the Maunalua Bay reef flat community, its removal also represents a massive disturbance. More than 1.36 million kg of vegetation was removed from the reef flat. The mudweed habitat also had an average sediment depth of 2.6 cm (Conklin 2009). Manual removal of mudweed, including its holdfast, leaves little or no sediment on the cleared substratum (Conkin 2009). This disturbance opens space that can be exploited by nonindigenous species.

It appears that, in terms of species richness, mudweed removal was not associated with an abnormally high number of nonindigenous species. Two to three nonindigenous species were identified in each of the time-periods following mudweed removal. This compares favorably to the number found during a survey of nonindegenous species on Hawai'i's coral reefs. Considering only polychaetes, molluscs, and peracarids (*i.e.*, the higher taxa containing all nonindigenous species identified in the present study), an average 6.86 (range: 3 – 11) nonindigenous species were found on seven coral reefs located near shipping ports or small-craft harbors on Kauai, Molokai, Maui, and Hawaii (Coles *et al.* 2006). Our count of the number of nonindigenous species may be low; about two-dozen identifications in the present study are higher-level (more inclusive) taxa. These groups may include nonindigenous species. This possibility should not cause doubt about the above comparison because the same individuals performed identifications in both studies.

A larger concern with mudweed removal is that the disturbance may permit high abundances of nonindigenous species. For instance, at 3-months post-removal the cryptogenic (and early-colonizing) tanaid, *Leptochelia dubia*, reached significantly higher abundance than seen in any other habitat/treatment. Its abundance did attenuate over time, and became statistically indistinguishable from the other native habitats by six months.

This rapid increase and eventual die-off of nonindigenous species in general, and *Leptochelia dubia* in particular, may be a normal course of events in disturbed sedimentary habitats. Guerra-García & García-Gómez (2006) report that *Leptochelia dubia* appears in newly available substrate even when not detected in surrounding areas. A review by Thistle (1981) suggests it is common for many early-colonizing species to first exceed then die off to background levels. Thus the early, and significant, increase in nonindigenous species abundance associated with mudweed removal may not be cause for concern.

Concurrent with the rapid increase and die off of *Leptochelia dubia* in plots cleared of mudweed was opposite pattern for decapod crustaceans. They were absent from the 3-month post-removal treatment, but increased through time to become statistically indistinguishable from any native habitat. These results suggest that the cleared areas had at least partially recovered from the disturbance of mudweed removal.

In general, the univariate statistical analyses performed in this study suggest that, after nine months, areas cleared of mudweed were indistinguishable from native habitats. Multivariate statistics suggest the mudweed-removal treatments are most similar to the sand habitat; however, removal treatments are located at an edge of the ordination plot (rather than between reference habitats). This pattern suggests that mudweed removal resulted in unique endpoint communites, rather than that the communities represent a transition state between two or more habitats. Further, cumulative species richness in sand is nearly double that of the 9-month post-removal treatment (although mean values are not significantly different); many species found in the sand habitat have clearly not established themselves in the sediments of the mudweed-removal areas.

There are at least two explanations for the difference between invertebrate communities in sand and where mudweed was removed. First, not enough time has passed, given the large areal scale of the habitat-restoration efforts. Although small patches of disturbed sedimentary habitats often resemble their pre-disturbance state within a short time, the areas from which mudweed has been removed are so large that some species may not have yet reached the central portions. Guerra-García & García-Gómez (2006) note that in large disturbed sedimentary areas, the edge-to-surface ratio is small and that central locations may have long recovery times. Alternatively, the sediments in the sandy and cleared areas may be fundamentally different. The sand habitat in this study was large (10 – 100s of square meters) relative to the sediments occurring in the areas cleared of mudweed (typically much less than 1 m^2). The sediments in the latter areas may be far more ephemeral (*i.e.*, the associated invertebrate communities may be in a much-more-frequently disturbed habitat). Related to the small sediment patches found in mudweed-cleared areas, hard-bottom surrounds the sediments and dominates the total area. Longenecker (2001) noted that many macrofaunal invertebrates have distinct microhabitat preferences. Thus, the small-scale combination of microhabitats in areas cleared of mudweed might, reasonably, not be expected to host the same set of species found in the sand habitat.

Even when considering the above caveats, it appears the removal of the invasive alga, *Avrainvillea amadelpha*, achieved the common, immediate goals of habitat restoration. However, the ultimate goal of habitat restoration is an ecosystem that remains stable without further human assistance (SER 2004). Whether this will occur remains to be seen. At the end of a four-year experiment, Peyton (2009) found that *Avrainvillea amadelpha* was unable recolonize space it once occupied when the seagrass *Halophila hawaiiana* was present. Importantly, this manipulative experiment was conducted at the margin of seagrass and mudweed canopies. Results of a concurrent three-year study suggest that, within areas of 100% mudweed cover, *Avrainvillea amadelpha* will re-occupy space at levels seen prior to its removal (Conklin 2009). The contradictory results of these smaller-scale but longer-term mudweed-removal experiments make it difficult to predict the endpoint of the large-scale removal project examined in the present study.

Effects on Fishes

The changes to invertebrate communities after mudweed removal may be expected to influence the distribution and abundance of fishes that feed on small, mobile invertebrates. Several authors suggest that food availability strongly influences the distribution and abundance of reef fishes (Clarke 1992, Polunin & Klumpp 1992, Risk 1997) and there are strong, positive relationships between the abundance of reef fishes and their food (Stewart & Jones 2001, Wilson 2001, Connell 2002, Gregson & Booth 2005). Longenecker (2007) examined the diets of six species representing 69.3% of the total small, cryptic individuals found on the forereef of Kaneohe Bay, Oʻahu, Hawaiʻi, and reported that each species specialized on a limited suite of invertebrate prey. He then compared densities of each fish and its suite of prey to find five significant regression equations and one strong trend, suggesting that the abundance of a given fish species within approximately 10-m^2 areas is strongly related to the abundance of its prey.

Of particular concern at Maunalua Bay is the possible effect of mudweed removal on the abundance of bonefish (*Albula*) species. For juvenile bonefish caught off the Florida Keys, four of the five important prey taxa were polychaetes, amphipods, copepods, and caridean shrimp (Snodgrass *et al.* 2008). With increasing bonefish size, amphipod importance declined, whereas the importance of brachyuran crabs increased (Snodgrass *et al.* 2008). In a separate study in the Florida Keys, Crabtree *et al.* (1998) found that a few prey taxa dominated the diet of (mostly adult) bonefish from the Florida keys: crabs (xanthids and portunids), shrimp (alpheids & penaeids), and a single fish species (a toadfish) made up 74.9% of the diet by weight.

We must emphasize that the relationships between the abundances of coral-reef fishes and their invertebrate prey at Maunalua Bay are not well-enough understood to predict exactly how fish populations (including bonefish) will change, if at all. However an examination of invertebrate abundances may permit reasonable suggestions about relative changes in fish populations. Total invertebrate abundance and, in particular, peracarid and decapod abundances decline significantly with the removal of mudweed (although after 6 months, decapod abundances are statistically indistinguishable from those in mudweed). Because of the similarity between mudweed and native algae invertebrate communities, populations of fishes feeding in algae-dominated habitats may decrease. If bonefish diet is similar in Florida and Hawaiʻi, an important prey type of juveniles (peracarids) decreases after mudweed removal, whereas an important prey type of adults (decapods) is not significantly different 6 months or more after mudweed removal. These results suggest a possible negative effect on the abundance of juvenile bonefish. However, the abundances of invertebrates associated with mudweed-removal treatments are, in general, indistinguishable from any native habitat. This raises the possibility that, from a food-availability perspective, mudweed-removal treatments will support fish populations similar to those found in Hawai‘i’s native reef-flat habitat.

ACKNOWLEDGMENTS

Dwayne Minton and Eric Conklin of the Nature Conservancy Hawaii Chapter provided crucial technical support by providing a suite of sampling coordinates for each habitat/treatment. Dwayne Minton also processed sediment samples and reviewed a draft manuscript. Scott Godwin identified cnidarians and crabs. This project was made possible through support provided by the Department of Commerce, National Oceanic and Atmospheric Administration and The Nature Conservancy, under the terms of Cooperative Agreement NA09NMF4630312. The content and opinions expressed herein are those of the authors and do not necessarily reflect the position or the policy of the NOAA or The Nature Conservancy, and no official endorsement should be inferred.

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APPENDIX I

Sample coordinates and associated data

Appendix I. Coordinates, date, and vegetation biomass of 8 sampling points in each of 7 treatments. R = mudweed, L = native algae, G = native seagrass, S = sand, 3MO = 3-month mudweed removal treatment, 6MO = 6-month mudweed removal treatment, 9MO = 9-month mudweed removal treatment.

Sample	Latitude	Longitude	Date	Vegetation (g)	Sediment weights (g)					
					>355	355-246	246-125	125-63	63-45	<45
R30	21.27901	-157.731	29-Sep-10	11.39	22.013	0.374	0.776	0.603	0.025	0.019
R32	21.27987	-157.731	4-Nov-10	135.91	9.744	0.509	1.618	2.286	0.259	0.277
R33	21.28039	-157.732	29-Sep-10	199.92	5.566	0.264	0.454	0.257	0.035	0.010
R34	21.28173	-157.732	4-Nov-10	48.35	8.299	0.451	0.979	0.746	0.205	0.107
R37	21.28037	-157.731	4-Nov-10	148.63	16.547	2.778	2.629	0.938	0.153	0.218
R38	21.27961	-157.730	4-Nov-10	36.13	4.767	0.731	1.830	1.083	0.098	0.103
R40	21.28044	-157.730	29-Sep-10	23.84	13.580	2.612	3.840	2.040	0.535	0.395
R43	21.28096	-157.727	29-Sep-10	92.55	6.362	1.353	1.231	0.430	0.087	0.175
L16	21.27940	-157.729	29-Sep-10	17.08	15.444	0.347	0.385	0.077	0.000	0.003
L17	21.27940	-157.729	29-Sep-10	0.90	14.936	0.157	0.206	0.050	0.000	0.000
L20	21.27953	-157.729	4-Nov-10	11.01	5.851	0.956	1.863	1.452	0.134	0.082
L21	21.27953	-157.729	29-Sep-10	152.96	5.918	0.261	0.362	0.216	0.016	0.107
L21	21.27953	-157.729	4-Nov-10	66.39	10.043	0.354	0.424	0.219	0.016	0.026
L22	21.27953	-157.729	29-Sep-10	72.00	14.906	0.946	1.708	0.826	0.062	0.029
L23	21.27954	-157.729	29-Sep-10	7.90	6.365	0.530	0.920	0.455	0.042	0.052
L25	21.27981	-157.729	4-Nov-10	21.60	21.183	2.612	4.592	2.858	0.319	0.327
G01	21.27870	-157.729	29-Sep-10	9.44	17.508	2.200	2.372	0.971	0.059	0.070
G02	21.27870	-157.729	29-Sep-10	15.31	25.258	2.526	3.667	1.744	0.133	0.000
G07	21.27887	-157.729	4-Nov-10	4.05	9.005	2.798	2.950	1.441	0.111	0.061
G08	21.28036	-157.729	4-Nov-10	7.27	22.332	3.879	9.491	5.568	0.436	0.414
G09	21.28036	-157.729	29-Sep-10	4.72	19.177	1.876	4.499	2.736	0.231	0.130
G11	21.28025	-157.729	29-Sep-10	3.20	29.917	5.001	9.920	8.699	1.012	0.966

Sample	Latitude	Longitude	Date	Vegetation (g)	Sediment weights (g)					
					>355	355-246	246-125	125-63	63-45	<45
G14	21.28003	-157.729	4-Nov-10	5.85	23.598	7.477	17.065	12.048	1.147	1.030
G15	21.27995	-157.729	4-Nov-10	10.96	22.793	3.493	7.146	6.660	0.676	0.904
S26	21.28067	-157.729	29-Sep-10	0.00	28.191	2.440	3.153	0.590	0.130	0.000
S27	21.28040	-157.729	29-Sep-10	0.00	21.551	1.498	3.386	1.508	0.156	0.102
S28	21.28032	-157.729	29-Sep-10	0.00						
S44	21.28038	-157.729	4-Nov-10	0.00	27.523	3.319	3.571	1.595	0.120	0.172
S45	21.28126	-157.732	4-Nov-10	0.00	11.643	2.310	2.123	2.034	0.568	0.299
S46	21.28120	-157.733	4-Nov-10	0.00	19.340	2.767	3.277	4.733	1.695	0.771
S47	21.28117	-157.733	4-Nov-10	0.00	11.617	1.315	0.505	0.069	0.012	0.034
S48	21.28065	-157.733	4-Nov-10	0.00	22.851	1.820	1.207	0.327	0.042	0.042
3M03	21.27988	-157.731	8-Dec-10	11.18	10.933	1.134	2.723	1.052	0.065	0.001
3M04	21.27993	-157.731	8-Dec-10	0.00	8.054	1.198	3.070	0.026	0.631	0.297
3M05	21.28135	-157.732	8-Dec-10	2.82	14.055	1.950	3.720	3.762	0.871	0.300
3M06	21.28012	-157.732	8-Dec-10	5.58	17.536	0.827	1.542	0.778	0.052	0.201
3MO8	21.28152	-157.732	8-Dec-10	0.00	1.920	0.329	0.607	0.800	0.241	0.077
3M09	21.28134	-157.732	8-Dec-10	1.83	8.322	1.965	3.742	3.104	0.794	0.421
3M10	21.28155	-157.732	8-Dec-10	0.64	14.070	3.250	3.287	2.878	0.767	0.360
6M01	21.28060	-157.731	8-Dec-10	12.56	13.741	0.637	0.759	0.455	0.070	0.055
6M03	21.28142	-157.731	8-Dec-10	0.00	13.275	1.473	2.824	1.824	0.697	0.271
6M04	21.27939	-157.732	8-Dec-10	14.91	6.295	0.695	2.099	1.502	0.128	0.083
6M06	21.27940	-157.732	8-Dec-10	0.00	11.465	0.697	1.024	0.272	0.011	0.012
6M07	21.28060	-157.731	8-Dec-10	0.00	11.574	2.245	2.228	0.360	0.064	0.052
6M08	21.28149	-157.730	8-Dec-10	0.00	5.235	0.482	0.900	0.567	0.147	0.115
6M09	21.28124	-157.730	8-Dec-10	0.17	4.503	0.465	1.949	1.078	0.278	0.179
6M10	21.27950	-157.732	8-Dec-10	11.96	2.600	0.355	0.435	0.136	0.000	0.000

Sample	Latitude	Longitude	Date	Vegetation (g)	Sediment weights (g)					
					>355	355-246	246-125	125-63	63-45	<45
9M01	21.27939	-157.731	8-Dec-10	0.00	19.362	1.534	3.691	0.885	0.038	0.000
9M02	21.28020	-157.731	8-Dec-10	1.10	1.107	0.146	0.218	0.068	0.000	0.000
9MO5	21.28001	-157.730	8-Dec-10	0.00	17.825	1.312	3.836	2.766	0.120	0.062
9M06	21.28017	-157.731	8-Dec-10	5.22	11.891	1.185	2.498	0.743	0.066	0.043
9M07	21.28023	-157.731	8-Dec-10	2.83	17.143	2.573	3.996	1.347	0.120	0.069
9M08	21.28034	-157.731	8-Dec-10	0.00	3.650	0.311	0.555	0.280	0.036	0.000
9M09	21.27909	-157.731	8-Dec-10	0.00	15.845	0.420	2.718	0.953	0.045	0.022
9M10	21.28008	-157.731	8-Dec-10	0.61	23.040	1.636	1.779	0.477	0.021	0.086

APPENDIX II

Abundance of invertebrates identified, by sample

Higher Taxon	Binomial	Author	01G	02G	07G	08G	09G	11G	14G	15G	16L	17L	20L	21La	21Lb	22L	23L	25L	26S	27S
CNIDARIA	*Epiphellia* spp.		1	1	1	1	1		1							1		1	1	1
ANNELIDA																				
POLYCHAETA																				
Amphinomidae	*Amphinome rostrata*	(Pallas, 1766)																		
Amphinomidae	*Eurythoe complanata*	(Pallas, 1766)												1	4					
Amphinomidae	*Hipponoe gaudichaudi*	Audouin & Milne Edwards, 1830																		
Capitellidae	*Capitella capitata*	(Fabricius, 1780)	2						1	1					2			1		
Capitellidae	*Scyphoproctus "1"*	Gravier, 1904	5	1																
Chaetopteridae	*Mesochaetopterus sagittarius*	(Claparede, 1870)		10				16	2								1			
Chaetopteridae	*Phyllochaetopterus socialis*	(Claparede, 1870)																	2	1
Chaetopteridae	*Phyllochaetopterus verrilli*	Treadwell, 1943	11	10										3	2	2	1	1		
Cirratulidae	*Cirriformia crassicollis*	(Kingberg, 1866)																		
Cossuridae	*Cossura coasta*	Kitamori, 1960									1					1				
Eunicidae	*Marphysa corallina*	Kinberg, 1865												1						
Eunicidae	*Nematoneris unicornis*	Schmarda, 1861	1					1							1					
Lumbrineridae	*Lumbrineris dentata*	Hartmann-Schroeder, 1965		3					1	2					1					
Nereidae	*Neanthes arenaceodonta*	Moore, 1903	2																	
Nereidae	*Neanthes succinea*	Frey & Leuckart, 1847			2				1	1										
Phyllodocidae	UNID "1"							1												
Sabellidae	UNID "1"																			
Spionidae	UNID "1"					3	2		4	2	1					1				
Spionidae	UNID "2"							1												
Spirorbidae	*Neodexiospira foraminosa*	(Moore & Bush, 1904)																		
Syllidae	UNID spp.		6	4	3			2							2	1		1	1	
Terebellidae	*Loimia* "1"	Malmgren, 1866												1						
Terebellidae	*Lysilla ubianesis*	Caullery, 1944																		
Terebellidae	UNID "1"											1								
UNIDENTIFIED	UNID spp.																		3	
SIPUNCULA	UNID spp.														1	1				3
MOLLUSCA																				
GASTROPODA																				
Calyptraeidae	*Crepidula aculeata*	(Gmelin, 1791)																		
Cerithiidae	*Bittium impendens*	(Hedley, 1899)												2						
Cerithiidae	*Cerithium boeticum*	Pease, 1860													1					
Cerithiidae	*Cerithium rostratum*	Sowerby, 1855																		
Cerithiidae	*Cerithium* spp.							1									1			1
Cerithiidae	*Cerithium zebrum*	Kiener, 1841		3	3	3	2	13	1	3	5	4		4	3	1		2	4	8
Cerithiidae	*Ittibittium parcum*	(Gould, 1861)			2			2	2	1	2			2	1			1		1
Cerithiopsidae	UNID "1"																			
Columbellidae	*Mitrella loyaltensis*	(Hervier, 1900):						1	1										1	1
Columbellidae	*Mitrella rorida*	(Reeve, 1859)																		
Columbellidae	*Mitrella* "1"																			
Columbellidae	*Seminella peasei*	(von Martens & Langkavel, 1871)																		
Elachisinidae	*Elachisina robertsoni*	Kay, 1979																		
Epitoniidae	*Laeviscala sandwichensis*	(Nyst, 1871)								1										
Fasciolariidae	*Peristernia chlorostoma*	(Sowerby, 1825)																		1

28S	44S	45S	46S	47S	48S	30R	32R	33R	34R	37R	38R	40R	43R	3M03	3M04	3M05	3M06	3M07	3M08	3M09	3M10	6M01	6M03	6M04	6M06	6M07	6M08	6M09	6M10	9M01	9M02	9M05	9M06	9M07	9M08	9M09	9M10
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						10	4			1																						4	2			1	4
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					3	10			1			2	6																							1	
							1	1															1														
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						2				4		2						1																			
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3	1		2	2		2				1				3			5	4		1	1	1										1	2	5	1		
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Higher Taxon	Binomial	Author	01G	02G	07G	08G	09G	11G	14G	15G	16L	17L	20L	21La	21Lb	22L	23L	25L	26S	27S
Fissurellidae	*Diodora granifera*	(Pease, 1861)																		1
Haminoeidae	*Atys kuhnsi*	Pilsbry, 1917																		
Haminoeidae	*Atys semistriata*	Pease, 1860							1											
Haminoeidae	*Haminoea ovalis*	Pease, 1868																		
Hipponicidae	*Antisabia foliacea*	(Quoy & Gaimard, 1835)																		
Hipponicidae	*Hipponix pilosus*	(Deshayes, 1832)																		
Hydrobiidae	*Tryonia porrecta?*	(Mighels, 1845)																		
Marginellidae	*Volvarina nevilli*	(Jousseaume, 1875)																		
Naticidae	UNID "1"																			
Neritidae	*Smaragdia bryanae*	Pilsbry, 1917			1	1	3	5	3	1			1						1	
NUDIBRANCHIA															1					1
Phasianellidae	*Tricolia variabilis*	(Pease, 1861)			1							1								
Pyramidellidae	*Evalea peasei*	(Dautzenberg & Bouge, 1933)						1												
Pyramidellidae	*Odostomia gulicki*	Pilsbry, 1918																		
Rissoidae	*Merelina granulosa*	(Pease, 1862)			1															
Rissoidae	*Rissoina cerithiiformis*	Tryon, 1887																		
Rissoidae	*Rissoina costata*	A. Adams, 1851									1									
Rissoidae	*Schwartziella triticea*	(Pease, 1861)																		
Rissoidae	*Stosicia hiloense*	(Pilsbry & Vanatta, 1908)																		
Rissoidae	*Zebina bidentata*	(Philippi, 1845)																		
Scaliolidae	*Finella pupoides*	A. Adams, 1860												1				1		
Stomatellidae	*Synaptocochlea concinna*	(Gould, 1845)																		
Thiaridae	*Melanoides turberculata*	(Müller, 1774)								1										
Triphoridae	*Iniforis aemulans*	(Hinds, 1843)		1																
Triphoridae	*Mastonia cingulifera*	(Pease, 1861)																		
Triphoridae	UNID spp.											1								
Trochidae	*Alcyna ocellata*	(A. Adams, 1861)																		
Trochidae	*Alcyna subangulata*	(Pease, 1861)																		
Trochidae	*Euchelus gemmatus*	(Gould, 1845)								1		1			1			3		
Trochidae	*Gibbula marmorea*	(Pease, 1861)																		
Trochidae	UNID "1"																			
Trochidae	*Trochus intextus*	Kiener, 1850						1												
Turbinidae	*Collonista candida*	(Pease, 1861)																		
Turbinidae	*Leptothyra rubricincta*	(Mighels, 1845)		1					1									1		3
Turbinidae	*Leptothyra verruca*	(Gould, 1845)																		
Turbinidae	*Turbo sandwicensis*	Pease, 1861																		
Turridae	*Kermia pumila*	(Mighels, 1845)																		
Vermetidae	UNID spp.										1				1				1	
UNIDENTIFIED	UNID "1"																			
BIVALVIA																				
Arcidae	*Barbatia nuttingi*	(Dall, Bartsch & Rehder, 1938)																		
Arcidae	*Barbatia* "1"																			
Carditidae	*Cardita thaanumi*	(Dall, Bartsch & Rehder, 1938)																		
Lucinidae	*Ctena bella*	(Conrad, 1837)																		2
Mytilidae	*Brachidontes crebristriatus*	(Conrad, 1837)																		
Nuculidae	*Nucula hawaiensis*	Pilsbry, 1921			1															
Sportellidae	*Hitia ovalis*	Dall, Bartsch & Rehder, 1938											1	2						

28S	44S	45S	46S	47S	48S	30R	32R	33R	34R	37R	38R	40R	43R	3M03	3M04	3M05	3M06	3M07	3M08	3M09	3M10	6M01	6M03	6M04	6M06	6M07	6M08	6M09	6M10	9M01	9M02	9M05	9M06	9M07	9M08	9M09	9M10
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Higher Taxon	Binomial	Author	01G	02G	07G	08G	09G	11G	14G	15G	16L	17L	20L	21La	21Lb	22L	23L	25L	26S	27S
ARTHROPODA																				
OSTRACODA	UNID "1"						1													
STOMATOPODA	UNID spp.													1		1				
LOPHOGASTRIDA	UNID "1"																	1		
AMPHIPODA																				
Amphilochidae	*Amphilochus kailua*	Barnard, 1970								1			3							
Amphilochidae	*Amphilochus likelike*	Barnard, 1970																		
Amphilochidae	*Amphilochus menehune*	Barnard, 1970						1						1		2	1			
Ampithoidae	*Ampithoe akuolaka*	Barnard, 1970															1			
Ampithoidae	*Ampithoe kaneohe*	Barnard, 1970			1								6	16	6	6				
Ampithoidae	*Ampithoe ramondi*	Audouin, 1828															1			
Ampithoidae	*Ampithoe waialua*	Barnard, 1970													1					
Ampithoidae	*Cymadusa filosa*	Savigny, 1816	1		2								1							
Ampithoidae	*Cymadusa hawaiensis*	(Schellenberg, 1938)					1													
Ampithoidae	*Cymadusa oceanica*	Barnard, 1955																		
Aoridae	*Aoroides columbiae*	Walker, 1898																		
Aoridae	*Bemlos intermedius*	(Schellenberg, 1938)																1		
Aoridae	*Bemlos macromanus*	Shoemaker, 1925										1							1	
Aoridae	*Bemlos pualani*	(Barnard, 1970)	1		4						1		4	2	11	12	4	2		
Aoridae	*Bemlos waipio*	(Barnard, 1970)																		
Aoridae	*Grandidierella makena*	(Barnard, 1970)								1									1	
Aoridae	*Lembos kamanu*	Barnard, 1970																		
Corophiidae	*Ericthonius brasiliensis*	(Dana, 1853)			1															
Eusiridae	*Tethygeneia pacifica*	(Schellenberg, 1938)											2	2						
Isaeidae	*Gammaropsis atlantica*	Stebbing, 1888			2															
Isaeidae	*Gammaropsis pokipoki*	Barnard, 1970																		
Isaeidae	*Ledoyerella haleiwa*	(Barnard, 1970)																		
Ischyroceridae	*Ischyrocerus kapu*	Barnard, 1970																		
Ischyroceridae	*Neoischyrocerus lilipuna*	(Barnard, 1970)																		
Leucothoidae	*Anamixis stebbingi*	Walker, 1904																		
Leucothoidae	*Leucothoe hyhelia*	Barnard, 1965			1						1			2		1				
Melitidae	*Elasmopus hooheno*	Barnard, 1970														3				
Melitidae	*Elasmopus molokai*	Barnard, 1970			1									5						
Melitidae	*Eriopisella upolu*	Barnard, 1970	5	21	10		4	3	7	1	2	4	2	4	1			6	4	2
Melitidae	*Gammarella amikai*	(Barnard, 1970)												1	3		1			
Melitidae	*Maera* "1"	Barnard, 1970											2				2			
Melitidae	*Mallacoota insignis*	(Chevreux, 1901)					1	1					5	36	3	14	2			
Melitidae	*Melita pahuwai*	Barnard, 1970										2	1				18			
Melitidae	*Quadrimaera kaiulani*	(Barnard, 1970)														3				
Melitidae	*Quadrimaera quadrimaena*	(Dana, 1853)																		
Neomegamphopidae	*Konatopus paao*	Barnard, 1970									1									
Stenothoidae	*Stenothoe haleloke*	Barnard, 1970																		1
UNIDENTIFIED	UNID "1"																			
ISOPODA																				
Anthuridae	*Amakusanthura inornata*	(Miller & Menzies, 1952)															1			
Janiridae	*Carpias algicola*	(Miller, 1941)			2							1	1	8		11	1			

28S	44S	45S	46S	47S	48S	30R	32R	33R	34R	37R	38R	40R	43R	3M03	3M04	3M05	3M06	3M07	3M08	3M09	3M10	6M01	6M03	6M04	6M06	6M07	6M08	6M09	6M10	9M01	9M02	9M05	9M06	9M07	9M08	9M09	9M10
								1																1											1		
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							1				1													1					1			1		1			
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							1	1							3																						
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								10	1	10	1		2																								
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						1	20	35	3	18	12	5					1							3													
							3																														
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						1																															
						2	8	25		1	5										1			1					5					1			1

Higher Taxon	Binomial	Author	01G	02G	07G	08G	09G	11G	14G	15G	16L	17L	20L	21La	21Lb	22L	23L	25L	26S	27S
Paranthuridae	*Paranthura ostergaardi*	Miller & Menzies, 1952			1															
Sphaeromatidae	UNID "1"			3								1		2						
TANAIDACEA																				
Apseudidae	*Apseudes tropicalis*	Miller, 1940	7	24	36		2	4	2			2	13	3	4	6	2		5	
Leptocheliidae	*Leptochelia dubia*	(Kroyer, 1842)				1		1			1								2	2
CUMACEA	UNID spp.																			
DECAPODA																				
Alpheidae	*Alpheus lobidens*	De Haan, 1850													1					
Alpheidae	*Alpheus paracrinitus*	Miers, 1881												1				1		
Alpheidae	*Alpheus rapax*	Fabricius, 1798		2				2												
CARIDEA	UNID "1"	Dana, 1852												1						
Crangonidae	UNID "1"	Haworth, 1825															1			
Penaeidae	UNID "1"	Rafinesque, 1815																		
Pilumnidae	*Pilumnus* spp.			1						2					2			2	2	1
Processidae	*Processa* "1"	Ortman, 1890	1												1					
ECHINODERMATA																				
OPHIUROIDEA	UNID spp.			1	1								1		1					1
HOLOTHUROIDEA	UNID spp.									1					1	1	1			
HEMICHORDATA	UNID spp.		1		1	1	2		1	2					3		1	1	1	

28S	44S	45S	46S	47S	48S	30R	32R	33R	34R	37R	38R	40R	43R	3M03	3M04	3M05	3M06	3M07	3M08	3M09	3M10	6M01	6M03	6M04	6M06	6M07	6M08	6M09	6M10	9M01	9M02	9M05	9M06	9M07	9M08	9M09	9M10
						1	2	3			1	1												1										2			
						4											2	1																		2	
		6				6	17	18	4	19	10	23	13		5		1	3	2		1	3	1	5	1				2	1		2	5		2	1	4
1	4		1				2							6	7		1	2	7	4	19	6	6		2				1			3			3		
																														1				2			
						2		6	1	1		2	8																								
																						1					1							2		1	
										1																											
1	1	1		1																				1	1			1	1				1	1		1	
						1							1																					1			
1	1																1						1	1													
				1	1	1				1													1														
1							1		1	1	1	1	1																							1	