Impacts of exotic mangroves and chemical eradication of mangroves on tide pool fish assemblages

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ABSTRACT: Fish were sampled from tide pools in Hawaii to determine how exotic mangroves *Rhizophora mangle* and the use of herbicides to chemically eradicate them are impacting tide pool fish assemblages. Ecological parameters were compared among mangrove-invaded, native vegetated, and non-vegetated tide pools before and after mangroves had been chemically eradicated. Native fish densities were higher than exotic fish densities in all treatments, were dominated by flagtails *Kuhlia xenura*, did not differ among treatments, and 1 yr after herbicidial eradication of mangroves, were greater than or equal to pre-control densities. Exotic fish densities did not differ between mangrove and native vegetated tide pools, were dominated by mollies *Poecilia* sp., were significantly lower in non-vegetated vs. vegetated pools, and did not differ before and after mangrove eradication. Significantly smaller native flagtails and exotic mollies were present in mangrove tide pools than in all other treatments. Our data suggests that exotic mangroves in Hawaii are not having an adverse effect on native fish assemblages in tide pools, and may actually provide nursery habitat for native and exotic fish. Furthermore, the presence of vegetation and not its origin may be more influential on exotic fish assemblages. Finally, our data suggests that if chemical eradication of mangroves negatively affected tide pool fish assemblages, those effects are short-lived. Future studies should attempt to quantify the ecological value of native versus exotic vegetation in supporting native (or exotic) fish assemblages.

KEY WORDS: *Rhizophora mangle* · Invasive species · Non-native species · Nursery habitat · *Kuhlia xenura* · *Poecilia* · Hawaii · Pacific Island

INTRODUCTION

Mangroves in novel ecosystems

Native mangrove forests provide important habitat for many species of resident and transient fish during high tides. Structural complexity resulting from tree trunks, prop roots, buttresses, and pneumatophores provides partial refuge from predation (Rönnbäck et al. 1999, Laegdsgaard & Johnson 2001, Ellis & Bell 2004). Algae and invertebrates that colonize tree roots and mangrove sediments are important food resources for various nekton species (Manson et al. 2005, Lin et al. 2007, Lugendo et al. 2007). However, most if not all studies documenting the fish habitat values of mangroves have been conducted within the native range of mangrove tree species. It is unclear how the invasion of coastlines by exotic mangroves alters fish habitat or whether exotic mangrove forests provide similar fish habitat value outside their native range. It is also unclear whether the invasion of native coastal ecosystems provides improved conditions for the invasion of other exotic fish, shrimp, or crabs.

Over 60 species of mangroves can be found on Pacific Islands throughout Oceania (Duke et al. 1998, 2002). Isolation of many Pacific Islands, such as Tahiti and Hawaii, has prevented the natural colonization of their coastlines by any of these mangrove tree species despite the fact that these islands share similar climatic and geological features with islands that support extant mangrove forests (Allen 1998). In 1902, *Rhizophora mangle* seedlings from Florida were planted along the shorelines of Molokai Island to minimize erosion (Walsh 1967). Today, *R. mangle* is present on all 5 major Hawaiian Islands due to intentional plantings and spread of propagules via interisland currents (Allen 1998, Bantilan-Smith et al. 2009) and has established populations in habitats that range from mudflats to vegetated coastal wetlands to tide pools. In its native new world range, *R. mangle* provides valuable fish habitat (Thayer et al. 1987, Lorenz et al. 1997). However, it is unclear how exotic *R. mangle* is impacting native fish assemblages along invaded coastlines of the Hawaiian and Society Islands. This is especially interesting as *Rhizophora* species native to other Pacific Islands (e.g. Federated States of Micronesia, Australia) provide habitat for several species of cosmopolitan and congeneric fish (Vance et al. 1996, Rönnbäck et al. 1999, MacKenzie & Cormier 2012) also found in the Hawaiian Islands.

Impacts of exotic mangroves

The colonization of mudflats by mangroves is thought to degrade native bird feeding and nursery habitat as well as provide refuge for bird predators such as mongoose or cats (Allen 1998, Rauzon & Drigot 2002). Exotic stands of mangroves on Oahu and Molokai Islands increased densities of exotic epifaunal and infaunal invertebrates, and caused shifts in food web structure compared to adjacent sand flats. Both of these impacts were attributed to increased structural complexity from mangrove roots coupled with shifts in organic matter inputs (Demopoulos et al. 2007, Demopoulos & Smith 2010).

Modified hydrology from increased structural complexity of mangrove roots and large inputs of organic matter (e.g. mangrove leaf litter) to invaded coastal areas have been suggested as mechanisms that may negatively impact native nekton habitat in Hawaii (Allen 1998, Fronda et al. 2008), yet few studies have examined this. Indeed, degradation of nekton habitat has been reported in coastal ecosystems invaded by exotic plants in other parts of the world. Decreased

densities of mummichog larvae and juveniles in *Phragmites australis*-invaded marshes versus native *Spartina* spp. marshes were attributed to a reduced number of water-filled depressions and altered hydrological cycles that resulted from increased organic matter inputs and stem densities of invasive *P. australis* (Able et al. 2003, Osgood et al. 2003, Raichel et al. 2003). While similar impacts may occur in mangrove-invaded coastlines of Pacific Islands, comparisons of fish densities among intertidal mangroves and sand flats on Molokai Island using drop nets revealed no significant differences, although mangroves generally harbored higher densities of exotic molly fish *Poecilia* sp. (Nakahara 2007). Mangroves invading tide pools may have greater impacts on fish assemblages that utilize these habitats because pools form discrete subtidal units to which fish are restricted at low tide and neap tidal cycles. Leaf litter from mangrove trees can also accumulate in tide pools and potentially lead to anoxic conditions through organic matter breakdown (Fronda et al. 2008). Negative impacts to tide pools would not only be ecological through loss of native biodiversity, but cultural and economic as well, as tide pools supply traditional food sources (i.e. snails, sea cucumbers) and support tourism by providing snorkeling areas protected from rip tides or wave action (Flanders 2007).

The invasion of coastlines by *Rhizophora mangle* has also negatively impacted the cultural values of these areas. Prop roots and trunks can destroy archeologically significant structures such as rock walls built by Hawaiians for fish ponds or heiau platforms (i.e. Hawaiian temples) (Allen 1998, Rauzon & Drigot 2002). As a result of the negative impacts exotic mangroves are having on the ecological, cultural, and economical value of Hawaiian coasts, efforts to remove or control mangroves have increased. However, these efforts have been costly and time consuming. For example, the removal of 20 acres of *R. mangle* from Oahu island required nearly 20 yr of volunteer efforts and 2.5 million dollars (Rauzon & Drigot 2002). Clearly, more cost-effective and labor-efficient techniques are needed.

Study objectives

Mangroves around tide pools in Kapoho, Hawaii serve as model ecosystems for examining the impacts of mangrove invasion on tide pool fish assemblages. Here, replicate tide pools differ in vegetation cover (mangrove, native vegetation, open), but not in sub-

strate (i.e. basalt), tidal inundation, and ground water and nutrient inputs. This is especially important as the latter 2 factors can vary significantly along the coast of Hawaii Island (Johnson et al. 2008). Furthermore, a planned effort to test the effectiveness of herbicides at eradicating mangroves and their ability to spread to non-vegetated open tide pools and adjacent uncolonized areas allowed us to examine how tide pools and nekton assemblages would respond to this eradication technique.

The objectives of the study were to document the structure of fish communities associated with these different tide pools and determine whether chemical eradication of mangroves would have any impact on nearshore fish assemblages. Assuming that there was minimal inter-annual variance in fish populations, we hypothesized that (1) fish assemblages associated with mangrove tide pools would be dominated by densities and biomass of exotic fish species, (2) fish assemblages associated with native and non-vegetated tide pools would be dominated by densities and biomass of native fish species, (3) densities and biomass of fish assemblages associated with mangrove tide pools would shift from exotic- to native-dominated after mangrove eradication, and

(4) mangrove eradication via herbicide would have minimal negative impacts on densities and biomass of native fish assemblages that utilize tide pools.

MATERIALS AND METHODS

Study site

The Kapoho tide pools are located on the eastern coast of Hawaii Island, Hawaii, USA (19° 29′ 10″N, 154° 49′ 19″ W) (Fig. 1). The area is a sunken basalt bench comprising several shallow tide pools that are only connected to each other during the highest of tides and that provide habitat for juveniles and adults of many reef-associated fish species (Friedlander et al. 2007). The abundant fish and coral populations in the tide pools are an important component of Hawaii's tourism industry as they attract many snorkelers each year (Flanders 2007). This area was granted protection in 2003 as a Marine Life Conservation District, due to recognition that it provides fish nursery habitat for the area's coastline. *Rhizophora mangle* is thought to have been introduced in the mid-1960s and now covers approximately 9.3 ha.
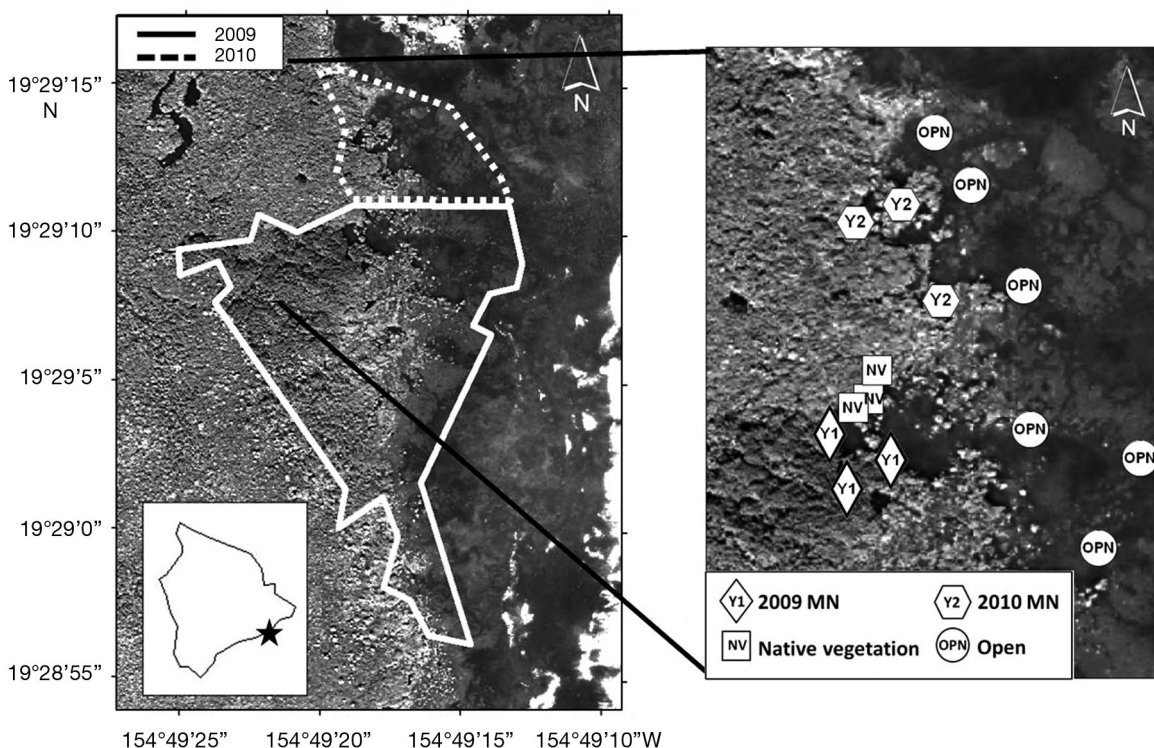

Fig. 1. Location of Kapoho tide pools on Hawaii Island. Solid line encloses area of mangroves treated with herbicide in 2009 (7.3 ha), dashed line encloses area of mangroves treated in 2010 (2 ha). Aerial photos: USDA NRCS (2007)

Other dominant vegetation cover includes native hau *Hibiscus tiliaceus* and milo *Thespesia populnea* trees.

Study design

The impacts of mangroves and chemical eradication of mangroves on fish communities in Kapoho tide pools were examined using a before-after-control-impact (BACI) design. Fish were sampled from 6 mangrove vegetated, 3 native vegetated, and 6 non-vegetated tide pools in 2008 (before mangrove eradication), in 2009 (during mangrove eradication), and in 2010 (after mangrove eradication). Mangrove vegetated tide pools were surrounded by mangrove trees, native vegetated tide pools were surrounded by milo and hau, and non-vegetated tide pools were predominantly surrounded (>50%) by uncolonized basalt. Mangrove propagules were occasionally removed from non-vegetated pools to maintain these open sites. Only 3 native vegetated pools were sampled because only 3 pools could be identified within our study area that met the above criteria. After the initial sampling period in 2008, the majority of mangroves (7.3 ha) were chemically treated by a non-profit environmental group (Malama O Puna) from June 2008 until May 2009. Holes were drilled in the trunks of mangrove trees >1 m high in coastal areas surrounding 3 of the mangrove tide pools (impacted, hereafter referred to as 2009 MN). Mangrove trees were then injected with 1 ml of Aquamaster™ (53.8% glyphosate) per 2.54 cm of tree basal diameter for trees ≥5 cm diameter and 0.3 ml per 2.54 cm of diameter for trees <5 cm. Smaller trees (<1 m) were sprayed with a mixture containing 0.3% Habitat™ (28.7% imazapyr), 0.3% methylated seed oil surfactant and 0.2% marker dye. The remaining 3 mangrove (2010 MN), 3 native vegetated (NATVEG) and 6 non-vegetated tide pools (OPEN) functioned as control pools. As differences in coastal water chemistry can result from differences in groundwater temperatures (e.g. presence/absence of hot springs), substrate age, or presence/absence of cess pools, mangrove, native vegetated and non-vegetated control tide pools were located within the same watershed as the treated areas. Inter-annual difference in densities and biomass of fish were thus considered to indicate a treatment effect as visual surveys conducted in these tide pools over the past 30 yr have shown minimal inter-annual variation (Friedlander et al. 2007, Walsh et al. 2009).

Immediately after the sampling period in 2009, remaining stands of mangroves (2.0 ha) were eradicated from the end of June 2009 until May 2010 as described above, with the exception that trees were injected with 0.5 ml of Habitat™ per 2.54 cm of tree basal diameter for trees ≥5 cm diameter and 0.1 ml per 2.54 cm of diameter for trees <5 cm. Habitat™ was used in the second year because smaller dosages were required and proved to be more effective than Aquamaster™ (A. Kobsa unpubl. data). Living mangroves in the previously treated area were retreated or removed by hand. This resulted in 2 groups of impacted pools: 2009 mangrove (mangroves chemically eradicated before 2009 fish sampling; 2009 MN) and 2010 mangrove tide pools (mangroves chemically eradicated before 2010 fish sampling; 2010 MN). Native vegetated and open pools functioned as control pools. From here on, these 4 groups of pools will be referred to as 2009 MN, 2010 MN, NATVEG, and OPEN, respectively (Fig. 1).

Two independent techniques were used to monitor fish communities in Kapoho tide pools: visual surveys and fyke nets. Visual surveys allowed us to compare fish abundance and community composition within the tide pools among the different treatments. Fyke nets allowed us to compare abundances and community composition of fish assemblages accessing flooded vegetated surfaces adjacent to tide pools.

Visual surveys

Fish communities were sampled using visual surveys conducted in all 4 treatments 2 h before and after peak low tides in May 2008 (before mangrove eradication) and June 2009 and 2010 (after mangrove eradication) using standard belt transect methodology (Brock 1954). Visual surveys were conducted over this 4 h time period and during the neap tidal cycle each year to ensure that pools sampled were discrete units; all pools and their respective transects were sampled once over a 2 d period. Ten minute long surveys were conducted in large treatment pools (area = 180 to 260 m^2) along 25 m long × 2 m wide transects, with 3 m buffers on each end. In smaller tide pools (area = 50 to 100 m^2), 5 min surveys were conducted along 10 m long × 2 m wide transects. In the vegetated treatments, visual surveys were conducted near the locations of the fyke nets. In the 2 larger OPEN tide pools (area > 200 m^2), two 25 m long × 2 m wide belt transect visual surveys were conducted simultaneously by 2 surveyors so that surveys could be treated as discreet samples. Visual surveys recorded fish species and total length. Total length was estimated to the nearest cm for fish up to 10 cm long; fish greater than 10 cm were

placed into 5 cm bins (i.e. 10 to 15 cm, 15 to 20 cm, etc.). Fish densities (no. m^{-2}) were determined by dividing the total number of fish observed along a transect by the area of that transect. Individual fish biomass values were estimated using length-weight regressions from www.fishbase.org or Kulbicki et al. (2005). Total fish biomass (g m^{-2}) was equal to the sum of biomass along each transect divided by the area of the transect.

Fyke nets

Fish communities leaving the flooded surfaces adjacent to the 2009 MN, 2010 MN, and NATVEG pools during the ebb spring tide were sampled using 3 mm mesh mini-fyke nets. Fyke nets were deployed during the full moon phase in May 2008 (before mangrove eradication), in June 2009 (during mangrove eradication) and in June 2010 (after mangrove eradication). Three fyke nets were deployed in the 3 replicate pools of each treatment; treatments were sampled on consecutive days. Fyke nets were placed directly in front of vegetation at low tide with openings facing vegetated areas. The bottom edges of the fyke side wings were secured into the substrate using concrete nails or tent stakes; the tops of the wings were tied to the secured bottom edges using daisy chain knots, thereby minimizing the area obstructed from fish and invertebrates attempting to access the flooded mangrove prop roots or native vegetation. At or near slack high tide, the wings of the fyke net were released and lifted through the water so that the fish exiting the vegetation with the falling tide would be caught in the net. Nets were then sampled 6 h later at the next low tide and fish were identified to species, weighed to the nearest mg, and total lengths measured to the nearest mm. As the area of flooded vegetation sampled could not be accurately measured, fish densities and biomass units are reported as catch per unit effort (CPUE), where the same effort (6 h of soak time per fyke net) was used to normalize data (Arthington et al. 2005).

Physicochemical parameters

Temperature (°C), specific conductivity (mS), pH, and dissolved oxygen concentrations (mg l^{-1}) were continuously measured in each of the 3 vegetated treatments (2009 MN, 2010 MN, and NATVEG pools) each year using YSI™ 600XLM data sondes. Two sondes were deployed into 2 of the 3 replicate pools

for each treatment on consecutive days by attaching to the sides of the fyke nets at or near slack high tide.

In 2009, during mangrove eradication, we were able to collect water samples from all 4 treatment pools (2009 MN, 2010 MN, NATVEG, OPEN) for nutrient analyses. In each pool, 50 ml of water was sampled at or near low tide to minimize mixing from adjacent pools. Water samples were then filtered through a GF/F filter into acid-washed centrifuge tubes and returned to the laboratory on ice where they were stored frozen until they could be analyzed. Nutrients were measured on a Technicon Pulse 2 Autoanalyzer and included ammonium (NH_4^+) (USGS 1-2525-89), nitrate and nitrite (ΣNO_3^-) (USEPA 353.2), soluble reactive phosphorus (PO_4^{3+}) (USEPA 365.1), total nitrogen (TN) (Shimadzu TNM-1), and total phosphorus (TP).

Statistical analyses

Dissolved oxygen concentrations, water temperatures, specific conductivity, and pH were compared from similar tidal cycles (full moon, spring tide) at similar times of the day (18:00 h). Comparisons were made near dusk to minimize the influence of the sun on water temperature and dissolved oxygen. All parameters from each treatment pool were averaged from 18:00 to 19:00 h in each year. Values were then compared among years (2008, 2009, 2010) as well as among treatments (2009 MN, 2010 MN, NATVEG) using a 2-way analysis of variance (ANOVA). Nutrients were compared among treatments using a 1-way ANOVA.

Fish densities and biomass from visual surveys and fyke nets were compared between fish type (exotic vs. native) and among treatments using a 3-way factorial ANOVA. Fixed effects of the model included fish type, treatment, year, along with all three 2-way interactions and one 3-way interaction. Densities of *Kuhlia xenura* and *Poecilia* sp. from visual surveys and fyke nets were also compared among treatments and years using a 2-way factorial ANOVA. Densities of these 2 fish species were compared as they represented the dominant species collected from the tide pools.

Species richness was determined by summing up the total number of fish species observed or collected from each site; Shannon-Wiener index of diversity (*H'*) and evenness (*J*) were calculated as described by Krebs (1989). Species richness, diversity, and evenness from visual surveys and fyke nets were then compared between years as well as among sites using a 2-way factorial ANOVA.

Size classes of native flagtails *Kuhlia xenura* and exotic mollies *Poecilia* sp., the most abundant species in fyke net samples, were compared between years and among treatments using a 2-way ANOVA. Size classes were pooled within each treatment in each year and average lengths were then compared. Size class analysis was only conducted on fyke net samples because fish were measured to the nearest mm as opposed to visual surveys, where fish were measured to the nearest cm (<10 cm) or placed into 5 cm bins (>10 cm).

Community compositions from visual surveys and fyke net samples were compared at the species level among treatments and years using a 2-way crossed analysis of similarities test (ANOSIM). Community composition from visual surveys and fyke net samples were also compared across years for each individual treatment using 1-way ANOSIMs. ANOSIM estimates community similarity using species composition and abundances in a non-parametric permutation procedure applied to a Bray-Curtis similarity matrix (Clarke & Warwick 1994). For each significant ANOSIM test, pair-wise comparisons were made between each treatment or year using a SIMPER analysis, which extracts similarities, re-ranks them, repeats the ANOSIM procedure, and identifies species that are contributing to differences in species assemblages.

Fish densities and biomass from visual surveys and fyke net samples did not meet assumptions of normality and equal variance and were therefore log (x+1)-transformed prior to statistical analysis. All ANOVAs accounted for repeated measures (over time) on each pool, with covariance structures set as an autoregressive of order 1 (i.e. measurements in the same pool in 2008 were potentially more correlated with 2009 than 2010). Post-hoc analyses were conducted using the Tukey-Kramer method. All ANOVAs were performed in PROC MIXED from SAS 9.1 (2002, SAS Institute) at an α level of 0.05, while similarity and diversity analyses were performed in the PRIMER statistical package (v. 6.1.9 2007) (Clarke & Warwick 1994, Carr 1997).

RESULTS

Mangrove control

Over 13 000 mangrove trees were treated with glyphosate in 2008 and over 2000 trees with imazapyr in 2009. Both chemicals appeared to eradicate mangroves as most trees were dead and defoliated 1 yr later, although the dead tree trunks and prop

roots that remained could still provide potential habitat structure around treated mangrove pools. Light levels, although not quantitatively measured, were much higher in tide pools after mangrove eradicate. In 2009, immediately after the larger mangrove area had been eradicated, algal blooms appeared in all sample tide pools but were largely absent in 2010.

Physicochemical parameters

Average dissolved oxygen (DO), temperature, specific conductivity, and pH were all similar among the 3 different vegetated treatments (Fig. 2). Dissolved oxygen, specific conductivity, and pH were significantly lower in 2009 than in 2008 or 2010 (p < 0.01, $F = 7.03$, df = 2; p < 0.01, $F = 8.8$, df = 2; p < 0.01, $F = 9.6$, df = 2, respectively). All 3 variables were also lower in 2010 than in 2008, but this was not significant. Temperature did not significantly differ among years, but was greater in 2009 than in 2008 or 2010.
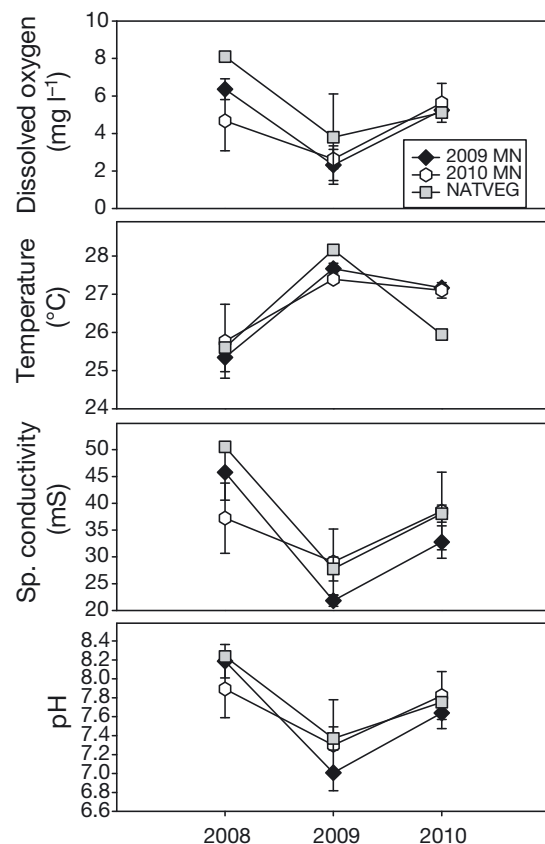

Fig. 2. Average (±1 SE) values of dissolved oxygen, temperature, specific conductivity, and pH measured in mangrove (MN) and native vegetated (NATVEG) tide pools in 2008, 2009, and 2010. Values were taken every 10 min and were averaged from 18:00 to 19:00 h

Concentrations of NH_4^+, PO_4^-, and TP were all below the level of detection (1.0, 0.25, and 0.25 μM, respectively). Total dissolved nitrogen and ΣNO_3^- ranged from 9.3 to 26.0 μM and 6.0 to 28.4 μM, respectively. The high amounts of ΣNO_3^- relative to TDN suggest that TDN was largely made up of ΣNO_3^-; dissolved organic forms of nitrogen were a minor component. Comparisons could not be made between years as data were not collected in 2008 or 2010. Comparisons among the 4 treatments revealed no significant difference in either TDN or ΣNO_3^- concentrations.

Visual surveys

A total of 50 fish species (46 native, 4 exotic) were surveyed from tide pools over the 3 yr period (Table 1). Total fish densities within tide pools averaged across years did not significantly differ among the 4 different treatments (2009 MN, 2010 MN, NATVEG, OPEN) (Table 2, Fig. 3A). After the initial application of herbicides to the 2009 MN sites in 2009, fish densities averaged across all 4 treatments were significantly and 2 to 3× lower (2.1 ± 0.5 m^{-2}) compared to pre-mangrove eradication (2008) (4.4 ± 0.6 m^{-2}) or post mangrove eradication (2010) densities (6.1 ± 1.0 m^{-2}) (p < 0.001, $F = 20.4$, df = 2). One year later (2010), total fish densities had increased, such that they were significantly greater than 2009 densities (p < 0.001, $F = 20.4$, df = 2), but were not significantly different from 2008 densities. Examination of individual treatments across time revealed that 2009 fish densities were lower than pre-mangrove eradication densities (2008) in all treatments, but this was only significant in NATVEG pools (Site × Year:

Table 1. Average (±1 SE) fish densities (no. m^{-2}) from visual surveys in 2008, 2009, and 2010. Tide pool treatments: MN: mangroves eradicated; NATVEG: native vegetation; OPEN: non-vegetated. Status: N: Hawaiian endemic; IP: Indo-Pacific; E: exotic; CCG: circumglobal. **Bold** taxa are exotic species

Taxon	Status	2009 MN	2010 MN	NATVEG	OPEN
2008					
Abudefduf abdominalis	N	0.17 ± 0.10	0.17 ± 0.06	0.05 ± 0.05	0.23 ± 0.07
Abudefduf sordidus	IP	0.13 ± 0.08	0.14 ± 0.05	–	0.12 ± 0.02
Acanthurus triostegus	IP	0.33 ± 0.20	0.63 ± 0.32	0.44 ± 0.25	0.55 ± 0.08
Arothron meleagris	IP	0.01 ± 0.01	–	–	–
Blennidae	N	–	–	–	0.01 ± 0.01
Cephalopholis argus	**E**	**–**	**–**	**–**	**0.01 ± 0.01**
Chaetodon auriga	IP	0.01 ± 0.01	–	–	0.01 ± 0.01
Chaetodon lunula	IP	0.04 ± 0.02	0.02 ± 0.02	0.03 ± 0.03	0.03 ± 0.01
Chlorurus sordidus	IP	–	0.09 ± 0.09	–	0.05 ± 0.03
Gomphosus varius	IP	–	0.13 ± 0.08	–	0.11 ± 0.02
Kuhlia xenura	N	1.66 ± 1.24	0.62 ± 0.34	3.11 ± 0.76	1.01 ± 0.94
Kyphosus sp.	IP	–	0.02 ± 0.02	–	–
Lutjanus fulvus	**E**	**–**	**0.02 ± 0.02**	**–**	**–**
Mugil cephalus	CCG	0.01 ± 0.01	0.43 ± 0.07	0.34 ± 0.21	0.22 ± 0.11
Parupeneus multifasciatus	IP	–	–	–	0.01 ± 0.00
***Poecilia* sp.**	**E**	**2.16 ± 0.77**	**0.62 ± 0.62**	**2.54 ± 0.74**	**–**
Scarus sp.	IP	–	–	–	0.06 ± 0.05
Scarus psittacus	IP	–	0.10 ± 0.10	–	0.5 ± 0.14
Scarus rubroviolaceus	IP	–	–	–	0.01 ± 0.01
Sphraena barracuda	CCG	0.01 ± 0.01	0.01 ± 0.01	–	–
Stethojulius balteata	N	–	–	–	0.01± 0.01
Stegastes fasciolatus	IP	–	–	–	0.01 ± 0.01
Thalassoma duperrey	N	0.13 ± 0.08	0.30 ± 0.13	0.39 ± 0.19	0.61 ± 0.12
Thalassoma trilobatum	IP	–	0.01 ± 0.01	–	0.02 ± 0.01
Total		4.66 ± 1.97	3.29 ± 0.33	6.89 ± 1.45	3.56 ± 0.91
2009					
Abudefduf abdominalis	N	0.08 ± 0.06	0.39 ± 0.19	0.03 ± 0.02	0.09 ± 0.03
Abudefduf sordidus	IP	0.17 ± 0.06	0.21 ± 0.01	–	0.14 ± 0.02
Abudefduf vaigiensis	IP	–	0.01 ± 0.01	–	–
Acanthurus blochii	IP	0.11 ± 0.09	–	–	0.01 ± 0.01
Acanthurus nigrofuscus	IP	–	0.02 ± 0.02	–	0.01 ± 0.01
Acanthurus triostegus	IP	0.31 ± 0.28	0.7 ± 0.18	0.08 ± 0.06	0.54 ± 0.14

Table 1 (continued)

Taxon	Status	2009 MN	2010 MN	NATVEG	OPEN
Blennidae	N	–	0.01 ± 0.01	–	–
Canthigaster amboinensis	IP	–	0.02 ± 0.02	–	–
Cephalopholis argus	**E**	**0.01 ± 0.01**	**0.01 ± 0.01**	**–**	**0.01 ± 0.01**
Chaetodon auriga	IP	0.01 ± 0.01	–	–	0.02 ± 0.01
Chaetodon ephippium	IP	0.01 ± 0.01	–	–	–
Chaetodon lunula	IP	0.06 ± 0.03	0.05 ± 0.04	0.04 ± 0.04	0.01 ± 0.01
Encrasicholina purpurea	N	–	0.08 ± 0.08	–	–
Gomphosus varius	IP	–	0.11 ± 0.04	–	0.05 ± 0.02
Kuhlia xenura	N	–	0.47 ± 0.47	–	0.25 ± 0.17
Kyphosus sp.	IP	0.01 ± 0.01	0.03 ± 0.03	0.01 ± 0.01	0.02 ± 0.0
Labroides phthirophagus	N	–	–	–	–
Lutjanus fulvus	**E**	**0.04 ± 0.03**	**0.02 ± 0.01**	**–**	**0.01 ± 0.0**
Mugil cephalus	CCG	0.02 ± 0.02	0.05 ± 0.05	0.06 ± 0.06	–
Mulloidichthys flavolineatus	IP	0.16 ± 0.16	–	–	–
Neomyxus leuciscus	IP	–	0.03 ± 0.03	–	–
Parupeneus porphyreus	N	–	–	–	0.01 ± 0.01
***Poecilia* sp.**	**E**	**2.33 ± 2.33**	**–**	**–**	**–**
Sphraena barracuda	CCG	0.03 ± 0.01	–	–	–
Scarus sp.	IP	0.01 ± 0.01	0.05 ± 0.05	–	0.05 ± 0.03
Scarus psittacus	IP	0.03 ± 0.02	–	–	0.01 ± 0.01
Stegastes fasciolatus	IP	–	–	–	0.01 ± 0.01
Thalassoma duperrey	N	0.57 ± 0.33	0.42 ± 0.16	0.36 ± 0.12	0.31 ± 0.02
Thalassoma trilobatum	IP	–	0.01 ± 0.01	–	0.01 ± 0.01
Total		3.96 ± 1.57	2.68 ± 1.2	0.60 ± 0.02	1.57 ± 0.33
2010					
Abudefduf abdominalis	N	–	0.17 ± 0.07	0.21 ± 0.12	0.32 ± 0.1
Abudefduf sordidus	IP	0.09 ± 0.06	0.11 ± 0.03	0.01 ± 0.01	0.28 ± 0.03
Abudefduf vaigiensis	IP	–	–	–	0.05 ± 0.05
Acanthurus blochii	IP	0.03 ± 0.03	0.01 ± 0.01	–	–
Acanthurus nigrofuscus	IP	–	–	–	–
Acanthurus triostegus	IP	0.18 ± 0.15	0.5 ± 0.32	1.27 ± 0.52	0.91 ± 0.16
Arothron hispidus	IP	–	–	–	0.01 ± 0
Asterropteryx semipunctatus	IP	–	0.03 ± 0.03	–	0.13 ± 0.03
Blennidae	N	0.02 ± 0.02	–	–	–
Canthigaster jactator	N	–	–	–	0.01 ± 0
Cephalopholis argus	**E**	**0.02 ± 0.02**	**0.01 ± 0.01**	**–**	**0.01 ± 0**
Chaetodon auriga	IP	–	–	–	0.02 ± 0.01
Chanos chanos	IP	0.01 ± 0.01	–	–	–
Chaetodon lunula	IP	0.04 ± 0.03	0.01 ± 0.01	0.1 ± 0.08	0.04 ± 0.01
Chlorurus sordidus	IP	–	–	–	0.28 ± 0.13
Gymnothorax sp.	IP	0.01 ± 0.01	0.01 ± 0.01	–	–
Gnatholepis sp.	IP	0.04 ± 0.02	–	–	–
Gomphosus varius	IP	–	0.02 ± 0.02	–	0.18 ± 0.09
Kuhlia xenura	N	2.73 ± 1.42	3.14 ± 1.74	7.08 ± 0.84	0.6 ± 0.58
Labroides phthirophagus	N	–	–	–	–
Lutjanus fulvus	**E**	**0.01 ± 0.01**	**–**	**–**	**–**
Mugil cephalus	CCG	0.08 ± 0.08	0.11 ± 0.09	0.01 ± 0.01	0.04 ± 0.02
Mulloidichthys flavolineatus	IP	0.01 ± 0.01	0.07 ± 0.07	–	–
Neomyxus leuciscus		–	0.01 ± 0.01	–	0.26 ± 0.12
Parupeneus pleurostigma	IP	–	–	0.03 ± 0.03	–
Plectroglyphidodon imparipennis	IP	–	–	–	0.01 ± 0.01
***Poecilia* sp.**	**E**	**0.34 ± 0.29**	**0.65 ± 0.65**	**2.04 ± 0.95**	**–**
Scarus jv.	IP	0.04 ± 0.04	–	–	0.19 ± 0.09
Scarus psittacus	IP	–	0.14 ± 0.14	–	0.22 ± 0.09
Sphraena barracuda	CCG	–	0.01 ± 0.01	–	–
Stethojulius balteata	N	–	–	–	0.02 ± 0.01
Stegastes fasciolatus	IP	0.01 ± 0.01	–	–	0.07 ± 0.02
Thalassoma duperrey	N	0.28 ± 0.28	0.17 ± 0.06	0.46 ± 0.18	0.87 ± 0.15
Thalassoma trilobatum	IP	0.01 ± 0.01	–	0.02 ± 0.02	0.02 ± 0.01
Valamugil engeli	**E**	**–**	**0.22 ± 0.18**	**0.96 ± 0.39**	**–**
Total		3.95 ± 1.67	5.41 ± 2.2	12.18 ± 1.38	4.56 ± 0.54

Table 2. Average (±1 SE) densities of total fish, *Poecilia* sp., and *Kuhlia xenura* from visual survey and fyke net data. **Bold** values indicate significant differences (*p < 0.05, **p < 0.01, ***p < 0.001); different letters indicate significant differences among years in post-hoc comparisons

	2008	2009	2010	Average
VISUAL SURVEYS				
Total fish				
2009 MN	4.7 ± 2.0	4.0 ± 1.6	3.9 ± 1.7	4.2 ± 0.9
2010 MN	3.3 ± 0.3	2.7 ± 1.2	12.2 ± 1.4	6.0 ± 1.6
NATVEG	**6.9 ± 1.4**[a]	**0.6 ± 0.1**[b]	**5.4 ± 2.2**[***a]	4.3 ± 1.2
OPEN	3.6 ± 0.9	1.6 ± 0.3	4.6 ± 0.5	3.2 ± 0.5
Average	**4.4 ± 0.6**[a]	**2.1 ± 0.5**[b]	**6.1 ± 1.0**[***a]	
Kuhlia xenura				
2009 MN	1.7 ± 1.2	–	3.1 ± 1.7	1.5 ± 0.7
2010 MN	0.6 ± 0.3	0.5 ± 0.5	2.7 ± 1.4	1.4 ± 0.7
NATVEG	3.1 ± 0.8	–	7.1 ± 0.8	3.4 ± 1.1
OPEN	1.0 ± 1.0	0.3 ± 0.2	0.6 ± 0.6	0.6 ± 0.4
Average	**1.5 ± 0.5**[a]	**0.2 ± 0.1**[b]	**2.8 ± 0.8**[***a]	
Poecilia sp.				
2009 MN	2.2 ± 0.8	2.3 ± 2.3	0.3 ± 0.3	1.6 ± 0.8
2010 MN	0.6 ± 0.6	–	0.7 ± 0.7	0.4 ± 0.1
NATVEG	2.4 ± 0.7	–	2.0 ± 1.0	1.5 ± 0.5
OPEN	–	–	–	–
Average	**1.1 ± 0.4**[ac]	**0.5 ± 0.5**[b]	**0.6 ± 0.3**[*bc]	
FYKE NETS				
Total fish				
2009 MN	133.3 ± 84.6	125.7 ± 55.9	163.3 ± 32.2	**140.8 ± 31.3**[a]
2010 MN	36.0 ± 18.1	23.3 ± 9.2	66.0 ± 14.5	**41.8 ± 9.6**[b]
NATVEG	85.7 ± 10.3	81.3 ± 14.2	232.7 ± 99.2	**133.2 ± 38.3**[*a]
Average	**85.0 ± 28.8**[a]	**76.8 ± 22.4**[a]	**154.0 ± 38.8**[*b]	
Kuhlia xenura				
2009 MN	31.7 ± 13.2	8.0 ± 8.0	99.0 ± 10.0	46.2 ± 14.6
2010 MN	26.7 ± 21.9	0.7 ± 0.7	48.3 ± 11.6	25.2 ± 9.9
NATVEG	52.0 ± 12.4	5.7 ± 5.7	108.7 ± 43.3	55.4 ± 19.8
Average	**36.8 ± 9.1**[a]	**4.8 ± 3.0**[b]	**85.3 ± 16.2**[***a]	
Poecilia sp.				
2009 MN	95.0 ± 74.4	106.0 ± 51.2	58.0 ± 26.8	86.3 ± 28.1
2010 MN	4.3 ± 4.3	10.7 ± 10.7	3.0 ± 2.5	6.0 ± 3.6
NATVEG	26.7 ± 5.9	62.7 ± 6.1	61.7 ± 29.6	50.3 ± 10.7
Average	42.0 ± 25.5	59.8 ± 12.4	40.9 ± 21.7	

p < 0.001, *F* = 5.7, df = 6) (Table 2, Fig. 3A). One year later (2010), total fish densities from each treatment were similar to or greater than densities in 2008.

Native fish species densities were largely comprised of the flagtail *Kuhlia xenura* (Table 1). Densities of *K. xenura* averaged across years did not differ among treatments, although they were generally higher overall in native vegetated compared to mangrove or open pools (Table 2). After the initial application of herbicide to the 2009 MN tide pools in 2009, *K. xenura* densities averaged across pool treatments were significantly lower (0.2 ± 0.1 m^{-2}) compared to densities from 2008 (1.5 ± 0.5 m^{-2}) and 2010 (2.8 ± 0.8 m^{-2}) (p < 0.001, *F* = 21.8, df = 2). *K. xenura* did not significantly differ between 2008 and 2010. Exotic fish

densities were largely comprised of the molly hybrid complex *Poecilia* sp. *Poecilia* sp. were only observed in vegetated pools; densities averaged across years (±1 SE) did not significantly differ among mangrove and native vegetated pools (Table 2). *Poecilia* sp. densities averaged across all pool treatments were significantly different among years (p < 0.05, *F* = 3.93, df = 2), but this was due to significantly higher densities in 2008 (1.1 ± 0.3 m^{-2}) compared to 2009 (0.5 ± 0.5 m^{-2}). Densities in 2010 (0.6 ± 0.3 m^{-2}) did not significantly differ from 2008 or 2009 densities. In 2009, mollies were absent from all but one 2009 MN pool, where they represented 58 % of the total fish observed in that pool. In 2010, mollies were again present in 2009 MN, 2010 MN and NATVEG pools. Compared to 2008, poeciliid densities in 2010 were lower for 2009 MN pools, but were comparable for 2010 MN and NATVEG pools.

When total densities of native versus exotic fish were compared, significantly more native fish than exotic fish were observed in visual surveys in all 4 tide pool treatments (Site × Fish type: p < 0.01, *F* = 5.0, df = 3) as well as in each year (Year × Fish type: p < 0.5, *F* = 4.2, df = 2) (Fig. 3B,C). Total exotic fish densities were significantly greater in vegetated tide pools (2009 MN, 2010 MN, NATVEG) than in OPEN tide pools, while total native fish densities did not statistically differ among any of the types of tide pools. After the initial herbicide application to the 2009 MN tide pools in 2009, exotic and native fish densities averaged across treatments were significantly lower than in 2008 (pre-mangrove eradication) or 2010. Total exotic fish densities in 2010 were not significantly different from those in 2008, while total native fish densities were significantly higher in 2010. There were no significant interactions between year and treatments for either exotic or native fish comparisons.

Nearly twice as many species were observed in OPEN tide pools than in vegetated tide pool treatments (p < 0.01, *F* = 7.9, df = 2) when numbers of species were averaged across years. There were no significant differences when numbers of species were averaged across treatments and compared among years (Table 3). Diversity (*H'*) was significantly and 2× higher in OPEN tide pools compared to 2009 MN and NATVEG tide pools (p < 0.05, *F* = 5.3, df = 2), but was similar between OPEN and 2010 MN pools or
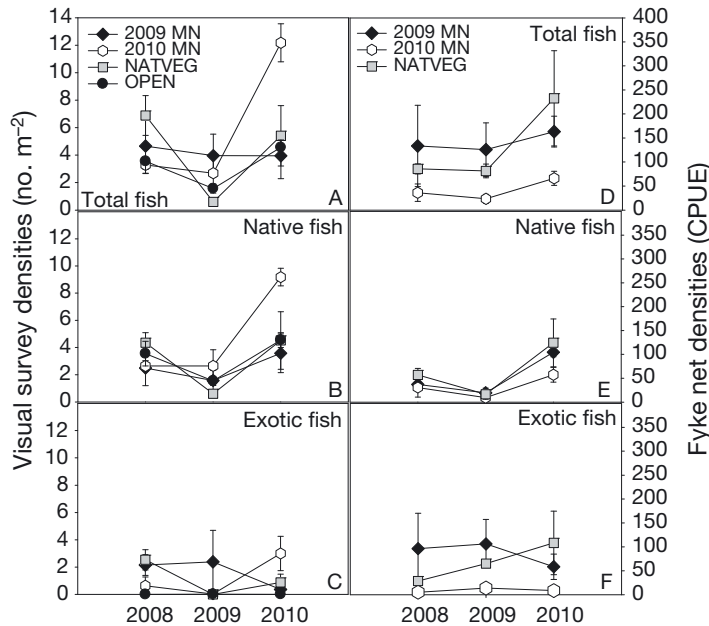
Fig. 3. Average fish densities (±1 SE) of (A,D) total, (B,E) native, and (C,F) exotic fish from (A,B,C) visual surveys (no. m^{-2}) in mangrove (MN), native (NATVEG), and non-vegetated (OPEN) tide pools and (D,E,F) fyke nets (catch per unit effort, CPUE) in MN and NATVEG tide pools. Total fish densities represent the sum of native and exotic fish densities

between any of the vegetated pools. Species were evenly distributed across tide pool treatments and time (Table 3). The 2-way crossed ANOSIM revealed that community structure differed significantly among treatments (R = 0.47, p < 0.001) due to differences between OPEN pools and all vegetated pools. SIMPER analysis revealed that dissimilarity between OPEN and vegetated pools averaged across years ranged from 55 to 73%, with higher densities of *Kuhlia xenura* and *Poecilia* spp. in vegetated pools averaged across years contributing 33 to 39% of that dissimilarity. In contrast, densities of reef-associated species, such as the convict tang *Acanthurus triostegus*, saddle wrasse *Thalassoma duperrey*, and palenose parrotfish *Scarus psittacus* averaged across years were greater in OPEN pools (0.67 ± 0.13, 0.60 ± 0.09, 0.24 ± 0.8 m^{-2}, respectively) compared to 2009 MN (0.27 ± 0.21, 0.33 ± 0.23, 0.01 ± 0.01 m^{-2}, respectively), 2010 MN (0.61 ± 0.27, 0.30 ± 0.12, 0.08 ± 0.08 m^{-2}, respectively), or NATVEG (0.60 ± 0.28, 0.40 ± 0.16, 0.0 ± 0.0 m^{-2}, respectively). Community structure was also significantly different among years (R = 0.39, p < 0.001), which was due to differences between 2009 (after initial herbicide treatment) and 2008 (pre-mangrove eradication) or 2010 (post-mangrove eradication). One-way ANOSIMs from each

individual treatment revealed that these interannual differences in species assemblages were only significant for OPEN pools (R = 0.44, p < 0.001), which was again due to differences between 2009 (after initial herbicide treatment) and 2008 (pre-mangrove eradication) or 2010 (post-mangrove eradication). Lower densities of *K. xenura*, *S. psittacus*, and *T. duperrey* in 2009 cumulatively contributed to 50% of dissimilarity between 2008 and 2009. Higher densities of *K. xenura*, *S. psittacus*, and *T. duperrey* in 2010 cumulatively contributed to 32% of dissimilarity between 2009 and 2010. Community structure between 2008 and 2010 was similar.

Table 3. Average (±1 SD) diversity values from visual survey and fyke net data. **Bold** values indicate significant differences (*p < 0.05, **p < 0.01, ***p < 0.001), different letters indicate significant post-hoc comparisons

|	2008	2009	2010	Average
VISUAL SURVEYS				
Species richness				
2009 MN	7.3 ± 3.8	9.0 ± 5.3	8.3 ± 6.8	**8.2 ± 4.8**[a]
2010 MN	9.0 ± 1.0	10.3 ± 4.0	9.7 ± 0.6	**9.7 ± 2.2**[a]
NATVEG	5.3 ± 0.6	3.3 ± 1.2	7.7 ± 0.6	**5.4 ± 2.0**[a]
OPEN	13.0 ± 3.4	11.7 ± 2.7	17.7 ± 4.3	**14.1 ± 4.2**[**b]
Average	9.5 ± 4.1	9.2 ± 4.4	12.2 ± 5.9	
Shannon-Wiener diversity (*H*′)				
2009 MN	1.2 ± 0.6	1.2 ± 1.0	1.0 ± 0.8	**1.1 ± 0.7**[a]
2010 MN	1.7 ± 0.4	1.8 ± 0.2	1.4 ± 0.3	**1.7 ± 0.3**[ab]
NATVEG	1.2 ± 0.2	0.9 ± 0.4	1.1 ± 0.6	**1.1 ± 0.4**[a]
OPEN	1.8 ± 0.4	1.7 ± 0.3	2.1 ± 0.3	**1.9 ± 0.3**[*b]
Average	1.5 ± 0.5	1.5 ± 0.6	1.5 ± 0.6	
Evenness				
2009 MN	0.6 ± 0.1	0.5 ± 0.4	0.5 ± 0.2	0.5 ± 0.2
2010 MN	0.7 ± 0.1	0.7 ± 0.2	0.6 ± 0.3	0.7 ± 0.2
NATVEG	0.8 ± 0.1	0.8 ± 0.1	0.6 ± 0.2	0.7 ± 0.2
OPEN	0.7 ± 0.1	0.7 ± 0.1	0.7 ± 0.1	0.7 ± 0.1
Average	0.7 ± 0.1	0.7 ± 0.2	0.6 ± 0.2	
FYKE NETS				
Species richness				
2009 MN	7.0 ± 1.7	6.0 ± 1.7	6.7 ± 2.1	6.6 ± 1.7
2010 MN	5.7 ± 1.2	6.3 ± 1.5	9.7 ± 2.1	7.2 ± 2.3
NATVEG	6.3 ± 0.6	5.7 ± 1.5	7.0 ± 1.7	6.3 ± 1.3
Average	**6.3 ± 1.2**[a]	**6.0 ± 1.4**[a]	**7.8 ± 2.2**[**b]	
Shannon-Wiener diversity (*H*′)				
2009 MN	1.1 ± 0.2	0.7 ± 0.1	1.2 ± 0.1	1.0 ± 0.3
2010 MN	0.7 ± 0.1	0.6 ± 0.4	1.1 ± 0.4	0.8 ± 0.3
NATVEG	1.1 ± 0.2	0.7 ± 0.2	1.3 ± 0.3	1.0 ± 0.3
Average	**1.0 ± 0.2**[a]	**0.6 ± 0.2**[b]	**1.1 ± 0.3**[***a]	
Evenness				
2009 MN	0.6 ± 0.2	0.4 ± 0.1	0.6 ± 0.1	0.5 ± 0.2
2010 MN	0.4 ± 0.1	0.3 ± 0.2	0.5 ± 0.2	0.4 ± 0.1
NATVEG	0.6 ± 0.1	0.4 ± 0.2	0.7 ± 0.1	0.6 ± 0.2
Average	**0.5 ± 0.1**[a]	**0.4 ± 0.1**[b]	**0.6 ± 0.1**[***a]	
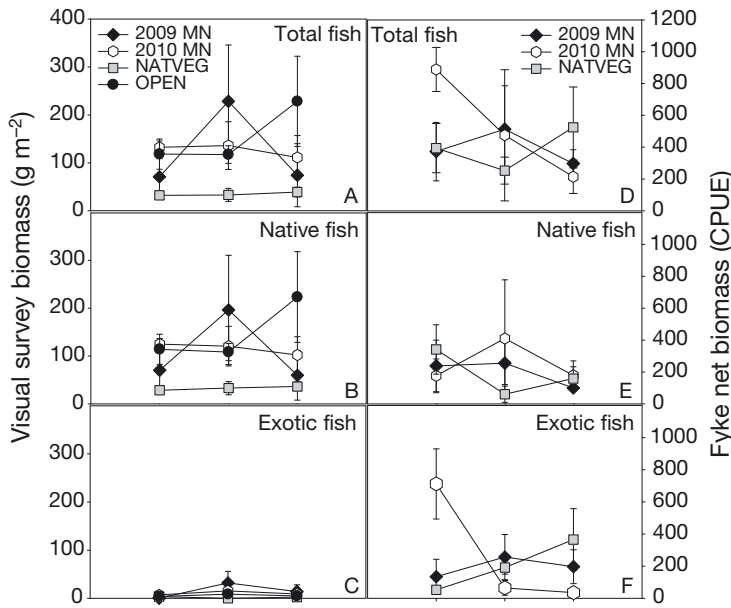
Fig. 4. Average fish biomass (±1 SE) of (A,D) total, (B,E) native, and (C,F) exotic fish from (A,B,C) visual surveys (g m^{-2}) in mangrove (MN), native (NATVEG), and nonvegetated (OPEN) tide pools and (D,E,F) fyke nets (catch per unit effort, CPUE) in MN and NATVEG tide pools. Total fish biomasses represent the sum of native and exotic fish biomasses

There were no significant differences in fish biomass among years or sites (Fig. 4A). Native fish biomass (110.9 ± 2.2 g m^{-2}) was significantly and over 10× greater than exotic fish biomass (8.0 ± 2.1 g m^{-2}) ($p < 0.001$, $F = 225.5$, df = 1). A significant interaction between fish and treatment ($p < 0.05$, $F = 2.8$, df = 3) was due to 2 to 4× more native fish biomass than exotic fish biomass in all 4 tide pool treatments as well as significantly more native fish biomass in the OPEN tide pools compared to 2010 MN and NATVEG tide pools (Fig. 4B,C).

Fyke nets

A total of 19 species (15 native, 4 exotic) were collected in fyke nets over the 3 yr period (Table 4), most of which are commonly reported from these tide pools (Walsh et al. 2009). Significantly higher densities of fish were sampled across years leaving the flooded surfaces of the 2009 MN (140.8 ± 31.3 m^{-2}) and NATVEG (133.2 ± 38.3 m^{-2}) tide pools than the 2010 MN tide pools (41.8 ± 9.6 m^{-2}) ($p < 0.01$, $F = 6.7$, df = 2) (Table 2, Fig. 3D). Fish densities averaged across treatments were significantly greater in 2010 (154.0 ± 38.8 m^{-2}) compared to pre-mangrove control (2008) (85.0 ± 28.8 m^{-2}) or 2009 (initial herbicide

application) fish densities (76.8 ± 22.5 m^{-2}) ($p < 0.05$, $F = 3.8$, df = 2). High variances across treatments resulted in no differences in average fish densities prior to mangrove eradication (2008) and immediately after herbicide was applied to the 2009 MN pools (2009).

In all 3 years, densities of native fish species accessing the flooded vegetated areas in Kapoho were largely comprised of *Kuhlia xenura* (Table 4). Densities of *K. xenura* leaving mangrove and native vegetation did not significantly differ (Table 2), while densities of *K. xenura* averaged across treatments were significantly lower after the initial application of herbicide in 2009 (4.8 ± 3.0 m^{-2}) compared to 2008 (pre-mangrove eradication; 36.8 ± 9.1 m^{-2}) and 2010 (post-mangrove eradication; 85.3 ± 16.2 m^{-2}) ($p < 0.001$, $F = 33.0$, df = 2). Densities of exotic fish species from fyke net samples were largely comprised of *Poecilia* sp., which had similar densities in mangroves and native vegetation as well over the 3 years sampled.

After the initial application of herbicide in 2009, there were significantly fewer native fish (15.0 ± 4.7 m^{-2}) compared to 2008 (41.6 ± 8.9 m^{-2}) or 2010 (95.4 ± 18.3 m^{-2}) ($p < 0.05$, $F = 5$, df = 2) (Fig. 3E), which also resulted in significantly fewer native fish than exotic fish accessing the flooded surfaces of treatments that year. There were no differences between 2008 and 2010 native fish densities, although 2010 densities were generally higher. There were no significant differences among exotic fish densities from fyke nets in 2008 (43.4 ± 25.56 m^{-2}), 2009 (61.8 ± 20.2 m^{-2}), or 2010 (58.6 ± 25.2 m^{-2}) (Fig. 3F).

The native shrimp *Palaemon debilis* was also a dominant portion of the nekton collected in the fyke net samples. Shrimp densities averaged across years did not differ significantly among tide pool treatments; shrimp densities averaged across habitats were significantly higher after initial herbicide application in 2009 compared to 2008 or 2010 ($p < 0.001$, $F = 14.21$, df = 2) (Fig. 5). There were no significant interactions between year and treatment.

More species were collected from fyke nets in 2010 than in 2008 or 2009 ($p < 0.01$, $F = 7.28$, df = 2). Diversity (H') and evenness (J) were significantly lower in 2009 than 2008 or 2010 ($p < 0.001$, $F = 24.7$, df = 2; $p < 0.001$, $F = 15.0$, df = 2, respectively) (Table 3). There were no differences between 2008 and 2010. Both 2- and 1-way ANOSIMs revealed that there were no significant differences in community structure in the nekton community accessing the vegetated areas adjacent to all 3 tide pool treatments or among years.

Table 4. Average (±1 SE) fish densities (catch per unit effort, CPUE) from 2008 fyke nets. Other details as in Table 1

Taxon	Status	2009 MN	2010 MN	NATVEG
2008				
Bathygobius cocosensis	CCG	2.00 ± 1.00	1.00 ± 1.00	3.00 ± 1.00
Cephalopholis argus	**E**	–	**0.67 ± 0.58**	–
Eleotris sandwicensis	N	0.33 ± 0.58	2.67 ± 3.06	–
Gymnothorax eurostus	IP	0.67 ± 0.58	–	–
Kuhlia xenura	N	31.67 ± 22.9	26.67 ± 37.86	52.00 ± 21.52
Lutjanus fulvus	**E**	–	**0.33 ± 0.58**	–
Mugil cephalus	CCG	2.33 ± 3.21	0.33 ± 0.58	1.67 ± 1.53
***Poecilia* sp.**	**E**	**95.00 ± 128.95**	**4.33 ± 7.51**	**26.67 ± 10.21**
Sphraena barracuda	CCG	–	–	0.33 ± 0.58
Valamugil engeli	**E**	**1.33 ± 2.31**	–	**2.00 ± 3.46**
Total		133.33 ± 146.62	36.0 ± 31.32	85.67 ± 17.9
2009				
Abudefduf abdominalis	IP	–	0.33 ± 0.33	–
Acanthurus triostegus	IP	–	1.00 ± 1.00	–
Bathygobius cocosensis	CCG	2.33 ± 0.33	4.67 ± 3.71	8.33 ± 4.63
Eleotris sandwicensis	N	3.33 ± 2.85	0.33 ± 0.33	0.33 ± 0.33
Gymnothorax eurostus	IP	0.33 ± 0.33	0.67 ± 0.33	–
Kuhlia xenura	N	8.00 ± 8.00	0.67 ± 0.67	5.67 ± 5.67
Mugil cephalus	CCG	4.33 ± 1.86	1.00 ± 1.00	2.00 ± 1.53
Oxyurichthys lonchotus cf.	IP	1.00 ± 1.00	0.33 ± 0.33	–
***Poecilia* sp.**	**E**	**106.00 ± 51.16**	**10.67 ± 10.67**	**62.67 ± 6.12**
Total		125.33 ± 55.84	19.67 ± 8.37	79.0 ± 13.2
2010				
Abudefduf abdominalis	IP	–	0.33 ± 0.33	–
Abudefduf sordidus	IP	0.33 ± 0.33	–	–
Acanthurus triostegus	IP	0.33 ± 0.33	1.33 ± 0.88	1.33 ± 0.67
Apogonidae		–	0.33 ± 0.33	–
Bathygobius cocosensis	CCG	3.67 ± 0.88	4 ± 3.06	5.33 ± 2.19
Eleotris sandwicensis	N	0.33 ± 0.33	0.67 ± 0.67	1 ± 0.58
Gobiidae		0.67 ± 0.67	0.33 ± 0.33	–
Gymnothorax eurostus cf.	IP	–	0.33 ± 0.33	–
Kuhlia xenura	N	99 ± 10.02	48.33 ± 11.61	108.67 ± 43.34
Mugil cephalus	CCG	–	1 ± 1	8 ± 7.02
Mulloidichthys flavolineatus	IP	0.33 ± 0.33	–	–
***Poecilia* sp.**	**E**	**58 ± 26.76**	**3 ± 2.52**	**61.67 ± 29.63**
Pristiapogon taeniopterus	IP	–	0.33 ± 0.33	–
Sargocentron sp.		–	0.33 ± 0.33	–
Valamugil engeli	**E**	**0.67 ± 0.67**	**5.67 ± 4.18**	**46.67 ± 37.95**
Total		163.33 ± 32.2	66 ± 14.53	232.67 ± 99.17

cantly smaller flagtails were also collected in 2008 (58.9 ± 2.3 mm) and 2010 (47.0 ± 0.7 mm) compared to 2009 (80.7 ± 4.8 mm) (p < 0.001, F = 19.27, df = 2). A significant interaction between year and treatment (p < 0.001, F = 7.1, df = 4) was largely due to significantly smaller flagtails being collected in 2008 and 2010 than in 2009 in the 2009 MN and NATVEG tide pools (Fig. 6).

Significantly smaller exotic mollies *Poecilia* sp. were collected in fyke nets from mangrove tide pools (2009 MN: 47.8 ± 0.7 mm; 2010 MN 46.3 ± 2.4 mm) compared to native vegetated tide pools (NATVEG: 56.5 ± 0.9 mm) (p < 0.001, F = 11.7, df = 2). Significantly smaller mollies were also collected in 2008 (46.7 ± 0.7 mm) and 2009 (52.0 ± 0.9 mm) compared to 2010 (63.3 ± 1.0 mm) (p < 0.001, F = 21.5, df = 2). A significant 2-way interaction (p < 0.05, F = 2.8, df = 4) revealed that these differences were due to significantly smaller mollies being collected from 2009 and 2010 MN pools compared to NATVEG pools, but only in 2008 and 2009. Fish were similar sized among treatments in 2010. Smaller mollies were also collected in 2008 and 2009 than in 2010 in all 3 vegetated treatments (Fig. 7).

There were no significant differences in fish biomass when years, treatments, or fish types were compared (Fig. 4D,E,F).

Fish size class distribution

Significantly smaller native flagtails *Kuhlia xenura* were collected in fyke nets from mangrove tide pools (2009 MN: 41.9 ± 1.0 mm; 2010 MN: 48.0 ± 1.2 mm) compared to native vegetated tide pools (NATVEG: 61.5 ± 1.6 mm) (p < 0.001, F = 7.3, df = 2). Signifi-

DISCUSSION

Surveys conducted within Kapoho tide pools prior to mangrove control revealed little to no inter-annual variation in species assemblages (Friedlander et al. 2007, Walsh et al. 2009). Quarterly nekton surveys conducted in 20 Hawaiian coastal wetlands also revealed minimal inter-annual variation in fish assemblages (MacKenzie & Bruland 2012). Similar fish assemblages over time from these 3 studies were attributed to (1) movement of fish being restricted to tidally discrete tide pools and coastal wetlands, and
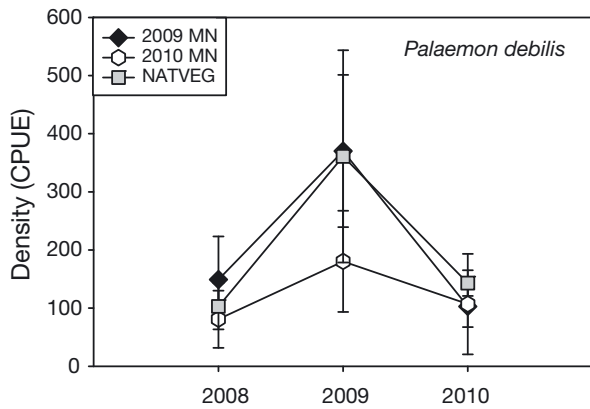
Fig. 5. *Palaemon debilis.* Average densities (±1 SE) of native shrimp from fyke nets (catch per unit effort, CPUE) in mangrove (MN) and native vegetated NATVEG) tide pools

Fig. 6. *Kuhlia xenura.* Number of individual native flagtail from each size class collected in fyke nets from mangrove (MN) and native vegetated (NATVEG) tide pools in 2008, 2009, and 2010

(2) many of the fish sampled having high site fidelity within Hawaiian ecosystems (e.g. *Scarus psittacus*, *Acanthurus blochii*, *Poecilia* sp.) (Meyer et al. 2010, MacKenzie & Bruland 2012). Thus, despite the fact that we only sampled once a year at the same time and we lacked an additional control site outside of the mangrove eradication area, we feel our data sets provided insight into how mangrove forests and the chemical eradication of those mangrove forests impact nearshore fish assemblages.

Exotic species can significantly alter the ecological function of an ecosystem and often create conditions that allow other exotic species to invade (Vitousek et al. 1997, Simberloff & Von Holle 1999). The exotic red mangrove *Rhizophora mangle* has altered hydrological inputs, organic matter dynamics, sedimentation patterns, and invertebrate food webs along invaded Hawaiian coastlines as well as increased numbers of exotic invertebrates (D'Iorio 2003, Demopoulos et al. 2007, Demopoulos & Smith 2010, Sweetman et al. 2010). Altered coastlines from invasive mangrove were also expected to create habitat more suitable for exotic fish species. While exotic fish densities were significantly higher in mangrove tide pools than non-vegetated tide pools, there were no differences when exotic fish densities were compared between mangrove and native vegetated tide pools. Furthermore, native fish densities and biomass were often similar to or significantly greater than exotic fish densities and biomass regardless of tide pool treatment. While these results did not support our first hypothesis, that mangrove tide pools would be dominated by exotic fish species, they partially supported our second hypothesis, that native vegetated and non-vegetated tide pools would be dominated by native fish species. The prevalence of native fish in mangrove tide pools complicated efforts to address Hypothesis 3, that fish assemblages associated with mangrove tide pools would shift from exotic- to native-dominated after mangroves had been chemically eradicated. Native fish densities generally increased after mangrove eradication (Figs. 3B,E & 4B,E), while densities of exotic fish species varied among years and treatments
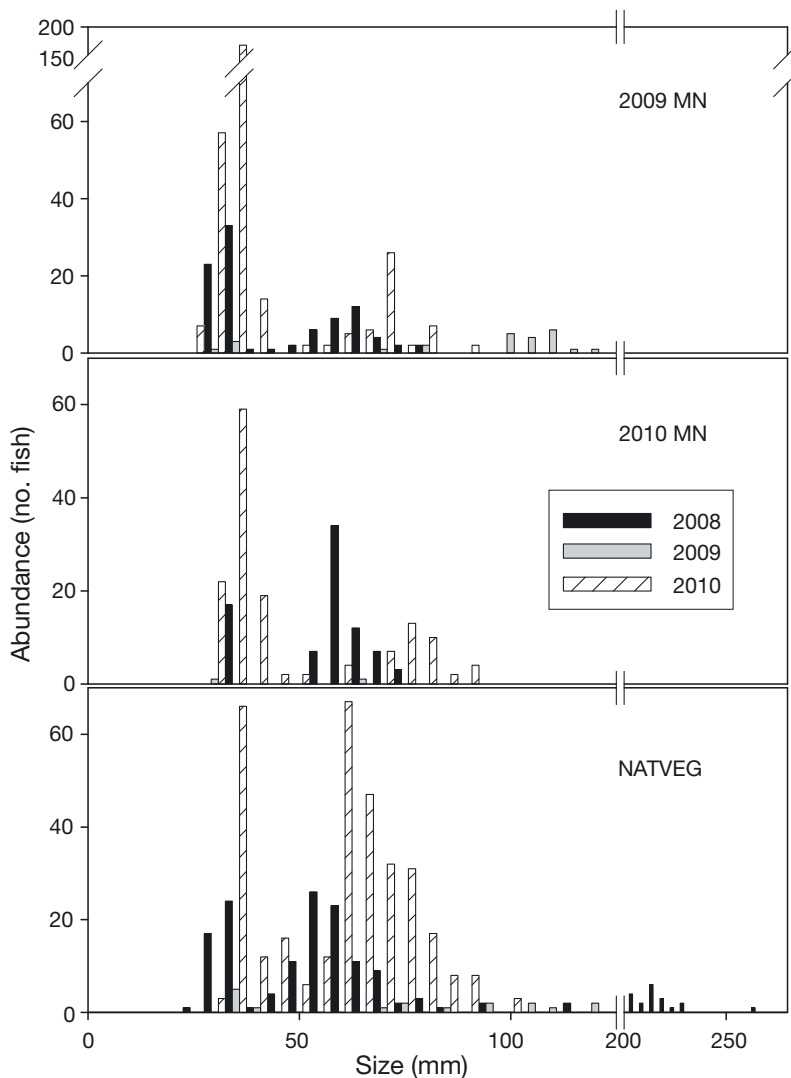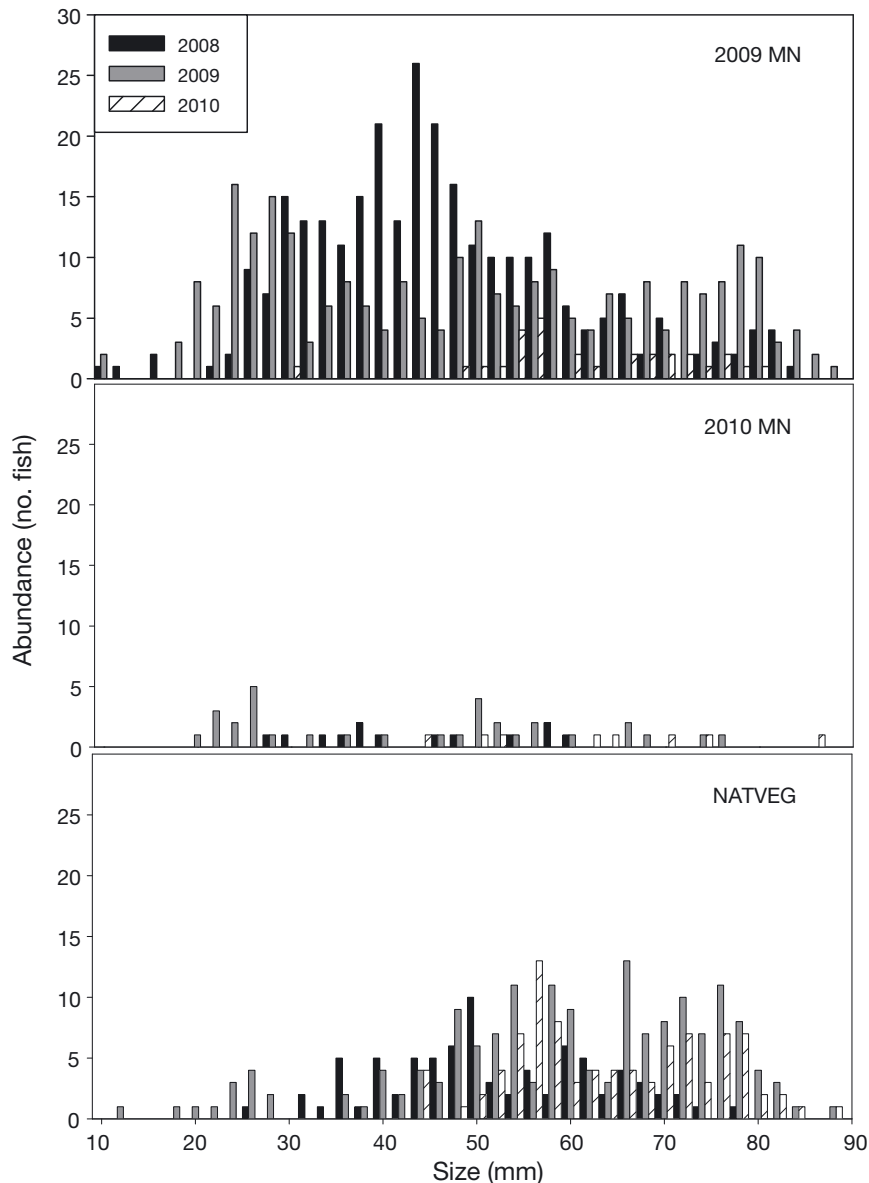
Fig. 7. *Poecilia* sp. Number of individual exotic mollies from each size class collected in fyke nets from mangrove (MN) and native vegetated (NATVEG) tide pools in 2008, 2009, and 2010

were not compared to native fish densities outside of the chemical eradication area. Additional control sites outside of Kapoho as well as future monitoring are needed to validate this and determine if there are any long-term impacts.

Facilitative interactions between exotic species

Densities of exotic species were expected to be greater than native species in mangrove-invaded tide pools due to facilitative interactions reported from other aquatic ecosystems. For example, the colonization of benthic habitat throughout the Great Lakes by the exotic zebra mussel *Dreissena polymorpha* has altered benthic structure, increased sediment accumulation and water clarity, and provided habitat more suitable for additional exotic species. Since the invasion of the Great Lakes by the zebra mussel, densities of exotic macrophytes, invertebrates, and fish have also increased, especially those that co-evolved with zebra mussels in the Caspian Sea (Ricciardi 2001, 2005). In Hawaii, the colonization of coastal areas by mangroves has decreased freshwater inputs (Demopoulos & Smith 2010, present study), increased sediment retention (D'Iorio 2003), and altered organic matter dynamics (Sweetman et al. 2010). While these impacts coupled with increased structural complexity from mangrove prop roots appear to provide habitat more suitable for exotic invertebrates (Demopoulos & Smith 2010), the impacts to fish communities are not entirely clear. Exotic fish densities did not differ between mangrove and native-vegetated pools, although densities were significantly higher in vegetated pools than non-vegetated open pools. Furthermore, native fish densities were generally greater than or equal to exotic fish densities in mangrove-vegetated pools. Thus, it appears that the presence of vegetation around pools influences

(Figs. 3C,F & 4C,F). Similar pre-eradication (2008) and 1 yr post-eradication (2010) native fish densities supported our fourth hypothesis that chemical eradication of mangroves would have minimal negative impacts on tide pool native fish assemblages. Similar native fish densities before and after chemical control suggest that if chemical control of mangroves impacted fish communities, it was acute and short lived. However, it remains unclear whether post-eradication native fish densities had been suppressed to some degree by the chemical treatment, as native fish densities within the Kapoho tide pools

exotic fish abundance, especially mollies, more than plant origin. A recent survey of nearly 40 coastal wetlands around the 5 main Hawaiian Islands revealed similar patterns, where high densities of exotic fish were present regardless of the wetland plant community structure (MacKenzie & Bruland 2012). Alternatively, lower densities of exotic fish from non-vegetated open pools may have resulted from the lack of vegetation and thus the lack of structure to avoid larger predatory fish, such as barracuda, snappers, or groupers that were present in all pool types. This may have also resulted in the lower total fish densities that were often observed in open pools during visual surveys. Predatory fish have been shown to decrease exotic fish densities (Moyle & Light 1996) and are thought to be an important component controlling exotic fish in Hawaiian coastal wetlands (MacKenzie & Bruland 2012).

With the exception of the 2010 MN pools in the 2010 visual surveys, there were no significant differences in native fish densities among mangrove, native, and non-vegetated pools. These overall patterns suggest that mangroves may not be negatively impacting native fish abundances in tide pools. These results agree with those reported from intertidal sand flats on Molokai Island (Nakahara 2007). Fish community structure, however, may be influenced by the presence of vegetation regardless of its origin, as evidenced by lower levels of species richness (S) and diversity (H') as well as significantly different fish assemblages in vegetated pools compared to non-vegetated open pools. Alternatively, these patterns may have been due to non-vegetated open pools being closer to the ocean than vegetated pools (Fig. 1). This would have allowed the migration of transient species from adjacent coral reefs during high spring tides and resulted in the higher number of reef-associated species that were present in non-vegetated open pools.

Comparison of size classes of the 2 dominant fish collected in fyke nets, the native flagtails and exotic mollies, revealed that significantly smaller fish were collected in mangrove fyke net samples compared to native vegetation. While size classes from visual surveys were not compared among treatments due to the resolution of fish measurements made using this technique, juvenile flagtails and mollies were often absent or in much lower densities in non-vegetated open tide pools than in vegetated ones. These results suggest that vegetated tide pools in general provide habitat for juvenile fish. This is in contrast with results from other studies that have shown that the invasion of native vegetated coastal areas by exotic plant spe-

cies decreased densities of young of year fish (Able et al. 2003, Osgood et al. 2003). In their native range, mangrove forests are important nursery habitat for many species of resident and transient fish (Cocheret de la Morinière et al. 2002, Sheridan & Hays 2003, Dorenbosch et al. 2006, MacKenzie & Cormier 2012) and are thought to provide feeding areas for juvenile fish (Lugendo et al. 2007) as well as refuge from predation (Vance et al. 1996, Primavera 1997, Ellis & Bell 2004). The increased structural complexity that has resulted from exotic mangrove roots and has increased invertebrate densities may also be providing an increased food source for juvenile fish as well as protection from predation. Interestingly, the congeneric flagtail *Kuhlia rupestris* is commonly found in or around native Micronesian mangroves and stable isotopes have shown that they use mangroves as feeding areas (R. A. MacKenzie unpubl. data). Future studies that combine dynamic measures (i.e. growth rates, production) with manipulation of movement of flagtails into mangroves are needed to fully understand if and how native Hawaiian juvenile flagtails are utilizing these novel habitats.

Impacts of mangrove control on tide pool fish assemblages and habitat

The application of the herbicides glyphosate and imazapyr to Kapoho mangroves proved to be a successful mechanism to chemically eradicate exotic mangroves and resulted in the successful eradication of 9.3 ha of mangroves. However, it remains unclear how the application of this herbicide impacted the physicochemical or biological function of these tide pools as our experimental design lacked a true control. Changes in physicochemical parameters were observed in all treatments immediately following mangrove eradication in 2009, despite the fact that only mangroves around the 2009 MN tide pools were treated. The lack of differences across treatments suggests changes in physicochemical patterns were a result of interannual variation. Alternatively, the mangrove eradication in 2009 in the 2009 MN tide pools could have influenced physicochemical parameters in all of the surrounding tide pools. While tide pools provide discreet habitat at low tide, these units are connected at the highest of tides when water is thoroughly mixed throughout the system.

The defoliation of mangroves that resulted after mangrove eradication increased water temperatures in tide pools and probably light levels as well. Algal blooms in 2009 were attributed to this increased

light. Algal blooms were also likely affected by nutrients leaching from standing dead mangrove trees as well as the large input of leaves that dropped into tide pools following the application of the herbicides. Large inputs of dead wood and defoliated leaf litter that follow natural and human disturbance events can be a major input of nutrients to mangrove forests (Paerl et al. 2001, Davis et al. 2004). Decomposition of this leaf litter and algae may have also lowered dissolved oxygen and pH levels. Alternatively, significantly fresher, warmer, and more acidic waters in 2009 compared to 2008, may have been due to increased inputs of geothermally warmed groundwater inputs in 2009. While these differences could have been due to tidal fluctuations between years, tides were actually higher in 2009 (0.78 ± 0.01 m) compared to 2008 (0.76 ± 0.0 m). Mangrove eradication likely increased inputs of groundwater, which would no longer have been evapotranspired by live trees before reaching the pool. While this has never been reported before from mangrove studies, the removal of exotic vegetation in other studies has significantly increased groundwater inputs through decreased evapotranspiration (Levine et al. 2003, Jovanovic et al. 2009). In 2010, water was still fresher, warmer, and more acidic than 2008, but these differences were not significant (except for temperature) or as great as those observed between 2009 and 2008. This was attributed to increased tidal inputs in 2010 (0.82 ± 0.01 m) offsetting increased groundwater inputs that resulted from mangrove eradication.

Lower fish densities in 2009 after the initial herbicide application were largely due to lower recruitment rates of young flagtails, as made evident by ANOSIM and SIMPER analyses, fewer small *Kuhlia xenura* in 2009 (Fig. 6), and similar levels of fish biomass across years (Fig. 4). Identifying the exact mechanisms responsible for lower recruitment rates of fish in 2009 were beyond the scope of the present study. Differing recruitment rates across years may have resulted from natural temporal fluctuations in flagtail assemblages, although little is known of their life histories (R. Nishimoto, Hawaii Division of Aquatic Resources, pers. comm.). It is unclear whether the herbicides were having a direct, adverse effect on the fish community as we did not measure herbicide concentrations in the water column. However, glyphosate was administered by injecting directly into the tree trunk and 100% of the herbicide reached the target organism with minimal overspray. Imazapyr, which was aerially broadcast and likely entered the water, has an extremely short half-life of 2 d and was expected to have quickly broken down. In a pond

study, imazapyr had completely broken down in the water column within 14 d (Mangels & Ritter 2000). Furthermore, glyphosate and imazapyr have been shown to have little impact on aquatic organisms when administered at the recommended dosages (Newton et al. 1984, Mangels & Ritter 2000). Our results and observations suggest that the indirect effects of mangrove eradication and not chemicals may have had a greater impact on fish habitat and thus fish communities in 2009, although these effects appear to have been short-lived. The low dissolved oxygen levels after herbicide application in 2009 were at or near levels (2 mg l^{-1}) considered to have lethal effects on many marine species (Vaquer-Sunyer & Duarte 2008). Algal blooms in 2009 may have also negatively impacted the habitat value of these tide pools for native *Kuhlia xenura*.

Densities of exotic mollies from visual surveys were lower in 2009 and 2010 compared to 2008. However, the lack of treatment or year effects on fyke net densities suggests that differences from visual survey data may have been due to mollies hiding in vegetated areas or dead mangrove trunks and prop roots that remained and were thus not counted. Furthermore, the eradication of mangroves was expected to reduce the densities of mollies, as stated in our fourth hypothesis. Lack of differences due to mangrove eradication was likely due to the fact that mollies can tolerate extreme fluctuations in dissolved oxygen, salinities, and temperatures (MacKenzie & Bruland 2012). Thus, the less-oxygenated, warmer water in 2009, which was thought to have negatively affected native fish densities, did not appear to affect exotic fish densities.

The native palaemonid shrimp *Palaemon debilis* appears to have temporarily benefitted from mangrove eradication. Significantly higher densities in 2009 fyke net samples compared to 2008 and 2010 densities were attributed to the massive inputs of leaf litter that occurred in the first year when mangroves were chemically treated. Increased leaf litter inputs following natural or human disturbance can provide food and shelter for shrimp populations (Crowl et al. 2001) and are thought to increase shrimp densities following major hurricanes or typhoons (Burkholder et al. 2004, Paerl et al. 2006, Stevens et al. 2006, MacKenzie & Cormier 2012). Alternatively, increased densities of shrimp in 2009 could have been a result of lower predation pressure from the reduced fish densities that also occurred in 2009. Shrimp are known to be an important food source for transient fish in other mangrove forests (Primavera 1997, Rönnbäck 1999), although this has yet to be documented in Hawaiian coastal ecosystems.

SUMMARY

Densities of native fish and fish community structure recovered to pre-mangrove eradication levels 1 yr after mangroves were successfully eradicated from Kapoho tide pools. It was not clear if the reduction in native fish densities or shift in community composition in 2009 during mangrove eradication was a result of the control treatment, increased groundwater inputs, or natural inter-annual variation in fish populations or if recovered fish populations represented fish populations outside of the Kapoho tide pools. Densities of exotic fish varied across sites and years with no consistent pattern. This may have been due to the fact that exotic fish were dominated by poeciliids, which can tolerate extreme fluctuations in dissolved oxygen, salinities, and temperatures (MacKenzie & Bruland 2012).

Exotic mangroves negatively impact the ecological function of coastal ecosystems in Hawaii (Demopoulos et al. 2007, Demopoulos & Smith 2010, Sweetman et al. 2010) and our results suggest that they may potentially reduce amounts of groundwater entering coastal areas. However, they do not seem to have an adverse effect on tide pool fish assemblages in Hawaii, except where mangroves are colonizing non-vegetated areas. Mangroves, therefore, may convert native species-rich, open tide pools to less diverse pools that support more exotic fish. Conversely, the presence of juvenile flagtails in flooded mangrove areas adjacent to tide pools and the general lack of young flagtails in non-vegetated pools suggests that mangroves may in fact be providing nursery habitat for native flagtails. The ability of exotic mangroves to provide nursery habitat for native species has interesting implications for Hawaii as well as for the Society Islands, where mangroves are also invasive. Additional studies are needed using stable isotopes, growth rates, or fish production to determine the ecological value of native versus exotic vegetation in supporting native (or exotic) fish assemblages.

Results revealed that if mangrove eradication on Kapoho tide pools had any negative effects on the fish community, those effects may have been acute and short lived. Two years after mangroves had been chemically eradicated, native fish densities and species richness were greater than or equal to pre-control densities and community structure did not significantly differ from pre-eradication community structure. Additional control sites outside of the treated area coupled with additional monitoring are needed to verify this as well as to determine if there are any long term effects from the mangrove eradication.

LITERATURE CITED

Able KW, Hagan SM, Brown SA (2003) Mechanisms of marsh habitat alteration due to *Phragmites*: Response of young-of-the year mummichog (*Fundulus heteroclitus*) to treatment for *Phragmites* removal. Estuaries 26: 484–494

Allen JA (1998) Mangroves as alien species: the case of Hawaii. Global Ecol Biogeogr Lett 7:61–71

Arthington AH, Balcombe SR, Wilson GA, Thoms MC, Marshall J (2005) Spatial and temporal variation in fish-assemblage structure in isolated waterholes during the 2001 dry season of an arid-zone floodplain river, Cooper Creek, Australia. Mar Freshw Res 56:25–35

Bantilan-Smith M, Bruland GL, MacKenzie RA, Henry A, Ryder CR (2009) A quantitative assessment of the vegetation and soils of coastal lowland wetlands in Hawai`i. Wetlands 29:1023–1036

Brock VE (1954) A preliminary report on a method of estimating reef fish populations. J Wildl Manag 18:297–308

Burkholder J, Eggleston D, Glasgow H, Brownie C and others (2004) Comparative impacts of two major hurricane seasons on the Neuse River and western Pamlico Sound ecosystems. Proc Natl Acad Sci USA 101:9291–9296

Carr MR (1997) PRIMER User manual: Plymouth routines in multivariate ecological research. Plymouth Marine Laboratories, Plymouth

Clarke KR, Warwick RM (1994) Change in marine communities: an approach to statistical analysis and interpretation. 2nd edn. PRIMER-E, Plymouth

Cocheret de la Morinière E, Pollux BJ, Nagelkerken I, Van der Velde G (2002) Post-settlement life cycle migration patterns and habitat preference of coral reef fish that use seagrass and mangrove habitats as nurseries. Estuar Coast Shelf Sci 55:309–321

Crowl TA, McDowell WH, Covich AP, Johnson SL (2001) Freshwater shrimp effects on detrital processing and nutrients in a tropical headwater stream. Ecology 82: 775–783

D'Iorio MM (2003) Mangrove and shoreline change on Molokai, Hawaii: assessing the role of introduced *Rhizophora mangle* in sediment dynamics and coastal change using remote sensing and GIS. PhD dissertation, University of California, Santa Cruz, CA

Davis SE III, Cable JE, Childers DL, Coronado-Molina C and others (2004) Importance of storm events in controlling ecosystem structure and function in a Florida Gulf Coast estuary. J Coast Res 20:1198–1208

Demopoulos AWJ, Smith CR (2010) Invasive mangroves alter macrofaunal community structure and facilitate opportunistic exotics. Mar Ecol Prog Ser 404:51–67

Demopoulos AWJ, Fry B, Smith CR (2007) Food web structure in exotic and native mangroves: A Hawaii-Puerto

Rico comparison. Oecologia 153:675–686

Dorenbosch M, Grol MGC, Nagelkerken I, van der Velde G (2006) Seagrass beds and mangroves as potential nurseries for the threatened Indo-Pacific humphead wrasse, *Cheilinus undulatus* and Caribbean rainbow parrotfish, *Scarus guacamaia.* Biol Conserv 129:277–282

Duke NC, Ball MC, Ellison JC (1998) Factors influencing biodiversity and distributional gradients in mangroves. Global Ecol Biogeogr Lett 7:27–47

Duke NC, Lo EYY, Sun M (2002) Global distribution and genetic discontinuities of mangroves—emerging patterns in the evolution of *Rhizophora.* Trees 16:65–79

Ellis WL, Bell SS (2004) Conditional use of mangrove habitats by fishes: Depth as a cue to avoid predators. Estuaries 27:966–976

Flanders LS (2007) Recommendations for a state management plan at the WaiOpae tide pools Kapoho, Hawaii. Hawaii Department of Land and Natural Resources, Honolullu, HI

Friedlander AM, Brown EK, Monaco ME (2007) Coupling ecology and GIS to evaluate efficacy of marine protected areas in Hawaii. Ecol Appl 17:715–730

Fronda R, Lane-Kamahele M, Harry B (2008) Removal of alien red mangrove from Kaloko-Honokohau National Historical Park. Tech Rep 162, National Park Resources Study Unit, Department of Botany, University of Hawai'i, Honolulu, HI

Johnson AG, Glenn CR, Burnett WC, Peterson RN, Lucey PG (2008) Aerial infrared imaging reveals large nutrient-rich groundwater inputs to the ocean. Geophys Res Lett 35:L15606, doi:10.1029/2008GL034574

Jovanovic NZ, Israel S, Tredoux G, Soltau L and others (2009) Nitrogen dynamics in land cleared of alien vegetation (*Acacia saligna*) and impacts on groundwater at Riverlands Nature Reserve (Western Cape, South Africa). Water SA 35:37–44

Krebs CJ (1989) Ecological methodology. Harper Collins, New York, NY

Kulbicki M, Guillemot N, Amand M (2005) A general approach to length–weight relationships for New Caledonian lagoon fishes. Cybium 29:235–252

Laegdsgaard P, Johnson C (2001) Why do juvenile fish utilise mangrove habitats? J Exp Mar Biol Ecol 257: 229–253

Levine JM, Vila M, D'Antonio CM, Dukes JS, Grigulis K, Lavorel S (2003) Mechanisms underlying the impacts of exotic plant invasions. Proc R Soc Lond B Biol Sci 270: 775–781

Lin HJ, Kao WY, Wang YT (2007) Analyses of stomach contents and stable isotopes reveal food sources of estuarine detritivorous fish in tropical/subtropical Taiwan. Estuar Coast Shelf Sci 73:527–537

Lorenz JJ, McIvor CC, Powell GVN, Frederick PC (1997) A drop net and removable walkway used to quantitatively sample fishes over wetland surfaces in the dwarf mangroves of the southern Everglades. Wetlands 17:346–359

Lugendo BR, Nagelkerken I, Kruitwagen G, Van Der Velde G, Mgaya YD (2007) Relative importance of mangroves as feeding habitats for fishes: A comparison between mangrove habitats with different settings. Bull Mar Sci 80:497–512

MacKenzie RA, Bruland GL (2012) Nekton community structure in coastal wetlands across the Hawaiian Islands. Estuaries Coasts 35:212–226

MacKenzie RA, Cormier N (2012) Stand structure influences

nekton community composition and provides protection from natural disturbance in Micronesian mangroves. Hydrobiologia 685:155–171

Mangels GA, Ritter A (2000) Estimated environmental concentration of imazapyr resulting from aquatic uses of Arsenal herbicide. Pesticide Registration Report # EXA 00-008, American Cyanamid Co., Princeton, NJ

Manson FJ, Loneragan NR, Skilleter GA, Phinn SR (2005) An evaluation of the evidence for linkages between mangroves and fisheries: a synthesis of the literature and identification of research directions. Oceanogr Mar Biol Annu Rev 43:483–513

Meyer CG, Papastamatiou YP, Clark TB (2010) Differential movement patterns and site fidelity among trophic groups of reef fishes in a Hawaiian marine protected area. Mar Biol 157:1499–1511

Moyle PB, Light T (1996) Biological invasions of fresh water: empirical rules and assembly theory. Biol Conserv 78: 149–161

Nakahara BA (2007) Utilization of mangrove habitat by megafauna along the southern coast of Molokai, Hawaii. MSc thesis, University of Hawaii at Manoa, Honolulu, HI

Newton M, Howard KM, Kelpsas BR, Danhaus R, Lottman CM, Dubelman S (1984) Fate of glyphosate in an Oregon Forest Ecosystem. J Agric Food Chem 32:1144–1151

Osgood DT, Yozzo DJ, Chambers RM, Jacobson D, Hoffman T, Wnek J (2003) Tidal hydrology and habitat utilization by resident nekton in *Phragmites* and non-*Phragmites* marshes. Estuaries 26:522–533

Paerl HW, Bales JD, Nusley LW, Buzzelli CP and others (2001) Ecosystem impacts of three sequential hurricanes (Dennis, Floyd, and Irene) on the United States' largest lagoonal estuary, Pamlico Sound, NC. Proc Natl Acad Sci USA 98:5655–5660

Paerl HW, Valdes LM, Joyner AR, Peierls BL and others (2006) Ecological response to hurricane events in the Pamlico Sound system, North Carolina, and implications for assessment and management in a regime of increased frequency. Estuaries Coasts 29:1033–1045

Primavera JH (1997) Fish predation on mangrove-associated penaids: the role of structure and substrate. J Exp Mar Biol Ecol 215:205–216

Raichel DL, Able KW, Hartman JM (2003) The influence of *Phragmites* (common reed) on the distribution, abundance, and potential prey of a resident marsh fish in the Hackensack Meadowlands, New Jersey. Estuaries 26: 511–521

Rauzon MJ, Drigot DC (2002) Red mangrove eradication and pickleweed control in a Hawaiian wetland, waterbird responses, and lessons learned. In: Veitch CR, Clout MN (eds) Turning the tide: the eradication of invasive species. IUCN SSC Invasive Species Specialist Group, IUCN, Gland and Cambridge

Ricciardi A (2001) Facilitative interactions among aquatic invaders: Is an 'invasional meltdown' occurring in the Great Lakes? Can J Fish Aquat Sci 58:2513–2525

Ricciardi A (2005) Facilitation and synergistic interactions among introduced aquatic species. In: Mooney HA, Mack RN, McNeely J, Neville LE, Schei PJ, Waage JK (eds) Invasive alien species: a new synthesis. Island Press, Washington, DC

Rönnbäck P (1999) The ecological basis for economic value of seafood production supported by mangrove ecosystems. Ecol Econ 29:235–252

Rönnbäck P, Troell M, Kautsky N, Primavera JH (1999) Dis-

tribution pattern of shrimps and fish among *Avicennia* and *Rhizophora* microhabitats in the Pagbilao Mangroves, Philippines. Estuar Coast Shelf Sci 48:223−234

Sheridan P, Hays C (2003) Are mangroves nursery habitat for transient fishes and decapods? Wetlands 23:449−458

Simberloff D, Von Holle B (1999) Positive interactions of nonindigenous species: invasional meltdown? Biol Invasions 1:21−32

Stevens PW, Blewett DA, Casey JP (2006) Short-term effects of a low dissolved oxygen event on estuarine fish assemblages following the passage of Hurricane Charley. Estuaries Coasts 29:997−1003

Sweetman AK, Middleburg JJ, Berle AM, Bernardino AF, Schander C, Demopoulos AWJ, Smith CR (2010) Impacts of exotic mangrove forests and mangrove deforestation on carbon remineralization and ecosystem functioning in marine sediments. Biogeosciences 7:2129−2145

Thayer GW, Colby DR, Hettler WF Jr (1987) Utilization of the red mangrove prop root habitat by fishes in South Florida. Mar Ecol Prog Ser 35:25−38

USDA NRCS (2007) Orthophoto Mosaic of the Island of Hawai'i, Hawai'i County, HI. US Department of Agriculture, Natural Resources Conservation Service, National Cartography and Geospatial Center

Vance DJ, Haywood MDE, Heales DS, Kenyon RA, Loneragan NR, Pendrey RC (1996) How far do prawns and fish move into mangroves? Distribution of juvenile banana prawns *Penaeus merguiensis* and fish in a tropical mangrove forest in northern Australia. Mar Ecol Prog Ser 131:115−124

Vaquer-Sunyer R, Duarte MC (2008) Thresholds of hypoxia for marine biodiversity. Proc Natl Acad Sci USA 105: 15452−15457

Vitousek PM, D'Antonio CM, Loope LL, Rejmánek M, Westbrooks R (1997) Introduced species: a significant component of human-caused global change. NZ J Ecol 21:1−16

Walsh GE (1967) An ecological study of a Hawaiian mangrove swamp. In: Lauff GH (ed) Estuaries. Horn-Shafer Company, Baltimore, MD

Walsh W, Sparks R, Barnett C, Couch C and others (2009) Long-term monitoring of coral reefs of the main Hawaiian Islands, Final Report. State of Hawaii Monitoring Report NA06NOS4260113, 2009 NOAA Coral Reef Conservation Program