

**THE INFLUENCE OF TOP-DOWN AND BOTTOM-UP FORCES ON BENTHIC REEF  
COMMUNITY STRUCTURE: AN EXPERIMENTAL ASSESSMENT AT KEWALO  
BASIN, O‘AHU.**

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## **CHAPTER 1. LITERATURE REVIEW**

## INTRODUCTION

In recent decades, coral reef ecosystems worldwide have undergone substantial long-term declines due to overfishing, pollution, disease, and coral bleaching (Gardner et al. 2003; Pandolfi et al. 2003, 2005; Sweatman et al. 2011; Wilkinson 2006). Since 1950, approximately 19% of the world's original area of coral reefs has been effectively lost (Wilkinson 2006). Coral reefs are worth more than \$375 billion in ecosystem goods and services to the annual global economy (Pandolfi et al. 2005) and about 30 million people are almost totally dependent on them for food and income from fishing, coastal protection, building materials and income from tourism (Wilkinson 2006). Therefore, it is imperative to effectively reduce threats to coral reef ecosystems as an essential step not only for successful ecological management and restoration of these ecosystems, but also a step for future cultural and socioeconomic livelihoods for those who depend on them (Cinner et al. 2009).

Over the past several decades, coral-dominance in many coastal reefs has shifted to fleshy turf- and/or macroalgal-dominance. This phenomenon is known as a phase shift and coral-algal phase shifts have become increasingly common worldwide (Done 1992; Hughes 1994; Lapointe 1997, 1999; Ledlie et al. 2007; McCook 1999; McManus & Polsenberg 2004; Rogers & Miller 2006; Smith et al. 2005; Stimson et al. 1996). Smith et al. (2010) recently argue that coral-algal phase shifts should be viewed as a shift in community structure away from reef-producing, calcium carbonate forms towards faster growing fleshy turf and/or macroalgal forms, an interesting position as ocean acidification further stresses calcifying animals and plants (Hoegh-Guldberg et al. 2007).

The shift from coral-dominance to fleshy turf- and/or macroalgal-dominance negatively impacts coral fecundity (Hughes et al. 2007), coral recruitment and settlement (Arnold et al.

2010; Birrell et al. 2005), and may be associated with the introduction of pathogens via smothering and abrasion of live coral tissue (Preskitt 2007), as well as the localized death of corals through active overgrowth (Jompa & McCook 2003). Coral-algal competition can result in changes to the benthic community structure and the physical structure of the reef (Birrell et al. 2008; Box & Mumby 2007; Done 1992; Hughes et al. 2007; Jompa & McCook 2003; Littler & Littler 1984; McCook 1999; McCook et al. 2001). A recent meta-analysis suggests that the frequency and geographical extent of phase shifts is far less common than the scientific literature indicates (Bruno et al. 2009); however that study uses the lack of macroalgae as the sole indicator for resiliency (Smith et al. 2010). Numerous other studies show that fleshy turf algae may be as or more detrimental to coral reef resiliency as larger macroalgae (Arnold et al. 2010; Birrell et al. 2005, 2008; Preskitt 2007).

Coral-algal phase shifts are largely attributed to external disturbances, such as overfishing resulting in a loss of "top-down" controls, and/or land-based pollution resulting in elevated "bottom-up" nutrient availability (Hughes et al. 1999, 2007; Lapointe 1997, 1999; Larned 1998; Littler et al. 2006; McCook 1999; McCook et al. 2001; Stimson et al. 1996, 2001; Smith et al. 2001, 2005, 2010). Although the effects of elevated nutrients strongly facilitate the shift from coral to macroalgae (Hatcher & Larkum 1983; Lapointe 1997; Larned 1998; McClanahan et al. 2003; Schaffelke & Klumpp 1998; Smith et al. 2001, 2010; Stimson et al. 1996), most recent experimental studies show that the loss of top-down controls are the main force driving coral-algal phase shifts on coral reefs (Belliveau & Paul 2002; Burkepile & Hay 2006, 2009; Diaz-Pulido & McCook 2003; Hatcher & Larkum 1983; Jompa & McCook 2003; McClanahan et al. 2005; McCook 1999; McCook et al. 2001; Okano 2010; Sotka & Hay 2009; Stimson et al. 2001; Thacker et al. 2001).



The loss of top-down controls, however, does not explain the abundance and distributions of benthic algae on tropical reefs alone (Lapointe 1999; Littler et al. 2006). To explain inconsistencies among results of these manipulative field experiments, some have suggested that earlier studies were not conducted on ecologically relevant time-scales (Smith et al. 2010) or did not use ecologically relevant levels of nutrient enrichment (Miller et al. 1999). The emerging perspective that both top-down and bottom-up controls are important in influencing benthic community structure is becoming more widely accepted as more ecologically appropriate field studies have been conducted (Littler et al. 2006; Smith et al. 2001, 2010). Other types of phase shifts from coral to corallimorpharia, soft corals, and sponges can occur from the loss of bottom-up controls alone (Nordstrom et al. 2009).

Herbivorous fish and urchins play an important role in structuring benthic reef communities (Bellwood et al. 2004; Carpenter 1986; Edmunds & Carpenter 2001; Hughes 1994; Jennings & Kaiser 1998; Lewis 1986; McCook 1999; McClanahan et al. 2003). In recent years there has been a decline in fisheries in many places throughout the world from overfishing (Friedlander & De Martini 2002; Jackson et al. 2001; Jennings & Polunin 1996, 1997; Koslow et al. 1988; Williams et al. 2006). Most experimental studies examining the effects of reduced herbivory find that it can alter species composition of benthic algae and cyanobacteria, as well as increasing their relative abundance and biomass (Sammarco 1983; Scott & Russ 1987; Smith et al. 2001, 2010; Wilkinson & Sammarco 1983). This suggests that a loss or decrease in herbivorous fish populations on a reef will favor an increase in fleshy turf and/or macroalgal abundance and biomass. Chael et al. (2010) find that a coral-algal phase shift on the Great Barrier Reef is strongly associated with low fish herbivore diversity and low abundances of algal browsers (predominantly Siganidae) and grazers/detritivores (Acanthuridae). The study suggests

that these functional groups of fish play an important role in reef resilience and therefore deserve particular protection.

Grazing of preferred macroalgae in the field by individual herbivorous fish species can be very intense and occur in short periods of time (15% decrease in original mass in 12h) (Mantyka & Bellwood 2007). Conklin (2007) find a trade-off between grazing of preferred macroalgae and the risk associated with acquiring the preferred species. Another study examining the behavior and diet composition of herbivorous fish found that all fish species investigated preferred epilithic algae and largely avoided macroalgae (Ledlie et al. 2007). Also, a field study in the Great Barrier Reef showed that both herbivorous and browsing fish species avoid high density patches of transplanted *Sargassum* sp. and preferentially graze on open patches of low density (Hoey & Bellwood 2011). This suggests that there may be a threshold for macroalgal density that once reached can suppress the grazing activity of herbivorous fish (Hoey & Bellwood 2011; Ledlie et al. 2007). These studies are compelling because they may indicate that there is a negative feedback loop where at the presence of a particular density of macroalgae can actually decrease the probability of a phase shift reversal.

Because most tropical reef algae are considered to be nutrient-limited, particularly dissolved inorganic nitrogen (DIN)-limited, addition of inorganic nutrients can relax nutrient limitations and quickly increase growth rates and biomass (Lapointe 1997, 1999; Larned 1998; Larned & Stimson 1996; McClanahan et al. 2003; Schaffelke & Klumpp 1998; Smith et al. 2004; Stimson et al. 1996). Larned (1998) compares tissue nitrogen to phosphorus ratios for macroalgae to the DIN to phosphorus (P) ratio in the water column and reports that N rather than P is the limiting nutrient in almost all species tested. However, Lapointe (1999) reports that the biomass of *Sargassum polyceratum* in DIN-rich water with high grazing increases significantly

with enrichment of P. Additionally, Schaffelke & Klumpp (1998) find that *Sargassum baccularia* is both N- and P-limited suggesting that both are important to take into consideration. Several other studies show that herbivorous fish display a preferential affinity to macroalgal plants with elevated nutrient concentrations (Boyer et al. 2004; Burkepile & Hay 2009; Stimson et al. 1996). This suggests that herbivorous fish preferentially select for more nutritious algae. If this hypothesis is true then phase shifts could occur even in the absence of overfishing if certain macroalgal species were being avoided by herbivorous fish. There is some experimental evidence supporting the hypothesis that grazing may not be strong enough to overcome the impacts of eutrophication (Worm & Lotze 2006).

In the main Hawaiian Islands (MHI) phase shifts have been observed and well-documented (Conklin 2007; Peyton 2009; Rodgers & Cox 1999; Russell 1987, 1992; Smith et al. 2002, 2004, 2005; Stimson et al. 1996, 2001). Algal blooms on coral reefs have been associated with negative ecological impacts on reefs (Smith et al. 2004, 2005). The most notorious phase shift in the MHI was first described in the 1960's and early 1970's in Kāneʻohe Bay, Oʻahu (Banner 1974; Smith et al. 1981). The overgrowth of coral by the macroalga *Dictyosphaeria cavernosa* in Kāneʻohe Bay has largely been attributed to nutrient-rich sewage discharge that occurred until 1977 in the bay (Done 1992; Smith et al. 1981; Stimson et al. 1996, 2001). Following the diversion of sewage discharge away from the bay the cover of *D. cavernosa* has steadily declined (Stimson et al. 2001; Stimson & Conklin 2008).

More recently, ephemeral blooms of the filamentous alga *Cladophora sericea* on West Maui have been associated with land-based pollution via groundwater seepage (Smith et al. 2005). Further, blooms of the invasive macroalgal species *Hypnea musciformis* and *Ulva*

*lactuca*, also on Maui, correlate with anthropogenic eutrophication via wastewater effluent from injection wells, and other land-based sources (Dailer et al. 2010).

Overfishing in the MHI has led to a grand mean fish standing stock biomass that is 260% lower than in the northwestern Hawaiian Islands (Friedlander & De Martini 2002). Overfishing depletes important key herbivorous fish species in the MHI, as well (Williams et al. 2008). Moreover, the overgrowth of reefs at the Waikīkī Marine Life Conservation District (MLCD) on O‘ahu by thick mats of the invasive alien macroalga *Gracilaria salicornia* has likely led to a 50% decline in fish biomass in the area due to reduced habitat quality (Williams et al. 2006). Therefore, an interaction or synergy between invasive algae, overfishing, and land-based pollution are the main factors driving phase shifts in the MHI. However, the relative strengths of these factors in driving phase shifts are not fully understood in the MHI.

Several factorial experiments independently and simultaneously manipulate nutrients and herbivory on coral-dominated reefs on Hawai‘i Island (Okano 2010; Smith et al. 2001, 2010). A study at Puakō shows that dramatic shifts in benthic reef community structure and biomass could occur in relatively short periods of time (Smith et al. 2001, 2010). This finding suggests that even on the healthiest of Hawaiian reefs, fleshy turf and/or macroalgal species are present, but are regulated by top-down and bottom-up forces present on the reef. Another study comparing two sites at Kealakekua Bay (Kaawaloa-MLCD and Kahauloa), also on Hawai‘i Island, reports that reduced herbivory alone and with elevated nutrients strongly influenced benthic reef community structure and biomass at both sites (Okano 2010). The effects of elevated nutrients alone were less clear. These studies together indicate that the dynamic relationship between top-down and bottom-up forces in coral reef ecosystems is very complex and needs to be investigated further.

The Relative Dominance Paradigm (RDP) is a conceptual model that predicts the competitive outcomes or alternative stable states for dominant photosynthetic organisms found on tropical reefs (Littler et al. 2006). The RDP, which was first proposed by Littler & Littler (1984), serves as a framework for understanding how the relative abundances of corals, crustose coralline algae (CCA), fleshy turf algae, and frondose macroalgae interact with complex environmental and biological factors, such as declining herbivory and eutrophication. Under conditions of high grazing and low nutrient availability the model predicts that large calcified coral or CCA forms will predominate. When nutrient availability is elevated and grazing remains intact the model suggests that grazing resistant CCA forms will predominate. Conversely, the model predicts that when grazing activity is reduced and nutrient availability remains low a shift from coral to fleshy turf algae is favored. Lastly, when grazing activity is reduced while nutrient availability remains elevated the model predicts that frondose macroalgae will predominate (Littler et al. 2006).

By identifying and understanding the factors driving phase shifts it may be possible to reverse the trajectories of decline (Pandolfi et al. 2005). Phase shift reversals can occur and have been well documented (Bellwood et al. 2006; Carpenter & Edmunds 2006; Smith et al. 2010; Stimson & Conklin 2008). For example, the recovery of high population densities of *Diadema* urchins in the Caribbean has been associated with increased coral recruitment, mainly of *Agaricia* and *Porites*, and reduced macroalgal cover (Carpenter & Edmunds 2006). Moreover, the substantial decrease in the cover of *D. cavernosa* in Kāneʻohe Bay likely occurred as a result of a prolonged rainy and cloudy period which reduced irradiance sufficiently enough to slow growth rates (Stimson & Conklin 2008). Further, Smith et al. (2010) independently and simultaneously excluded herbivores and elevated nutrients for one year on a Hawaiian reef and

found that benthic community trajectories could be reversed in two months following re-exposure to natural herbivore populations, even in the continued presence of elevated nutrients. Another herbivore exclusion study on the Great Barrier Reef found that communities dominated by macroalgae could be reverted to coral when exclusion cages were removed (Bellwood et al. 2006). Thus, identifying the factors that may lead to phase shift reversals can have strong implications for coral reef ecosystem management and restoration. Because most current management and restoration efforts are focused on the recovery of degraded reefs, understanding the roles of herbivores and nutrients on these reefs is necessary.

The aims of this study are to investigate the independent and simultaneous effects of reduced herbivory and elevated nutrients on benthic reef community structure on a degraded reef at the Kewalo Basin, O‘ahu. Further, this study will examine the effects of herbivore restoration on benthic community structure by re-exposing benthic communities to natural herbivore populations. More specifically, this study will test the following hypotheses:

1. Reduced herbivory (top-down forces) and elevated nutrients (bottom-up forces) will influence benthic community structure on a degraded reef on O‘ahu.
2. Benthic community trajectories can be reversed by restoring natural herbivory levels on a degraded reef.

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**CHAPTER 2. AN EXPERIMENTAL ASSESSMENT OF THE INDEPENDENT AND  
SIMULTANEOUS EFFECTS OF REDUCED HERBIVORY AND ELEVATED  
NUTRIENTS ON BENTHIC REEF COMMUNITY STRUCTURE AT KEWALO BASIN,  
O'AHU**

## **ABSTRACT**

In recent decades, coral-algal phase shifts have become increasingly common worldwide. Understanding the factors leading to these shifts can have strong implications for coral reef ecosystem management and restoration. The Relative Dominance Paradigm (RDP) is a conceptual model used to explain alternative stable states for dominant photosynthetic organisms found on tropical reefs. The RDP predicts that coral-algal phase shifts occur most commonly under conditions of low herbivory (top-down forces) and elevated nutrients (bottom-up forces). Using replicated settlement tiles, the effects of nutrient enrichment and herbivore exclusion on benthic community structure were analyzed for eight months on the reef shelf adjacent to Kewalo Basin, O‘ahu, Hawai‘i (9 m depth contour). Further, to restore natural herbivory levels herbivore exclusion cages were removed after six months of experimental manipulation. The results indicate that top-down forces independently and when combined with elevated nutrients strongly influence benthic community structure. However, the effects of nutrients on benthic community structure alone were less clear. In addition, re-exposure to natural herbivore populations shifted benthic community trajectories in two months, even in the continued presence of elevated nutrients. This research suggests that maintaining natural herbivory levels is critical for management of degraded reef ecosystems, even where continued pressure from fishing exists.

## INTRODUCTION

Over the past 50 years coral-algal phase shifts have become increasingly common on tropical coral reefs worldwide (Done 1992; Hughes 1994; Lapointe 1997, 1999; Ledlie et al. 2007; McCook 1999; McManus & Polsenberg 2004; Rogers & Miller 2006; Smith et al. 2005; Stimson et al. 1996). The ecological shift from a state of coral-dominance to filamentous turf- and/or macroalgal-dominance negatively impacts coral fecundity, recruitment, settlement, and is associated with the introduction of pathogens via smothering and abrasion of live coral tissue, as well as localized death of corals through active overgrowth (Arnold et al. 2010; Birrell et al. 2005; Hughes et al. 2007; Jompa & McCook 2003; Preskitt 2007).

Most studies conducted over the past several decades have attributed external disturbances, such as overfishing and eutrophication, to coral-algal phase shifts (Hughes et al. 1999, 2007; Lapointe 1997, 1999; Larned 1998; Littler et al. 2006; McCook 1999; McCook et al. 2001; Stimson et al. 1996, 2001; Smith et al. 2001, 2005, 2010). Top-down forces play an important role in structuring benthic reef communities (Bellwood et al. 2004; Carpenter 1986; Edmunds & Carpenter 2001; Hughes 1994; Jennings & Kaiser 1998; Lewis 1986; McCook 1999; McClanahan et al. 2003). According to a recent meta-analysis, top-down forces play a greater relative role than bottom-up forces in driving coral-algal phase shifts (Burkepile & Hay 2006). However, addition of inorganic nutrients can quickly increase growth rates and biomass of most tropical benthic reef algae (Lapointe 1997, 1999; Larned 1998; Larned & Stimson 1996; McClanahan et al. 2003; Schaffelke & Klumpp 1998; Smith et al. 2004; Stimson et al. 1996). While most recent experimental studies that have simultaneously manipulated herbivory and nutrient levels on tropical coral reefs have shown that the loss of top-down controls are the main force driving coral-algal phase shifts (Belliveau & Paul 2002; Burkepile & Hay 2006, 2009;



Diaz-Pulido & McCook 2003; Hatcher & Larkum 1983; Jompa & McCook 2003; McClanahan et al. 2005; McCook 1999; McCook et al. 2001; Okano 2010; Sotka & Hay 2009; Stimson et al. 2001; Thacker et al. 2001), this alone does not fully explain the abundance of benthic algae on tropical reefs (Lapointe 1999; Littler et al. 2006). Nutrients alone can strongly facilitate algal blooms (Dailer 2010; Smith et al. 2005; Worm & Lotze 2006); however, when in combination with reduced herbivory play a pronounced role in shifting benthic communities (Littler et al. 2006; Okano, 2010; Smith et al. 2001. 2010).

Phase shift reversals are possible and have been documented (Bellwood et al. 2006; Carpenter & Edmunds 2006; Smith et al. 2010; Stimson & Conklin 2008). For example, the recovery of high population densities of the sea urchin *Diadema antillarum* in the Caribbean has been associated with increased coral recruitment, mainly of *Agaricia* and *Porites*, and reduced macroalgal cover (Carpenter & Edmunds 2006). Moreover, the substantial decrease in the cover of *Dictyosphaeria cavernosa* in Kāneʻohe Bay following a prolonged rainy and cloudy period between January and June 2006 likely slowed growth rates by reducing irradiance leading to the decline (Stimson & Conklin 2008). Further, Smith et al. (2010) independently and simultaneously excluded herbivores and elevated nutrients for one year on a Hawaiian reef and found that benthic community trajectories could be reversed in two months following re-exposure to natural herbivore populations, even in the continued presence of elevated nutrients. Another herbivore exclusion study on the Great Barrier Reef found that communities dominated by macroalgae could be reverted to coral when exclusion cages were removed (Bellwood et al. 2006). Although in one case prolonged inclement weather was associated with the decline in a dominant macroalgal species responsible for the phase shift, in most other cases the reversal is associated with the recovery or return of natural herbivore populations. These studies seem to

provide additional evidence that the loss of top-down controls is the main force driving phase shifts on tropical coral reefs. Moreover, this suggests that increasing rates of herbivory are beneficial for restoration of overfished coral reefs. Thus, identifying the factors that may lead to phase shift reversals can have strong implications for coral reef ecosystem management and restoration.

There are different levels of intensity of degradation on coral reefs; however, the loss of coral communities resulting from declining rates of fecundity and recruitment of coral larvae are most commonly associated with degraded reefs (Bellwood et al. 2004; Richmond 1993). Because most current management and restoration efforts are focused on the recovery of degraded reefs understanding the roles of herbivores and nutrients on these reefs would seem necessary.

The aims of this study are to investigate the independent and simultaneous effects of reduced herbivory and elevated nutrients on benthic reef community structure on a degraded reef at the Kewalo Basin, O‘ahu, Hawai‘i. Further, this study will examine the effects of herbivore restoration on benthic community structure by re-exposing benthic communities to natural herbivory (simulating a phase shift reversal). More specifically, this study will test the following hypotheses:

1. Reduced herbivory (top-down forces) and elevated nutrients (bottom-up forces) will influence benthic community structure on a degraded reef on O‘ahu.
2. Benthic community trajectories can be reversed by restoring natural herbivory levels on a degraded reef.

## MATERIALS & METHODS

### *Study Site*

The study was conducted on the reef shelf adjacent to the Kewalo Basin on the south shore of O‘ahu, Hawai‘i (21.20° 90.3’ N, 157.80 ° 72.1’ W). This reef shelf has been heavily impacted by urbanization along the adjacent coastline (Figure 1) with coastal development and intense human uses (Brill 1992). The 30-acre Kaka‘ako Waterfront Park adjacent to the study site was built on a former municipal sanitary landfill (lined with plastic to prevent leakage). In addition, daily line-fishing activities from the rocky coastline are common, along with frequent spearfishing activities that take place in the outer portions of the reef. The reef slope begins at about 5 m depth and drops off into spur and groove formations with numerous sandy patches at about 8 -10 m depth. Coral cover is moderate to low at this site (< 20% live coral, mainly of *Porites lobata* and *Pocillopora meandrina*). Herbivore populations consist mainly of fish and sea urchins, although green sea turtles are also present (Tables 1-2). There are rich intertidal and shallow subtidal algal communities extant at the Kewalo Basin. However, the algal cover in the experimental area was very low, except for three weedy species present on dead coral and rock (*Asparagopsis taxiformis*, *Lyngbya majuscula*, *Tolypocladia glomerulata*). The study was conducted within a 600 m<sup>2</sup> area of reef crest at approximately 9 m depth and parallel to shore. The study site was approximately 150 m west of the Kilo Nalu Nearshore Reef Observatory, which is maintained by the University of Hawai‘i’s School of Ocean and Earth Science and Technology (SOEST) and provides real-time and archived data for mean currents/tidal height, current profiles, water quality, directional wave spectra, and wave characteristics (see website for archived data products for the period that this study was conducted: December 2010 - July 2011: <http://www.soest.hawaii.edu/OE/KiloNalu/>).

### *Experimental Design*

The design of this experiment was similar to the approach described in Smith et al. (2001, 2010) with the differences being that carbonate limestone was selected as the artificial substrate for this experiment to avoid skewing results from the affinity that crustose corallines have for PVC (Smith et al. 2010). Additionally, the total duration of this experiment was shorter than the Smith et al. (2010) study because of summer seasonal strong ocean swells that limited access to the site. Finally, the type of fertilizer, Yara Mila™, as well as the size and dimensions of tiles and cages used differed slightly.

A randomized four-way factorial block design was employed to examine the effects of reduced herbivory and elevated nutrients on benthic community structure. Six individual 10 x 10 m blocks were positioned adjacent to one another and parallel to shore (= 600 m<sup>2</sup>). Each block was divided into four 25 m<sup>2</sup> subplots. Within each subplot settlement tiles (58.06 cm<sup>2</sup> carbonate limestone tiles) were affixed to a plastic-coated metal rack (0.41 x 0.41 m) and directly cable-tied to the reef (48 racks total). Tile racks were randomly placed into one of four treatments: 1) control, 2) nutrient enrichment, 3) herbivore exclusion, and 4) both nutrient enrichment and herbivore exclusion. The experiment was deployed in late October/early November 2010. One tile from each rack was randomly collected via SCUBA each month for 8 months (Dec. 2010 - July 2011) following Smith et al. (2001).

Nutrient enrichment was achieved by filling 20.32 cm diameter unglazed clay flower pots with approximately 1.36 kg of 21-7-14 Yara Mila™ fertilizer (21.0% Total Nitrogen, 7% Available Phosphate, P<sub>2</sub>O<sub>5</sub>, 14.0% Soluble Potash, and 5.1% Combined Sulfur). The pots were then inverted and mounted onto plastic-coated base plates using Z-spar epoxy. The drainage hole near the top of the pot was rubber stopper plugged closed and the pots were secured at a distance

of 0.25 m from tile racks (Smith et al. 2001). Nutrient pots were scrubbed clean with brushes, washed, and refilled monthly.

Herbivore exclusion cages were assembled from 2.54 cm diameter plastic-coated metal wire mesh (0.41 x 0.41 x 0.41 m). The cages were secured over tile racks to exclude large herbivores. Cages were cleaned regularly of fouling organisms. Cage controls were not used due to a number of similar studies in the Hawaiian Islands that have found little to no significant caging effect (Okano 2010; Smith et al 2001; Stimson et al. 1996). Fish biomass and abundance of herbivore populations were surveyed once during month five of the experiment. Standard belt-transects were used to conduct the survey (25 x 4m transect, n=4 transects).

After six months of experimental manipulation herbivore exclusion cages were removed. The remaining tiles were exposed to natural levels of grazing for approximately two months with fertilizer still available. At two months, the tiles were then collected and the response variables were analyzed following Smith et al. (2010).

### *Response variables*

Upon collection, tiles were placed into pre-labeled plastic Ziploc® bags with seawater and transported to the Botany Department, University of Hawai'i in an ice chest. Tiles were frozen at -80°C prior to analysis. Each tile was thawed and rinsed in filtered seawater to remove all accumulated sediment and non-sessile invertebrates. All benthic algal species were identified to the lowest possible taxonomic unit and permanent microscope slides were prepared and examined using a compound microscope (Abbott 1999; Abbott & Huisman 2004). The abundance of individual species was calculated by estimating the percent cover for each species

within each cell of a 16-celled grid that was overlaid on top of the tiles and viewed under a stereomicroscope.

### *Statistical analyses*

The influence of each experimental treatment on community structure was analyzed using PRIMER v6 statistical software. Analysis of similarity (ANOSIM) was used to evaluate the similarity in benthic community structure at the species level for each month. Bray-Curtis similarity measures were calculated each month for all benthic species in all treatments and blocks. SIMPER was also used to determine the contributions of individual benthic species to the similarity in community structure for each month. Changes in community structure for each treatment over time were determined and visualized using non-metric multidimensional scaling (MDS) plots.

## RESULTS

### *Herbivore Survey*

The survey of reef herbivores conducted in April 2011 at the Kewalo Basin showed very low fish biomass (Tables 1, 2). The most abundant fish species were the brown surgeonfish *Acanthurus nigrofuscus* with  $0.128 \text{ g m}^{-2} \pm 0.041$  (mean  $\pm$  SE) and the saddle wrasse *Thalassoma duperrey* at  $0.18 \text{ g m}^{-2} \pm 0.056$  (mean  $\pm$  SE), which were also the most commonly observed fish species that grazed on the uncaged tiles throughout the experiment. *Thalassoma duperrey* is not known to be herbivorous, but rather omnivorous, therefore it is likely that this fish species was grazing on invertebrates on the uncaged tiles. *Echinothrix calamaris* and *Tripneustes gratilla* sea urchins (Lessios et al. 2001) were repeatedly observed grazing on uncaged tiles in all months. Further, urchins were disproportionately abundant around the uncaged tile racks at the time the survey was conducted. Although no parrotfish were observed during the survey, grazing marks were observed on live coral within the experimental area.

### *Composition of benthic communities*

A total of 159 taxa of benthic organisms were identified. This included 158 algal taxa: 29 macroalgae, 119 turf algae, and 10 crustose coralline algae (CCA) (Table 5). All sessile invertebrates were grouped together into one category, but consisted of only one unidentified polychaete species. No coral settled on the tiles during the sampling period.

### *Effects of herbivore exclusion and nutrient enrichment on benthic community structure*

The similarity in community structure between treatments was evaluated with ANOSIM. The major focus in this analysis was to demonstrate any significance of the global-R, which is the observed sample statistic for testing treatment differences (Clarke & Gorley 2006).

Additionally, MDS plots and SIMPER analyses were computed to help further assess the effects of herbivore exclusion and nutrients enrichment on benthic community structure in each month.

The results from the ANOSIM for month one indicated that significant differences between Cage/Fertilized (Fert) and Control (global-R = 0.316;  $p= 0.002$ ) and between Control and Fert (global-R = 0.316;  $p= 0.004$ ) treatments (Table 3). That these differences were already evident at this very early time point, suggests that nutrient limitation is extreme and that short term enrichments were very successful. The MDS plot for the same time period showed some grouping of data points by treatment, but clearly there was considerable overlap between other treatment groups given the low global-R value of 0.316 (Figure 2). SIMPER analyses indicated that filamentous turf species contributed more to the Cage and Cage/Fert treatments, while crustose prostrate forms contributed more to the Control and Fert treatments, despite losing two samples during collection in month one (for both Control and Cage treatments  $n=6$ ; both Fert and Cage/Fert  $n=5$ ). Abiotic factors of sand and/or open space on the experimental tiles contributed the most to similarity in all treatments for month one (Table 4).

For month two, the ANOSIM results revealed significant differences between Cage and Control treatments (global-R = 0.35;  $p= 0.004$ ) and between Cage/Fert and Control (global-R = 0.35;  $p= 0.002$ ) treatments (Table 3), suggesting that treatments in which herbivory was reduced are significantly different than controls. Again, the MDS plot showed some separation of data among treatments in which herbivores were excluded versus uncaged treatments. However, based on the low global-R value (global-R = 0.35), there was clearly still some overlap (Figure 3). Similar to month one, the SIMPER results indicated that sand and/or open space on the experimental tiles contributed the most to similarity in all treatments for month two (Table 4). Meanwhile, filamentous turf species contributed more to the Cage and Cage/Fert treatments,



while sessile invertebrates and CCA contributed more to the Control and Fert treatments. There were also unequal sample sizes in month two (for Control, Cage, and Cage/Fert treatments  $n=6$ ; Fert  $n=5$ ) because one sample was lost during collection.

The results from ANOSIM for month three indicated significant differences between Cage/Fert and Control treatments (global-R = 0.468;  $p= 0.002$ ), Cage and Control treatments (global-R = 0.468;  $p= 0.002$ ), Cage/Fert and Fert treatments (global-R = 0.468;  $p= 0.002$ ), and Cage and Fert (global-R = 0.468;  $p= 0.002$ ) treatments (Table 3). This suggests that both herbivore reduced treatments were significantly different from both controls and fertilized treatments. The MDS plot showed strong separation between both caged and both uncaged treatment groups (Figure 4). However the global-R value of 0.468 suggested that there may still be some overlap between some of the treatment groups. Again, SIMPER results for month three indicated that sand and/or open space on the experimental tiles contributed the most to similarity in all treatments (Table 4). Filamentous turf species contributed more to the Cage and Cage/Fert treatments, while sessile invertebrates and CCA contributed more to the Control and Fert treatments ( $n=6$  for all treatments in month three).

In month four, the results from ANOSIM revealed significant differences between Cage and Control (global-R = 0.717;  $p= 0.002$ ), Cage and Fert (global-R = 0.717;  $p= 0.005$ ), Cage/Fert and Control (global-R = 0.717;  $p= 0.005$ ), and Control and Fert (global-R = 0.717;  $p= 0.005$ ) treatments (Table 3). The only treatments not significantly different from one another were the herbivore reduced treatments. Even the fertilized treatment was significantly different from the control in month four. The MDS plots showed clear differences between treatments in which herbivores were excluded versus uncaged treatments, but the differences between the fertilized and control treatments were more difficult to visualize (Figure 5). The high global-R value of

0.717 confirmed that there were differences between caged and uncaged treatments. SIMPER results for month four indicated that sand and/or open space on the experimental tiles contributed the most to similarity in Control and Fert treatments, while CCA and macroalgae contributed the most to Cage and Cage/Fert treatments, respectively (Table 4). Macroalgae and filamentous turf species contributed more to the Cage and Cage/Fert treatments, while sessile invertebrates and CCA contributed more to the Control and Fert treatments. In month four, macroalgae were detected in the Cage and Cage/Fert treatments and CCA began to appear in the Cage/Fert treatment alone. There were unequal sample sizes in month four (both Control and Cage treatments  $n=6$ ; both Fert and Cage/Fert  $n=4$ ), associated with the loss of four samples due to a tsunami that occurred on March 11, 2011. One of the lost Cage/Fert samples was not recovered for the duration of the experiment.

For month five, the high global-R value of 0.719 suggested that there were clear differences between nearly all of the treatments; however, the results from ANOSIM did not detect significant pairwise differences (Table 3). The MDS plot revealed strong differences between treatments in which herbivores were excluded versus uncaged treatments (Figure 6). SIMPER results for this time period indicated that sand and/or open space on the experimental tiles contributed the most to similarity in Control and Fert treatments, while filamentous turf and macroalgae contributed the most to Cage and Cage/Fert treatments (Table 4). In month five, filamentous turf algae appeared in the Control and Fert treatments, with continued contributions from CCA in the Cage/Fert treatment. Once again, there were unequal sample sizes for month five (Control treatment  $n=6$ ; both Fert and Cage  $n=5$ ; Cage/Fert  $n=4$ ) due to the loss of an additional Cage sample to an early season swell. This lost Cage sample was not recovered for the duration of the experiment.

Results from ANOSIM for month six indicated significant differences between Cage/Fert and Control (global-R = 0.731;  $p= 0.002$ ), Cage and Control (global-R = 0.731;  $p= 0.002$ ), Cage/Fert and Fert (global-R = 0.731;  $p= 0.005$ ), and Cage and Fert (global-R = 0.731;  $p= 0.005$ ) treatments (Table 3). This indicates that both herbivore reduced treatments were significantly different from both controls and fertilized treatments. The MDS plot showed separation between all four treatments, not just between caged and uncaged treatments (Figure 7). Yet, the global-R value of 0.731 was slightly lower than the threshold value of 0.75 to consider all four treatments well separated. SIMPER results for month six indicated that sand and/or open space on the experimental tiles contributed the most to similarity in the Fert treatment only, while CCA contributed the most to the Control treatment and macroalgae contributed the most to Cage and Cage/Fert treatments (Table 4). There were unequal sample sizes in month six, as well (both Control and Fert treatments  $n=6$ ; Cage  $n=5$ ; Cage/Fert  $n=4$ ).

Herbivore exclusion cages were removed from both Cage and Cage/Fert treatments two months prior to the eight month sampling period. The results from ANOSIM for month eight revealed no significant pairwise differences after cages were removed (Table 3). The low global-R value (global-R = 0.457), nearly identical to month three (global-R = 0.468), indicates considerable overlap between treatment groups suggesting that there was a shift or reversal in benthic community trajectories in response to re-exposure to natural herbivory. The MDS plot showed a pattern of data points most consistent with patterns displayed in month one, two, and three of the experiment (Figure 8). Similar to early months, the SIMPER results for month eight indicated that abiotic sand and/or open space on the experimental tiles contributed the most to similarity in Control and Fert treatments, while sessile invertebrates and articulated coralline algae, contributed the most in the Cage and Cage/Fert treatments, respectively (Table 4).

Meanwhile, space opened in the Cage treatment and a shift towards the turf alga *Chondria simpliciuscula* occurred. For the Cage/Fert treatment, an increase in sessile invertebrate abundance and a similar shift towards the turf alga *Chondria simpliciuscula* was observed. There were unequal sample sizes in month eight (both Control and Fert treatments  $n=6$ ; Cage  $n=3$ ; Cage/Fert  $n=5$ ).

## DISCUSSION

Nearly 23% of the world's population lives within 100 km of the coast (Small & Nicholls 2003). Coastal environments are extremely susceptible to natural disasters and the effects of climate change-related disturbances (Adger et al. 2005). Because coral reef ecosystems are facing significant long-term declines on a global scale, minimizing threats of overfishing and nutrient pollution are imperative at the local level (Gardner et al. 2003; Pandolfi et al. 2005). With expected increases in human populations, it is likely that the fate of nearly all coral reefs is to become urbanized. Therefore, understanding the roles of herbivores and nutrients on these reefs is necessary.

The increase in coral-algal phase shifts worldwide (Done 1992; Hughes 1994; Lapointe 1997, 1999; Ledlie et al. 2007; McCook 1999; McManus & Polsenberg 2004; Rogers & Miller 2006; Smith et al. 2005; Stimson et al. 1996) urges a deeper and more thorough understanding of the factors underlying these shifts in order to more effectively manage and restore coral reef ecosystems. This is one of the few studies to examine the effects of reduced herbivory and elevated nutrients on a degraded reef (Burkepile & Hay 2009). Most other studies that have explored the role of top-down and bottom-up forces in the field have focused on healthy reefs (Diaz-Pulido & McCook 2003; McClanahan et al. 2002; Miller et al. 1999; Sotka & Hay; Thacker et al. 2001) where studies were conducted on very short time scales or were conducted on already coral-dominated reefs (Okano 2010; Smith et al. 2001, 2010). The results here indicate that top-down forces independently and when combined with elevated nutrients strongly influence benthic community structure on an urban reef adjacent to municipal uses with intense human use for recreation and fishing. However, the effects of nutrient enrichment alone were only significant in the short term. Experimentally restoring natural herbivory on a degraded reef

led to positive changes (reductions in algal cover) that supported the findings of Smith et al. (2010) on a relatively pristine, coral dominated reef. Re-exposure to natural herbivore populations shifted benthic community trajectories in two months, even in the continued presence of elevated nutrients.

The lack of significant effects from nutrient enrichment alone has been commonly found in these types of experiments (Burkepile & Hay 2009; Okano 2010; Thacker et al. 2001). Nutrient enrichment can increase feeding by herbivorous fish (Burkepile & Hay 2009) indicating that algal surplus, created by fertilization, will be rapidly consumed by herbivores if present in sufficient numbers (Smith et al. 2010). However, Smith et al. (2010) argued that if the time-scales for nutrient enrichment are ecologically relevant, significant differences in species composition will emerge.

#### *Disturbance regime*

This experiment was not conducted for a full year; however, it was conducted during the full time period in which the site can be safely accessed. In the late summer months, there are large swells on the south shore of O‘ahu. At the Kewalo Basin and surrounding areas the wave heights can be upwards of 6.10 m at these times (<http://www.soest.hawaii.edu/OE/KiloNalu/>). During these months there is strong surge and substantial movement of sand, potentially destroying the experimental set-up or leading to scouring effects that could possibly confound the results on this kind of field experiment (pers. obs.).

### *Other factors*

Given that the park adjacent to the reef shelf was built on a former municipal sanitary landfill, the potential for ambient nutrient levels to be elevated should be considered. Also, the nitrogen-footprint of the watershed that connects to the Kewalo Basin is considered moderate to high (Van Houtan et al. 2010). If background nutrients were sufficient to load benthic communities then one might not expect a response to the enrichment. It seems likely that ambient nutrients could have been interacting to confound the enrichment affect by elevating background levels.

The biomass of herbivorous fish at Kewalo Basin was very low, but unexpectedly similar overall abundances were determined when compared to protected reefs in fisheries management areas on the main Hawaiian Islands (Smith et al. 2010; Williams et al. 2006). The results from this study support the findings that top-down forces most strongly regulate benthic communities (Burkpile & Hay 2006, 2009). Here, nutrient enrichment did interact with reduced herbivory to structure benthic communities suggesting that nutrients can still play an important role in determining benthic composition. Although 29 macroalgal taxa were identified on settlement tiles in this study the site was nearly devoid of observable macro- and fleshy turf- algae at the time the experiment was conducted. The presence of the macroalga *Asparagopsis taxiformis*, the filamentous cyanobacterium *Lyngbya majuscula*, and the filamentous turf alga *Tolypocladia glomerulata* at the study site are likely the result of grazing resistance due to associated toxicity in these species (Arthur et al. 2008; Capper & Paul 2008; Manilal et al. 2010; Parsons et al. 2001, 2008). For example, a piscicidal assay of bioactive metabolites isolated from *A. taxiformis* led to behavioral anomalies and paralysis at low doses, and 100% mortality of tilapia in only 2 h at high doses (Manilal et al. 2010). Further, *Lyngbya majuscula* contains tumor producing

compounds that are thought to be associated with fibropapillomatosis in green sea turtles in Hawai‘i (Arthur et al. 2008). Incidental topical exposure of oral tumors in green sea turtles to broken *L. majuscula* filaments likely exposes the tumor tissue to these toxins during feeding (Arthur et al. 2008). Additionally, some toxic dinoflagellates have displayed host preference for *Tolypocladia glomerulata* in the Hawaiian Islands (Parsons et al. 2001; Parsons & Preskitt 2007). Moreover, palatability assays showed that *T. glomerulata* was only consumed after other preferred species had been consumed (Thacker et al. 2001). Based on this evidence for grazing resistance it is reasonable that herbivores may preferentially avoid these species in this reef at Kewalo Basin.

This study has demonstrated that algal species previously hypothesized to be absent on the reef at the Kewalo Basin can become dominant in response to reduced herbivory alone and in combination with elevated nutrients. One in particular, *Ulva lactuca*, was present in both herbivore excluded treatments, but never occurred on either the control or the fertilized treatments, as was also reported by Smith et al. (2001) at Puakō. Recently, *U. lactuca* has been shown to produce high concentrations of L-arginine, which is an essential amino acid in the synthesis of the herpes virus envelope associated with fibropapillomatosis in green sea turtles in Hawai‘i (Kawachi 2012; Van Houtan et al. 2010). These observations suggest that reducing herbivory alone and in combination with elevated nutrients at the Kewalo Basin can possibly have unforeseen detrimental effects on green sea turtles if increases in *U. lactuca* abundance were to occur at this site.

*Spyridia filamentosa* dominated in both the herbivore excluded treatments in months five and six of this experiment, however, the abundance was rapidly reduced following removal of the exclusion cages after month six. Molecular comparisons of the *Cox2-3* spacer and partial



LSU sequences of *S. filamentosa* indicated multiple introductions of this species to the Hawaiian Islands from two lineages (Conklin 2009). There are also morphological differences in branchlet cell dimensions between these two lineages (Conklin 2009). Based on these morphological differences the *S. filamentosa* from both herbivore excluded treatments in this experiment belong to the PAC lineage, with longer narrower shaped branchlet cells (Conklin 2009). The larger surface area of *S. filamentosa* in the PAC lineage is believed to promote sediment trapping; however, seagrass restoration efforts using *S. filamentosa* in Maunalua Bay, O‘ahu were unsuccessful (Conklin 2009). Molecular analyses would need to be done to be certain as to whether or not the *S. filamentosa* from Kewalo Basin is derived from a non-native lineage; however, Conklin (2009) found that most *S. filamentosa* samples collected on the south shore of O‘ahu were from non-native lineages. Considering the close proximity of the study site to the Honolulu Harbor it is possible that *S. filamentosa* at the Kewalo Basin represents an introduction to the archipelago. These results suggest that reduced herbivory alone and in combination with elevated nutrients at the Kewalo Basin may promote the abundance of a non-native lineage of *S. filamentosa*, as well as other possible cryptic non-native lineages.

This study has demonstrated that re-exposure to natural herbivore populations can shift benthic community trajectories in two months, even in the continued presence of elevated nutrients, suggesting that increasing rates of herbivory are beneficial for restoration of overfished urban coral reefs on O‘ahu. It needs to be noted that this benefit would be most effective in the absence of elevated nutrients (Smith et al. 2010). Spearfishing is very common in subtidal regions at the Kewalo Basin (pers. obs). A recent investigation into how specific gears select for susceptible and recovery-enabling species that may depend on coral reefs for feeding or habitat found that spear guns and traps target a high proportion of species likely to be affected by

bleaching and key for the recovery of corals, whereas line fishing catches the lowest proportion of susceptible and recovery-enabling species (Cinner et al. 2009). Selective bans or gear restriction (spears and traps) potentially can increase marine resource resiliency via top-down control.

Understanding the roles of top-down and bottom-up forces on tropical coral reefs are essential for effective management and restoration of these ecosystems. Coastal environments are extremely susceptible to natural disasters and the effects of climate change related disturbances (Adger et al. 2005). Thus, increasing resilience to disasters and disturbances would seem imperative for Pacific Islands. These types of manipulative field studies examining reduced herbivory and elevated nutrients are highly relevant and provide insight to increase the resiliency of coral reefs to all disasters and disturbances. For example, the effects of herbivore exclusion on bleached corals on the Great Barrier Reef indicated that the presence of large herbivorous fish are critical for increasing the resiliency of coral reefs to bleaching events (Hughes et al. 2007).

In the last two decades, a resurgence in community-based marine resource management has taken place in Vanuatu, Samoa, Cook Islands, Fiji, Palau, Hawai'i, Tuvalu, Kiribati, and Tonga (Johannes 2002). Locally Managed Marine Areas, which were first created in 1997 in Fiji, have been a very successful type of community-based marine resource management system and have spread throughout many of the south Pacific Islands (WRI 2008). These types of community-based marine resource management systems have been shown to increase the resiliency of coral reefs to natural disasters and disturbances (WRI 2008). Moreover, a comparison between national parks, co-managed reserves, and traditionally managed areas found that fish size and biomass were higher in all traditionally managed areas (McClanahan et al. 2006). These types of studies suggest that traditional management on Pacific Islands can

indirectly increase herbivorous fish biomass and abundance by conserving limited marine resources. Traditionally, in the Hawaiian Islands land and marine resources were managed by communities as a single integrated unit, i.e. the ahupua‘a (Berkes 2008). Community-based approaches that integrate management of land and marine resources would seem to be suitable for the Hawaiian and most other Pacific Islands. Although it is unlikely that traditional community-based marine resource management systems will be reinvigorated on O‘ahu, they have been adopted on some of the outer islands with some success (Gon 2003; Poepoe et al. 2007).

### *Conclusions*

In conclusion, this study has shown that top-down forces independently and when combined with elevated nutrients strongly influence benthic community structure at the Kewalo Basin. However, the effects of nutrient enrichment alone were only significant in the early stages of community development (first and fourth month). Experimentally restoring natural herbivory on a degraded reef in the Hawaiian Islands offers promise for longer term reef restoration, supporting the findings in Smith et al. (2010), that re-exposure to natural herbivore populations can shift benthic community trajectories in two months, even in the continued presence of elevated nutrients.

Management schemes that favor increased rates of herbivory, either directly or indirectly would be beneficial for restoration of the coral reef ecosystem at the Kewalo Basin, although management schemes that simultaneously reduce nutrient pollution would seem likely to work better.

Table 1. Fish Biomass for Kewalo Basin, O‘ahu.

Biomass estimates for fish surveyed within the experimental area at the Kewalo Basin, O‘ahu, Hawai‘i in April 2011 (25 x 4m, n=4 transects). Biomass was estimated in terms of mean g m<sup>-2</sup> ± SE.

<b>Family</b>	<b>Species</b>	<b>Biomass (g m<sup>-2</sup>) ± SE</b>
Acanthuridae	<i>Acanthurus achilles</i>	1.245 ± 0.000
Acanthuridae	<i>Acanthurus nigrofuscus</i>	0.831 ± 0.017
Acanthuridae	<i>Acanthurus olivaceus</i>	0.169 ± 0.045
Acanthuridae	<i>Acanthurus triostegus</i>	0.522 ± 0.082
Chaetodontidae	<i>Chaetodon ephippium</i>	0.061 ± 0.015
Pomacentridae	<i>Chromis vanderbilti</i>	0.346 ± 0.013
Cirrhitidae	<i>Cirrhitus pinnulatus</i>	0.462 ± 0.011
Labridae	<i>Coris venusta</i>	0.387 ± 0.053
Acanthuridae	<i>Ctenochaetus hawaiiensis</i>	0.144 ± 0.035
Pomacentridae	<i>Dascyllus albisella</i>	0.138 ± 0.035
Fistulariidae	<i>Fistularia commersonii</i>	0.956 ± 0.225
Labridae	<i>Halichoeres ornatissimus</i>	0.716 ± 0.065
Ostraciidae	<i>Ostracion meleagris</i>	0.425 ± 0.009
Cirrhitidae	<i>Paracirrhites arcatus</i>	0.413 ± 0.055
Cirrhitidae	<i>Paracirrhites forsteri</i>	0.385 ± 0.105
Mullidae	<i>Parupeneus multifasciatus</i>	0.693 ± 0.024
Pomacentridae	<i>Plectroglyphidodon imparipennis</i>	0.310 ± 0.028
Balistidae	<i>Rhinecanthus rectangulus</i>	0.875 ± 0.074
Pomacentridae	<i>Stegastes fasciolatus</i>	0.260 ± 0.038
Labridae	<i>Stethojulis balteata</i>	0.477 ± 0.039
Labridae	<i>Thalassoma duperrey</i>	0.681 ± 0.014
Labridae	<i>Thalassoma trilobatum</i>	0.472 ± 0.067

Table 2. Herbivore Abundances for Kewalo Basin, O‘ahu.

Individual abundances of herbivores surveyed in April 2011 at the reef outside of Kewalo Basin, O‘ahu, Hawai‘i (25 x 4m, n=4 transects). Abundance is expressed in terms of the mean number of individuals  $m^{-2} \pm SE$ .

<b>Organism</b>	<b>Species</b>	<b>Abundance (no. <math>m^{-2}</math>) <math>\pm</math> SE</b>
<b>Fishes</b>	<i>Acanthurus achilles</i>	0.028 $\pm$ 0.017
	<i>Acanthurus nigrofuscus</i>	0.128 $\pm$ 0.041
	<i>Acanthurus olivaceus</i>	0.003 $\pm$ 0.005
	<i>Acanthurus triostegus</i>	0.025 $\pm$ 0.03
	<i>Chaetodon ephippium</i>	0.003 $\pm$ 0.005
	<i>Chromis vanderbilti</i>	0.023 $\pm$ 0.029
	<i>Cirrhitus pinnulatus</i>	0.003 $\pm$ 0.005
	<i>Coris venusta</i>	0.005 $\pm$ 0.006
	<i>Ctenochaetus hawaiiensis</i>	0.003 $\pm$ 0.005
	<i>Dascyllus albisella</i>	0.003 $\pm$ 0.005
	<i>Fistularia commersonii</i>	0.005 $\pm$ 0.001
	<i>Halichoeres ornatissimus</i>	0.035 $\pm$ 0.024
	<i>Ostracion meleagris</i>	0.075 $\pm$ 0.048
	<i>Paracirrhites arcatus</i>	0.008 $\pm$ 0.009
	<i>Paracirrhites forsteri</i>	0.003 $\pm$ 0.005
	<i>Parupeneus multifasciatus</i>	0.025 $\pm$ 0.006
	<i>Plectroglyphidodon imparipennis</i>	0.058 $\pm$ 0.095
	<i>Rhinecanthus rectangulus</i>	0.033 $\pm$ 0.04
	<i>Stegastes fasciolatus</i>	0.01 $\pm$ 0.011
	<i>Stethojulis balteata</i>	0.05 $\pm$ 0.074
<i>Thalassoma duperrey</i>	0.18 $\pm$ 0.056	
<i>Thalassoma trilobatum</i>	0.005 $\pm$ 0.006	
<b>Echinoderms</b>	<i>Echinothrix calamaris</i>	0.028 $\pm$ 0.005
	<i>Tripneustes gratilla</i>	0.003 $\pm$ 0.005
<b>Reptiles</b>	<i>Chelonia mydas</i>	0.005 $\pm$ 0.006

Table 3. Global-R Values (ANOSIM). Global-R values and significance levels (%) for all pair-wise treatment differences during the eight month sampling period.

<b>Month</b>		<b>1</b>	<b>2</b>	<b>3</b>	<b>4</b>	<b>5</b>	<b>6</b>	<b>8</b>
<b>Sample statistic (Global-R)</b>		0.316	0.35	0.468	0.717	0.719	0.731	0.457
<b>Significance level (%)</b>	Cage, Cage/Fert	9.7	58.9	97.6	11.4	13.5	0.8	3.6
	Cage, Control	0.6	0.4*	0.2*	0.2*	0.8	0.2*	3.6
	Cage, Fert	55.8	0.9	0.2*	0.5*	0.8	0.2*	1.2
	Cage/Fert, Control	0.2*	0.2*	0.2*	0.5*	0.8	0.5*	0.9
	Cage/Fert, Fert	0.8	0.9	0.2*	2.9	0.8	0.5*	0.2*
	Control, Fert	0.4*	52.4	27.5	0.5*	0.8	2.4	41.1

\*significance p-value  $\leq 0.005$

Table 4. Species Contributions (SIMPER).

Percent contributions of benthic species or functional groups to similarity within each treatment over time based on the individual abundances (% cover) of each species. The top three major contributing species or functional groups are listed below.

Treatments	Month	Contribution of benthic species or functional group to similarity within treatment (% contribution)
Control	1	Sand/bare (42.63), <i>Hincksia indica</i> (14.89), CCA (8.77)
Fert	1	Sand/bare (36.23), <i>Hincksia indica</i> (26.78), <i>Lobophora variegata</i> (12.32)
Cage	1	Sand/bare (42.31), <i>Hincksia indica</i> (18.16), <i>Ceramium flaccidium</i> (7.87)
Cage/Fert	1	Sand/bare (55.65), <i>Asteronema breviararticulatum</i> (15.63), <i>Hincksia indica</i> (7.17)
Control	2	Sand/bare (26.30), invert (11.07), CCA (10.88)
Fert	2	Sand/bare (18.92), invert (10.37), <i>Sphacelaria</i> sp. (8.36)
Cage	2	Sand/bare (14.55), <i>Cladophora vagabunda</i> (9.85), <i>Ceramium flaccidium</i> (9.37)
Cage/Fert	2	Sand/bare (15.51), <i>Cladophora vagabunda</i> (14.96), <i>Ceramium flaccidium</i> (7.02)
Control	3	Sand/bare (16.18), invert (9.61), CCA (8.55)
Fert	3	Sand/bare (13.12), <i>Ceramium flaccidium</i> (7.44), CCA (6.69)
Cage	3	Sand/bare (10.75), <i>Chondria simpliciuscula</i> (7.31), invert (6.88)
Cage/Fert	3	Sand/bare (9.31), <i>Sphacelaria</i> sp. (7.24), CCA (6.91)
Control	4	Sand/bare (12.54), <i>Sphacelaria</i> sp. (9.39), invert (8.42)
Fert	4	Sand/bare (9.49), CCA (7.78), invert (7.55)
Cage	4	CCA (7.79), <i>Lobophora variegata</i> (7.30), <i>Jania adhaerens</i> (7.28)
Cage/Fert	4	<i>Spyridia filamentosa</i> (11.73), <i>Cladophora vagabunda</i> (8.87), <i>Hydrolithon farinosum</i> (7.52)
Control	5	Sand/bare (12.25), <i>Anotrichium secundum</i> (11.85), <i>Taenioma perpusillum</i> (8.96)
Fert	5	Sand/bare (9.21), <i>Sphacelaria</i> sp. (8.71), <i>Taenioma perpusillum</i> (7.49)
Cage	5	<i>Ptilothamnion cladophorae</i> (10.12), <i>Spyridia filamentosa</i> (9.22), <i>Cladophora vagabunda</i> (6.60)
Cage/Fert	5	<i>Hydrolithon farinosum</i> (7.23), <i>Cladophora vagabunda</i> (6.66), <i>Spyridia filamentosa</i> (6.57)
Control	6	CCA (9.53), <i>Anotrichium secundum</i> (8.58), <i>Sphacelaria</i> sp. (8.56)
Fert	6	Sand/bare (11.67), CCA (8.82), invert (8.41)
Cage	6	<i>Spyridia filamentosa</i> (11.41), <i>Hydrolithon farinosum</i> (6.68), invert (6.50)
Cage/Fert	6	<i>Spyridia filamentosa</i> (9.76), <i>Jania adhaerens</i> (9.61), invert (6.58)
Control	8	Sand/bare (14.08), CCA (9.82), <i>Calothrix</i> sp. (9.65)
Fert	8	Sand/bare (11.39), <i>Sphacelaria</i> sp. (11.15), CCA (8.50)
Cage	8	Invert (13.17), Sand/bare (12.11), <i>Chondria simpliciuscula</i> (7.43)
Cage/Fert	8	<i>Jania adhaerens</i> (8.59), invert (7.33), <i>Chondria simpliciuscula</i> (6.09)



Table 5. Species List.

List of all benthic photosynthetic species that settled on the experimental tiles at the Kewalo Basin during the eight month study period. The table shows the presence and/or absence of each species for all four treatments. Letters following each species name indicate the functional group to which the organism belongs (T = turf algae, M= macroalgae, CCA = crustose coralline algae).

	Control	Fertilized	Cage	Cage/Fert
<b>Marine Bacteria</b>				
<i>Chrysonephos lewisii</i> (T)	x	x		
<b>Diatoms</b>				
unidentified Diatoms (T)	x	x	x	x
<b>Cyanobacteria</b>				
<i>Anabaena</i> sp. (T)	x	x	x	x
<i>Calothrix</i> sp. (T)	x	x	x	x
<i>Lyngbya majuscula</i> (T)		x		
<i>Lyngbya</i> sp.1 (T)	x	x	x	x
<i>Lyngbya</i> sp.2 (T)		x		
<i>Lyngbya</i> sp.3 (T)		x		
<i>Symploca hypnoides</i> (T)			x	x
unidentified cyanobacteria (T)	x	x	x	x
<b>Green Algae</b>				
<i>Chaetomorpha indica</i> (T)	x	x	x	x
<i>Cladophora dotyana</i> (T)		x	x	
<i>Cladophora laetevirens</i> (T)		x	x	
<i>Cladophora sericea</i> (T)		x		
<i>Cladophora</i> sp. (T)	x	x	x	x
<i>Cladophora vagabunda</i> (T)	x	x	x	x
<i>Codium saccatum</i> (M)				x
<i>Derbesia fastigiata</i> (T)		x		
<i>Neomeris annulata</i> (M)			x	
<i>Neomeris</i> sp. (M)	x	x	x	x
<i>Neomeris vanbosseae</i> (M)		x	x	x
<i>Parvocaulis</i> sp. (T)	x	x	x	
<i>Ulva lactuca</i> (M)			x	x
<i>Ulva flexuosa</i> (M)	x			x
<i>Ulva linza</i> (T)		x		

<i>Ulva paradoxa</i> (T)	x	x	x	x
<i>Ulva</i> sp. (T)	x		x	x
<b>Brown Algae</b>				
<i>Asteronema breviarticulatum</i> (T)			x	x
<i>Asteronema rhodortonoides</i> (T)			x	x
<i>Asteronema</i> sp. (T)	x			
<i>Dictyota acutiloba</i> (M)	x		x	x
<i>Dictyota friabilis</i> (M)	x	x		x
<i>Dictyota sandwicensis</i> (M)				x
<i>Dictyota</i> sp. (M)		x		
<i>Dictyota stolonifera</i> (M)	x			x
<i>Distromium flabellatum</i> (M)	x	x	x	x
<i>Feldmannia lebelli</i> (T)	x	x	x	x
<i>Hincksia indica</i> (T)	x	x	x	x
<i>Lobophora variegata</i> (M)	x	x	x	x
<i>Padina melemele</i> (M)				x
phaeophyte-crustose (M)	x	x	x	
phaeophyte-flabellate (M)	x	x	x	x
phaeophyte-saccate (M)				x
<i>Spatoglossum</i> sp. (M)			x	x
<i>Sphacelaria nova-hollandae</i> (T)	x		x	
<i>Sphacelaria rigidula</i> (T)				x
<i>Sphacelaria</i> sp. (T)	x	x	x	x
<i>Sphacelaria tribuloides</i> (T)				x
<b>Red Algae</b>				
<i>Acrochaetium seriatum</i> (T)				x
<i>Aglaothamnion cordatum</i> (T)	x	x	x	x
<i>Amansia glomerata</i> (M)	x	x	x	x
<i>Amphiroa beauvoisii</i> (M)			x	x
<i>Anotrichium secundum</i> (T)	x	x	x	x
<i>Antithamnion decipiens</i> (T)			x	
<i>Antithamnionella breviramosa</i> (T)			x	x
<i>Asparagopsis taxiformis</i> (M)			x	
CCA-1 (CCA)	x	x		x
CCA-2 (CCA)		x	x	x
CCA-3 (CCA)			x	
CCA-4 (CCA)	x			
CCA-5 (CCA)	x	x	x	x
CCA-6 (CCA)	x		x	

CCA-7 (CCA)			X	X
CCA-8 (CCA)			X	
CCA-9 (CCA)	X	X		X
<i>Centroceras minutum</i> (T)	X	X	X	X
<i>Centroceras</i> sp. (T)				X
<i>Ceramium cingulum</i> (T)				X
<i>Ceramium clarionensis</i> (T)	X	X	X	X
<i>Ceramium codii</i> (T)	X		X	X
<i>Ceramium dumosertum</i> (T)			X	X
<i>Ceramium fimbriatum</i> (T)	X	X	X	X
<i>Ceramium flaccidium</i> (T)	X	X	X	X
<i>Ceramium hanaense</i> (T)	X	X	X	X
<i>Ceramium jolyi</i> (T)		X		
<i>Ceramium</i> sp. (T)	X			X
<i>Ceramium</i> sp.1 (T)			X	
<i>Ceramium vagans</i> (T)	X	X	X	X
<i>Champia parvula</i> (T)	X	X	X	X
<i>Champia viellardii</i> (T)	X	X	X	X
<i>Chondracanthus acicularis</i> (T)	X	X	X	X
<i>Chondria arcuata</i> (T)				X
<i>Chondria dangeardii</i> (T)	X	X	X	X
<i>Chondria minulata</i> (T)			X	X
<i>Chondria polyrhiza</i> (T)	X	X	X	X
<i>Chondria simpliciuscula</i> (T)	X	X	X	X
<i>Chondria</i> sp. (T)	X	X	X	X
<i>Corallophila huysmansii</i> (T)	X			
<i>Corallophila</i> sp. (T)			X	
<i>Crouania mageshimensis</i> (T)		X		X
<i>Dasya corymbifera</i> (M)			X	X
<i>Dasya kristeniae</i> (T)	X	X	X	X
<i>Dasya murrayana</i> (T)	X	X	X	X
<i>Dasya</i> sp.1 (T)	X	X	X	X
<i>Dasya</i> sp. 2 (T)	X			
<i>Dasya</i> sp. 3 (T)	X			
<i>Dotyella hawaiiensis</i> (T)			X	X
<i>Falkenbergia</i> (T)		X	X	
<i>Fernandosiphonia ecorticata</i> (T)		X	X	
<i>Gelidiella antipai</i> (T)	X	X	X	X
<i>Gelidiella</i> sp. (T)				X

<i>Griffithsia heteromorpha</i> (T)			X	
<i>Griffithsia</i> sp. (T)			X	X
<i>Griffithsia subcylindrica</i> (T)			X	
<i>Herposiphonia arcuata</i> (T)	X		X	X
<i>Herposiphonia crassa</i> (T)				X
<i>Herposiphonia delicatula</i> (T)	X	X	X	X
<i>Herposiphonia dubia</i> (T)	X	X	X	X
<i>Herposiphonia nuda</i> (T)	X	X	X	X
<i>Herposiphonia obscura</i> (T)	X	X	X	X
<i>Herposiphonia pacifica</i> (T)	X	X	X	X
<i>Herposiphonia parca</i> (T)		X		
<i>Herposiphonia secunda</i> f. <i>secunda</i> (T)		X	X	
<i>Herposiphonia</i> sp.1 (T)	X	X	X	X
<i>Herposiphonia</i> sp.2 (T)	X	X	X	X
<i>Herposiphonia</i> sp.3 (T)	X	X	X	X
<i>Herposiphonia</i> sp.4 (T)		X	X	
<i>Herposiphonia variabilis</i> (T)	X	X	X	X
<i>Heterosiphonia crispella</i> (T)	X		X	X
<i>Heterosiphonia</i> sp. (T)			X	
<i>Hydrolithon farinosum</i> (CCA)	X	X	X	X
<i>Hypnea spinella</i> (T)	X	X	X	X
<i>Hypoglossum minimum</i> (T)	X	X	X	X
<i>Jania adhaerens</i> (T)	X	X	X	X
<i>Jania pumila</i> (T)				X
<i>Jania</i> sp. (T)		X		X
<i>Laurencia majuscula</i> (M)	X			X
<i>Laurencia yamadana</i> (T)	X	X	X	X
<i>Lomentaria hakodatensis</i> (T)	X	X	X	X
<i>Malconema minimum</i> (T)	X		X	X
<i>Monosporus indicus</i> (T)	X	X	X	X
<i>Neosiphonia hawaiiensis</i> (T)	X	X	X	X
<i>Peysonnellia rubra</i> (M)	X	X	X	X
<i>Polysiphonia apiculata</i> (T)			X	
<i>Polysiphonia homoia</i> (T)	X	X	X	X
<i>Polysiphonia</i> sp.1 (T)	X	X	X	X
<i>Polysiphonia</i> sp.2 (T)	X	X	X	X
<i>Polysiphonia</i> sp.3 (T)	X	X	X	X
<i>Polysiphonia</i> sp.4 (T)			X	
<i>Polysiphonia</i> sp.5 (T)			X	

<i>Polysiphonia</i> sp.6 (T)		x		x
<i>Polysiphonia sphaerocarpa</i> (T)	x	x	x	x
<i>Polysiphonia subtilisima</i> (T)			x	x
<i>Polysiphonia tongatensis</i> (T)				x
<i>Polysiphonia-prostrate</i> (T)	x	x	x	x
<i>Ptilothamnion cladophorae</i> (T)		x	x	x
<i>Reticulocaulis mucosissimus</i> (M)			x	
<i>Scinaia furcata</i> (M)			x	x
<i>Spirocladia hodgsoniae</i> (T)		x	x	
<i>Spirocladia</i> sp. (T)	x	x	x	x
<i>Spyridia filamentosa</i> (M)	x		x	x
<i>Spyridia</i> sp. (M)		x		
<i>Taenioma perpusillum</i> (T)	x	x	x	
<i>Tolypiocladia glomerulata</i> (T)	x	x	x	x
unidentified Nemaliales (T)				x
unidentified rhodophyte (T)	x			
<i>Womersleyella pacifica</i> (T)	x	x	x	x
<i>Yamadaella caenomyce</i> (M)			x	x

Figure 1. Field Map of Kewalo Basin, O‘ahu, Hawai‘i. Photo Credit: Google Earth

The Kewalo Basin is located on the south shore of O‘ahu just east of the Honolulu Harbor and west of Ala Moana. The study was conducted within a 600 m<sup>2</sup> area offshore of the Kewalo Basin on the sloping reef crest at approximately 9 m depth. The picture shows GPS coordinates taken at the study site overlaid on a Google Earth image of the Kewalo Basin (points 005, 007, 008, 010).



Figure 2. MDS Plot of Community Similarity - December 2010.

The MDS plot displays the similarity in benthic community structure after one month of the experimental manipulation. Each data point represents the abundance (% cover) for each benthic species found on a single experimental tile. Treatments can be identified by the different shapes and colors of the data points. All replicates for all four treatments are shown (both Control and Cage treatments  $n=6$ ; both Fert and Cage/Fert  $n=5$ ). Data points that are closer to one another in two-dimensional space are more similar in terms of community abundance. The stress value indicates how well the community data are represented with the prospect of misinterpretation within acceptable levels of 0.2 or less (Clarke & Warwick 2001; Smith et al. 2010).

# MDS - Similarity of Communities

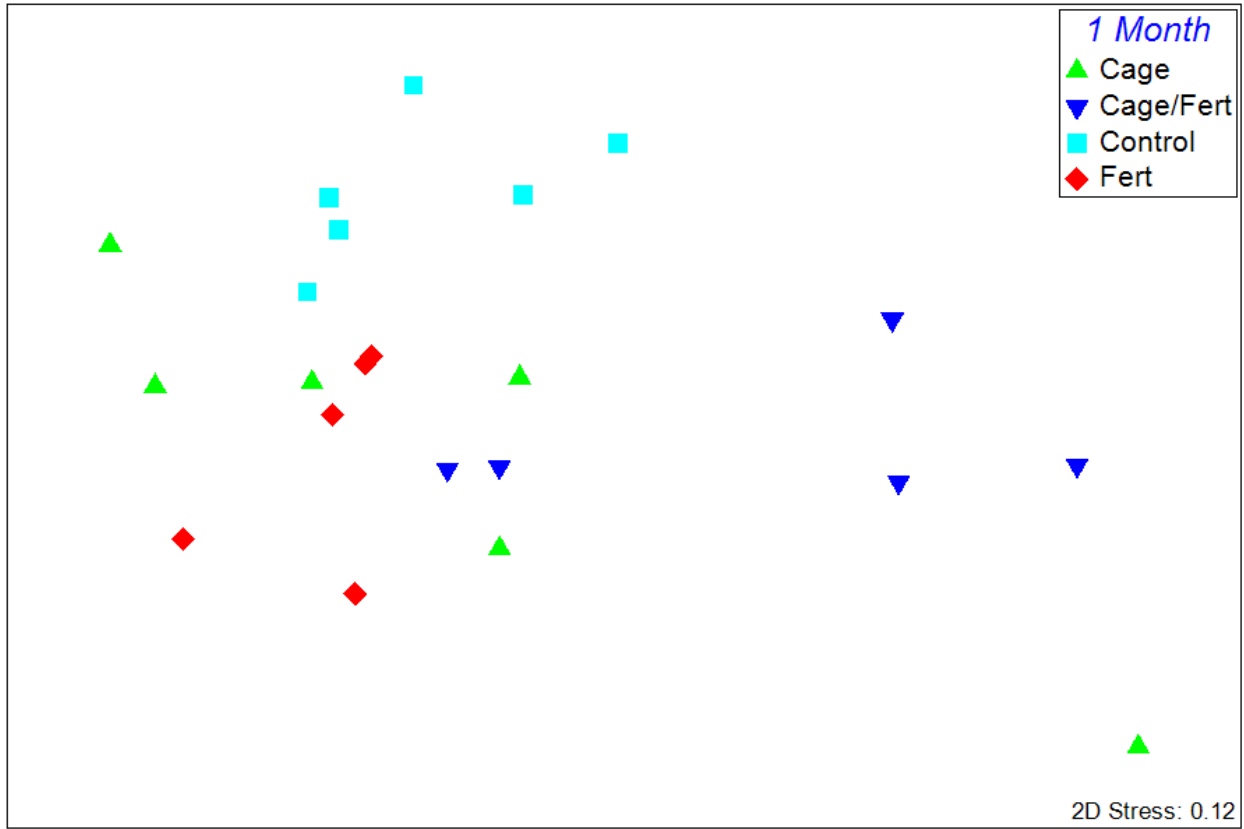




Figure 3. MDS Plot of Community Similarity - January 2011.

The MDS plot displays the similarity in benthic community structure after two months of the experimental manipulation (Control, Cage, and Cage/Fert treatments  $n=6$ ; Fert  $n=5$ ).

# MDS - Similarity of Communities

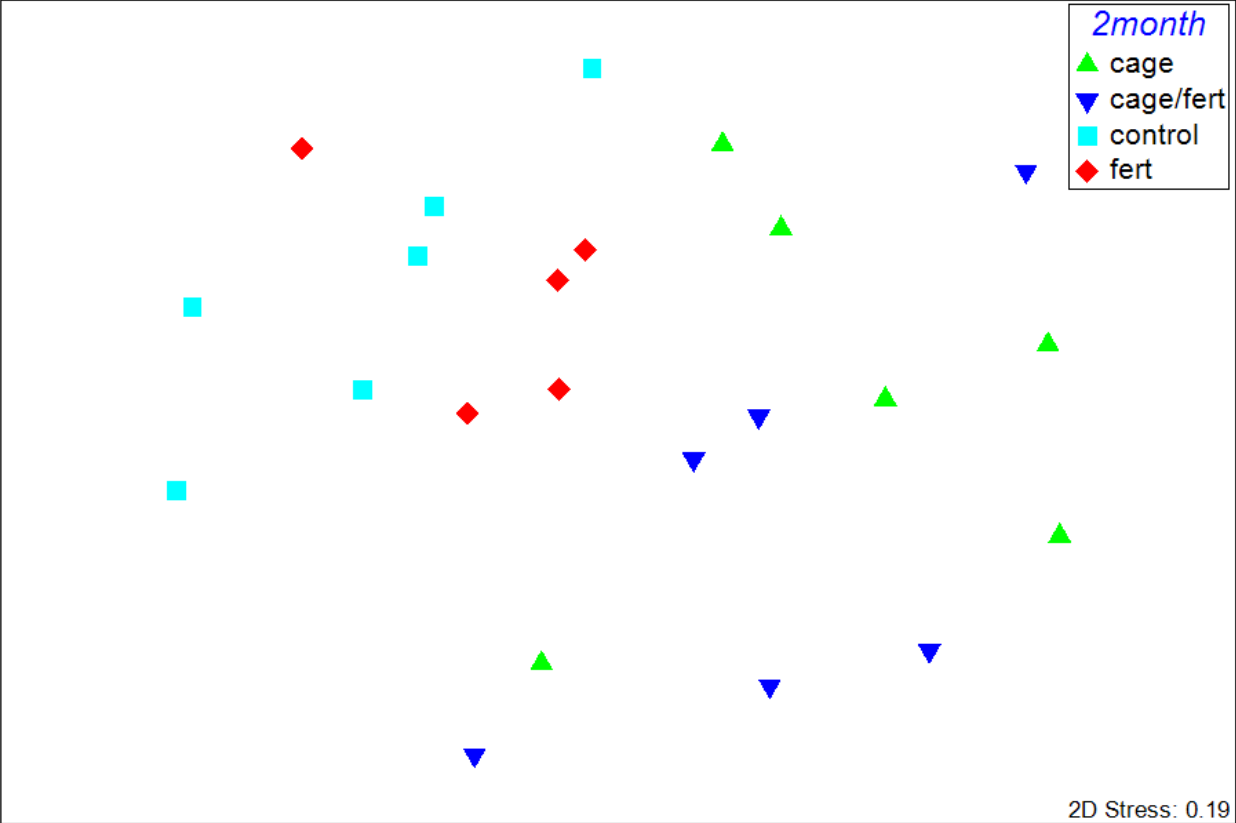


Figure 4. MDS Plot of Community Similarity - February 2011.

The MDS plot displays the similarity in benthic community structure after three months of the experimental manipulation ( $n=6$  for all treatments).

# MDS - Similarity of Communities

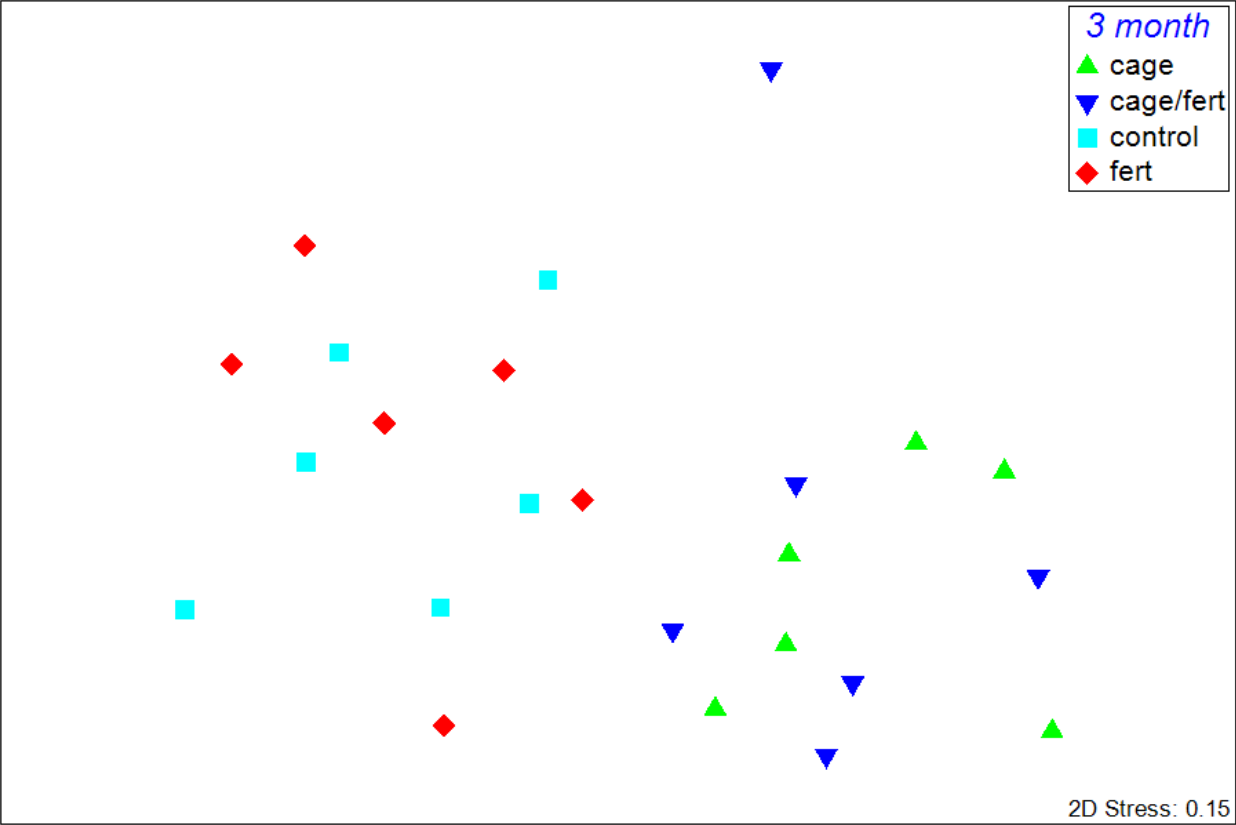


Figure 5. MDS Plot of Community Similarity - March 2011.

The MDS plot displays the similarity in benthic community structure after four months of the experimental manipulation (both Control and Cage treatments  $n=6$ ; both Fert and Cage/Fert  $n=4$ ).

# MDS - Similarity of Communities

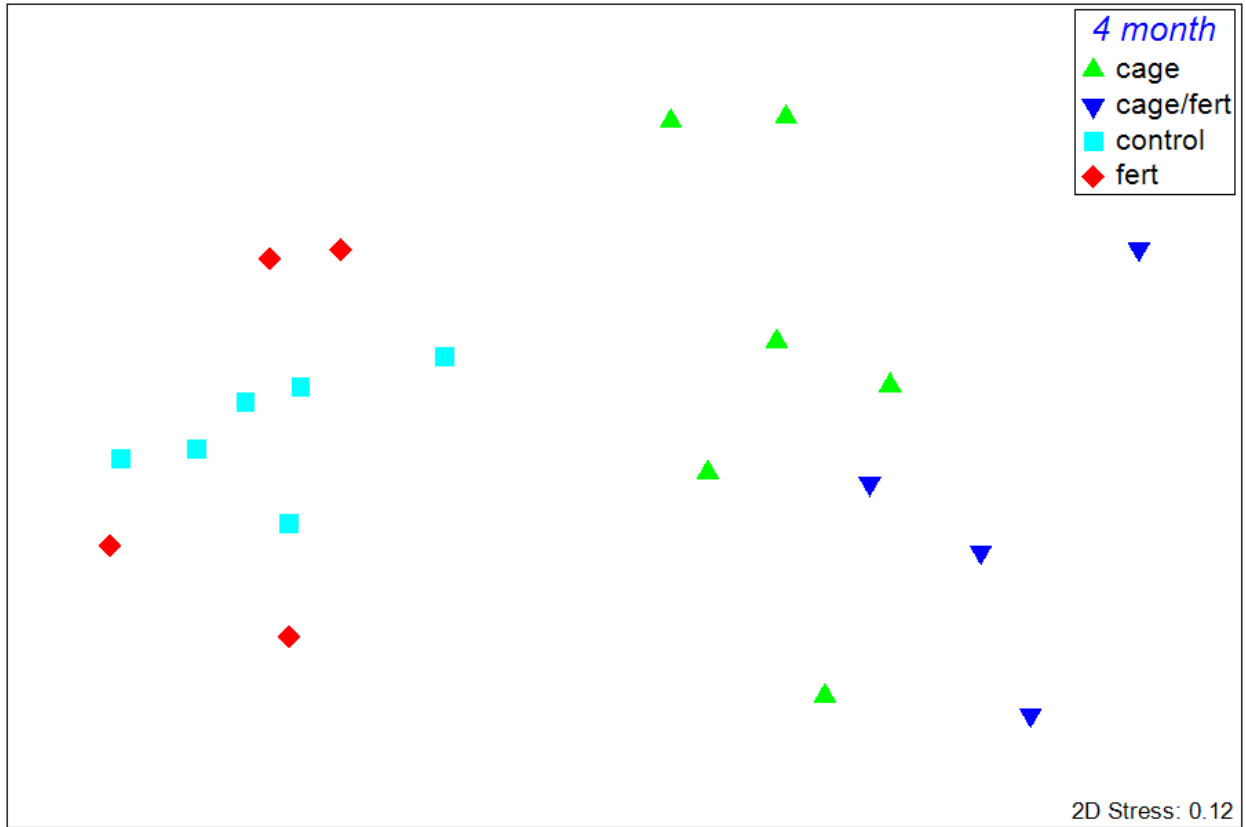


Figure 6. MDS Plot of Community Similarity - April 2011.

The MDS plot displays the similarity in benthic community structure after five months of the experimental manipulation (Control treatment  $n=6$ ; both Fert and Cage  $n=5$ ; Cage/Fert  $n=4$ ).

# MDS - Similarity of Communities

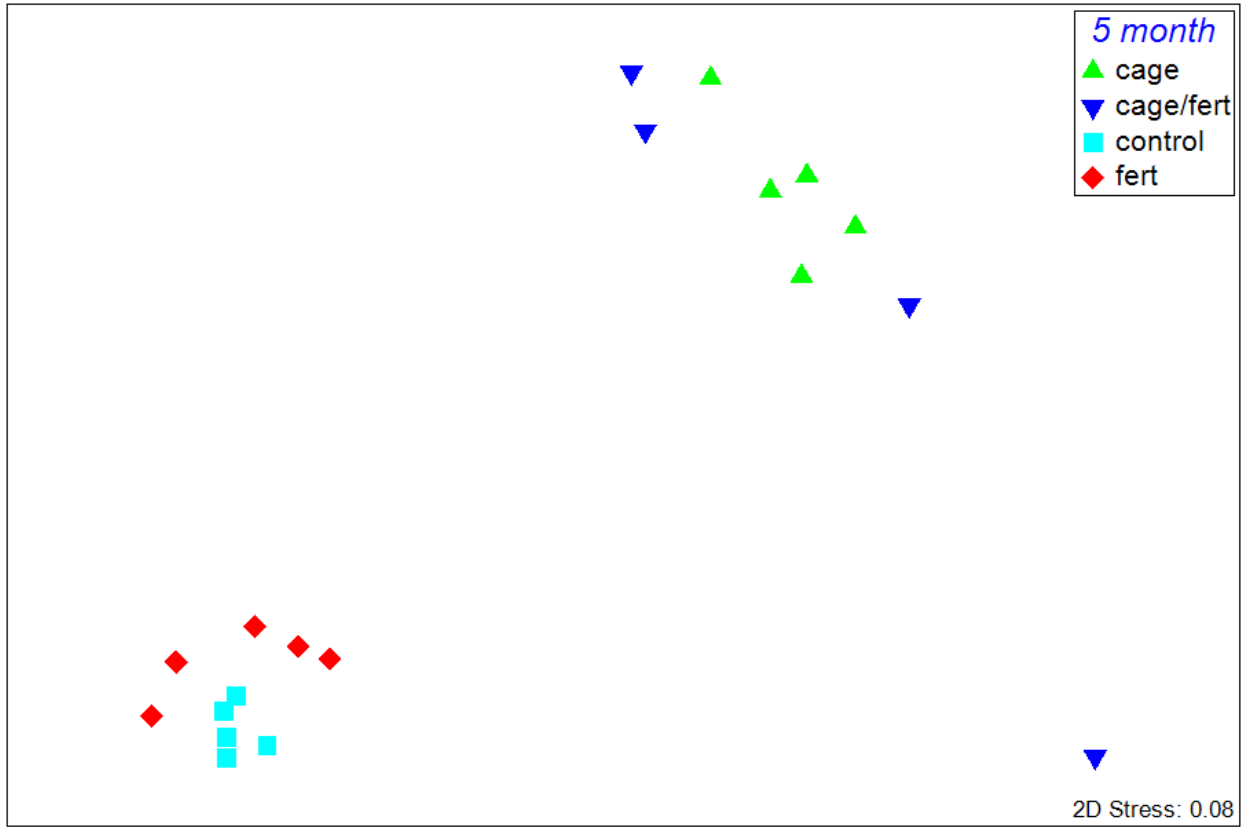




Figure 7. MDS Plot of Community Similarity - May 2011.

The MDS plot displays the similarity in benthic community structure after six months of the experimental manipulation (both Control and Fert treatments  $n=6$ ; Cage  $n=5$ ; Cage/Fert  $n=4$ ).

# MDS - Similarity of Communities

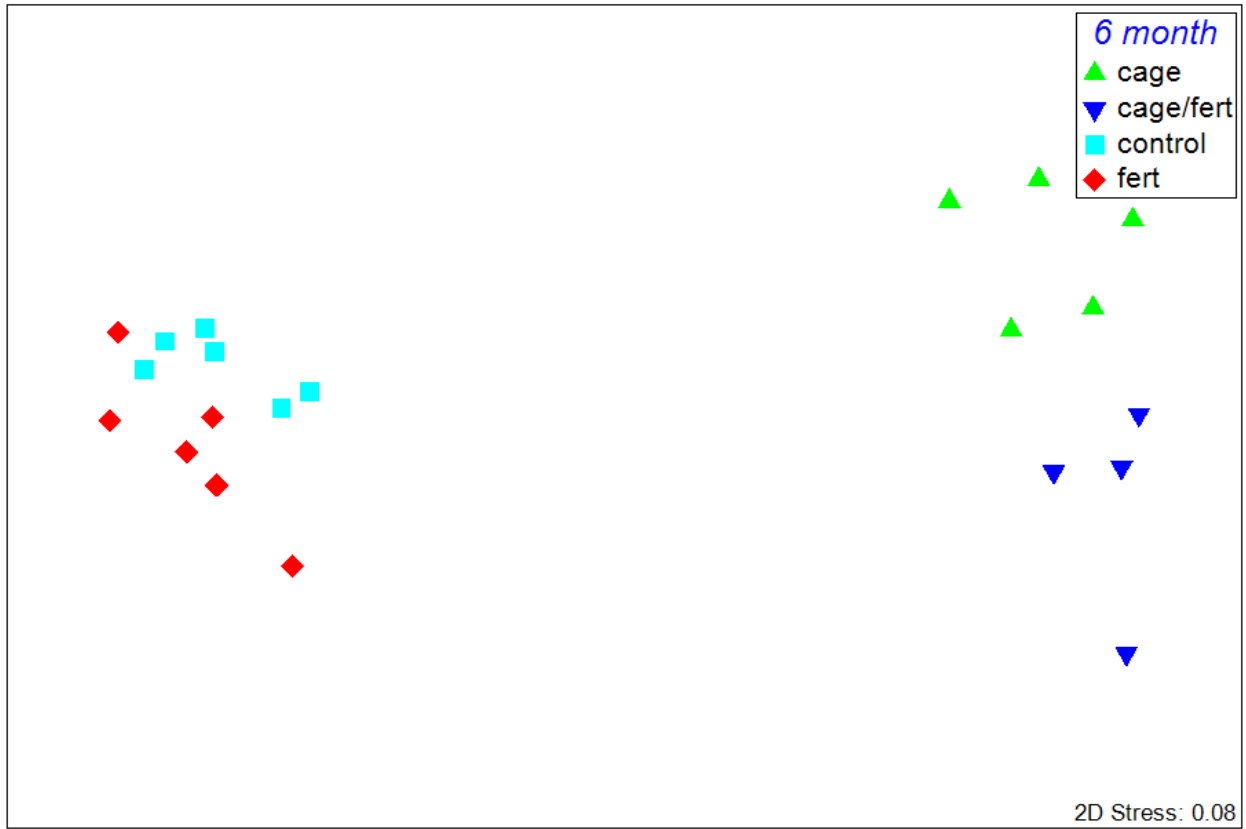
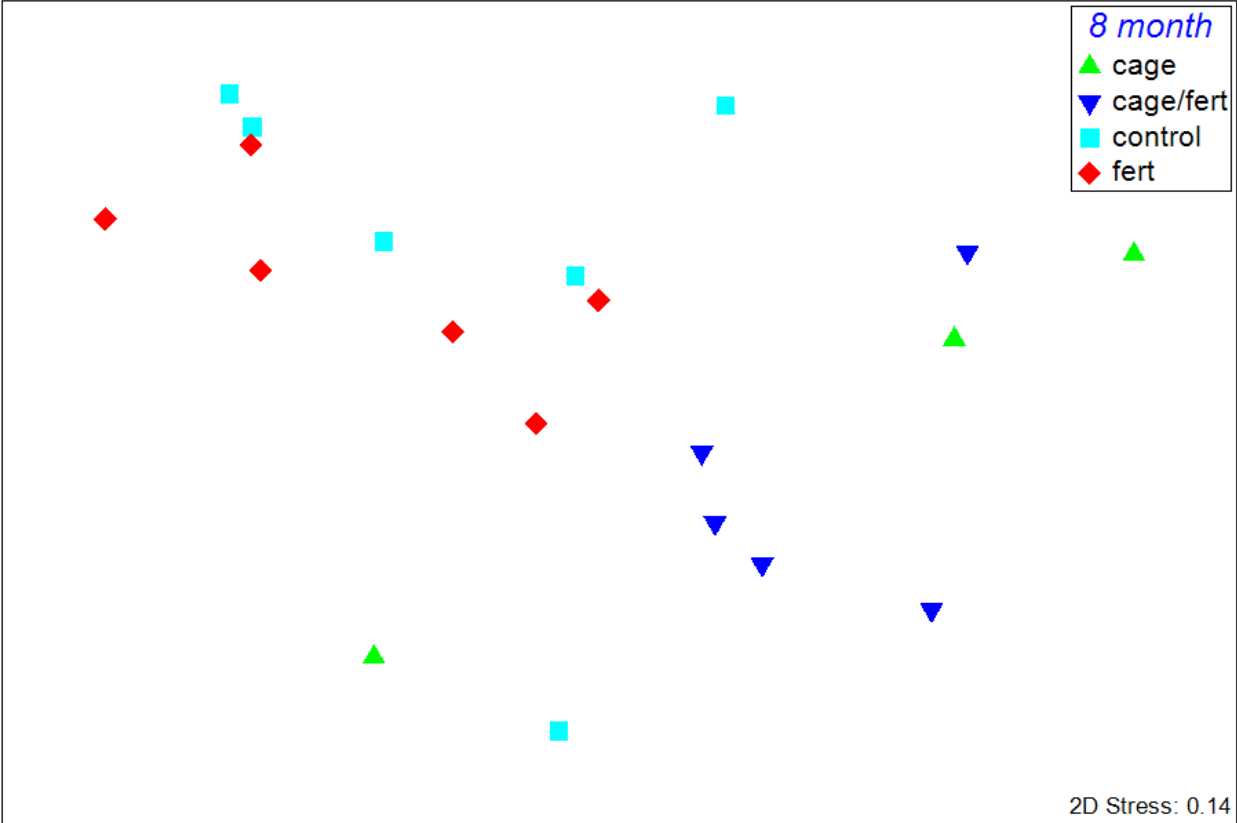


Figure 8. MDS Plot of Community Similarity - July 2011.

The MDS plot displays the similarity in benthic community structure after eight months of the experimental manipulation. Cages were removed from the Cage and Cage/Fert treatments two months prior to sampling to re-expose those communities to natural herbivory. Therefore, all treatments were exposed to the same levels of natural herbivory for two months (both Control and Fert treatments  $n=6$ ; Cage  $n=3$ ; Cage/Fert  $n=5$ ).

# MDS - Similarity of Communities (Cages removed after 6 month)



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## **CHAPTER 3. SYNTHESIS AND MANAGEMENT RECOMMENDATIONS**

### *Summary*

The increase in coral-algal phase shifts worldwide urges a deeper and more thorough understanding of the factors underlying them in order to more effectively manage and restore coral reef ecosystems. The results here indicate that top-down forces independently and when combined with elevated nutrients, strongly influence benthic community structure on an urban reef adjacent to municipal uses, and intense human use for recreation and fishing. However, the effects of nutrient enrichment alone were only significant in the short term. Experimentally restoring natural herbivory on a degraded reef led to positive changes (reductions in algal cover) that support the findings of Smith et al. (2010) on a relatively pristine, coral dominated reef. Re-exposure to natural herbivore populations shifted benthic community trajectories in two months, even in the continued presence of elevated nutrients. This research suggests that maintaining herbivore populations is critical even in management of urbanized reef ecosystems, where continued pressure from fishing exists.

### *Recommendations*

These types of manipulative field studies examining reduced herbivory and elevated nutrients are highly relevant and provide insight for management and restoration of coral reef ecosystems on the main Hawaiian Islands. Little is known about the effects of reduced herbivory and elevated nutrients on the windward side of O‘ahu or Hawai‘i Island. Further, implementing similar studies on Maui and Kaua‘i would be valuable and could help provide a more thorough calibration of the complex factors driving coral-algal phase shifts on the main Hawaiian Islands. Ultimately, these types of studies can help resource managers make better management decisions.

Management schemes that favor increased rates of herbivory, either directly or indirectly would be beneficial for restoration of the coral reef ecosystem at the Kewalo Basin, although management schemes that simultaneously reduce nutrient pollution would seem likely to work better. It is more difficult based on this experiment to offer specific recommendations on reducing nutrient pollution at this site; however, specific recommendations for increasing rates of herbivory can be offered. For example, protection of specific herbivorous target fish and urchin species on the reef at the Kahekili beach park on West Maui has been successfully implemented to address declining coral cover and increasing algal overgrowth. Considering that rotational management at the nearby Waikīkī-Diamond Head Fisheries Management Area (FMA) has not been effective, permanent closures specifically protecting herbivorous fish and urchins would seem most appropriate at the Kewalo Basin. The observations made in this experiment suggest that the herbivorous fish species *Acanthurus nigrofuscus* and the omnivorous fish species *Thalassoma duperrey*, as well as the sea urchin species *Echinothrix calamaris* and *Tripneustes gratilla* should be prioritized for protection on the reef adjacent to Kewalo Basin.