ANTHROPOGENIC STRESS, BIOEROSION, AND FARMING DAMSELFISH: POTENTIAL INTERACTIONS AND EFFECTS ON CORAL REEFS IN AMERICAN SAMOA

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Chapter 1. INTRODUCTION

Pomacentridae, the family commonly known as damselfishes, is one of the most abundant families of reef dwelling fish. Damselfish are small (few species exceed 15 cm total length), are abundant in most shallow tropical habitats, and can commonly be found anywhere where suitable shelter is available (Myers, 1999; Hoover, 1993). Pomacentrids have adapted various feeding strategies, with most species feeding as planktivores or herbivores. Of the herbivorous fish, some species are primarily foragers, which are mobile schooling fish that participate in grazing activities, and some are farmers (gardeners), which tend to be site attached, territorial species (Ceccarelli et al., 2005a). According to Ceccarelli et al. (2005b), farming damselfish are important to reef ecosystems because they occupy or control a large portion of the benthic substrate and can modify the benthic substrate to increase the cover of algae. Some direct and indirect effects of territorial behavior exhibited by farming damselfish include increasing coral recruitment, especially of rare coral species (Wellington, 1982), protecting surrounding corals from predation by *Acanthaster planci* and other corallivorous species (Ceccarelli et al., 2001), and decreasing rates of external bioerosion (Eakin, 1992). Additionally, Ceccarelli et al. (2002) and Sammarco and Carleton (1986) have correlated the presence of herbivorous damselfish (*Stegastes* spp.) with local increases in internal bioerosion of corals and a proliferation of invertebrate macrofauna and benthic algae. Bioerosion is the removal or destruction of coral and carbonate structures via chemical or physical actions of biological entities. According to Hutchings (1986), coral substrates do not become heavily bored by bioeroding organisms until the living veneer of the coral dies. Farming

damselfish that kill coral and increase available substrate for the recruitment of algae and the establishment of algal gardens can increase rates of internal bioerosion by facilitating the recruitment and survival of bioeroding organisms (Glynn, 1997).

Bioeroding organisms on a reef can be categorized as internal or external bioeroders, as well as macroborers or microborers. Major internal macrobioeroders are sponges, sipunculans, and polychaetes, while prominent external bioeroders include certain species of parrotfish and sea urchins. Bioerosion alters the overall coral cover and structural form of corals present on the reef (Syms, 1998) and is a significant biological process affecting the long-term persistence of coral reefs and reef-associated species around the world. The accretion of calcium carbonate, which makes up the structure of tropical reefs, and bioerosion are in a delicate balance with each other. Anthropogenic stress, including the potential influence of global climate change on the ocean, can alter the carbonate balance such that coral (calcium carbonate) accretion may slow, and coral reefs may enter a phase dominated by bioerosion (Perry, 1998). Humans also have the potential to significantly alter this balance by affecting the density of external bioeroders on reefs though fishing and other harvesting activities, and via land use patterns in coastal watersheds that alter the transport of nutrients to reef ecosystems. Nutrient availability has been found to substantially increase bioerosion on reefs (Sanders *et al.*, 2005; Chazottes *et al.*, 2002; Scott, 1988). Increases in dissolved organics and/or particulates, increases the food available to macrobioeroding organisms, which can increase the recruitment success and stimulate growth rates of bioeroders, thereby increasing overall rates of internal bioerosion (Hallock, 1988). Additionally, eutrophic conditions, in which

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phosphate levels are elevated, inhibit the calcification process, slowing rates of coral accretion (Highsmith, 1980).

In the chapters that follow, various methods for measuring bioerosion are explored, and the effects of anthropogenic stress on the density of farming damselfish and their algal gardens is linked to changes in rates of internal bioerosion. In order to observe potential changes in bioerosion and the effect such changes have on coral reefs, scientists need an accurate and effective tool to monitor bioerosion. The research described in Chapter 2 explores both resource intensive and a rapid field technique that can be used to measure bioerosion of coral substrates, comparing the results for ease of use, reliability, statistical variability, and the scale at which each method is effective. The three methods explored herein are (1) volume displacement, (2) rubble count, which was first described by Holmes *et al.* (2000), and (3) digital area analyses. Chapter 3 describes a field survey, whereby the density of farming damselfish and percent cover of damselfish algal gardens at each site were determined, and the benthic substrate was analyzed for percent cover of coral and algae. A water quality report produced by the American Samoa Environmental Protection Agency (ASEPA), which classified watersheds as either minimally, intermediately, or extensively influenced, was then used to look for significant differences in the benthic composition of reefs based on relative levels of anthropogenic stress. Bioerosion measurements from Chapter 2 were then correlated with the ASEPA ratings, and an analysis was made of how a potential web of interactions may exist, whereby increasing human influence in watersheds and/or coral reefs may modify the effects that herbivorous damselfish have on local rates of coral bioerosion.

American Samoa, including the islands of Ofu, Olosega, and Tutuila, was selected for this research. A map of American Samoa (Figure 2-1) and description of each study site is presented in Chapters 2 and 3. This region has the unique property of possessing a collection of islands that vary in the amount of anthropogenic stress to which they are exposed, ranging from an island with a commercial harbor and tuna canneries, to somewhat isolated islands that have only a single Samoan village. Additionally, the coral composition and geologic structure of American Samoa are such that there are a number of readily accessible reef flats and back reef lagoons of considerable size that have extensive tracts of damselfish algal gardens. These islands, therefore, provided the appropriate biota and environmental conditions to address the research questions outlined below:

1. How do results from less resource and time intensive methods of measuring bioerosion - specifically volume displacement and rubble count techniques - compare to results obtained using image analysis software and digital photos of coral cross-sections? (Chapter 2)

2. Is there a positive correlation between the intensity of anthropogenic stress in coastal watersheds and the density of farming damselfish (and damselfish algal gardens)? (Chapter 3)

3. Is the level of anthropogenic stress in a watershed significantly correlated with rates of internal coral bioerosion? (Chapter 3)

4. Does anthropogenic stress alter the effect farming damselfish have on rates of coral bioerosion? (Chapter 3)

Damselfish algal gardens are a prominent feature of coral reefs around the world, and can occupy, in some cases, up to 50 percent of the solid benthic substrate (Klumpp and Polunin, 1989; Sammarco and Williams, 1982). Therefore, the relationship between damselfish and coral, and their effects on the structural integrity of coral reefs, is an important aspect of coral reef ecology that deserves attention. Because farming damselfish can readily establish algal gardens on recently dead coral, eutrophication or other forms of anthropogenic stress that kill coral tissue are expected to be positively correlated with the abundance of damselfish and damselfish algal gardens. To date, the abundance and distribution of farming damselfish have not been correlated with eutrophic conditions or local anthropogenic activities. By examining the effects of anthropogenic stress on bioerosion and the abundance of damselfish and their algal gardens at a number of sites, this thesis suggests how human activities, specifically in coastal environments, may have direct and indirect effects on the structure of coral reef habitats and the diversity and composition of species found there.

Chapter 2. TECHNIQUES FOR MEASURING INTERNAL BIOEROSION OF CORALS

ABSTRACT

As scientific efforts continue to focus on the sustainability of coral reefs and their inhabitants, our understanding of bioerosion and the development of appropriate methods for quantifying coral bioerosion are of increasing importance. In attempts to determine an efficient and reliable technique for evaluating bioerosion intensity, three methods were applied to a set of coral rubble samples. Rubble count (described by Holmes *et al.*, 2000) and volume displacement techniques were compared against the well-published digital image analysis method for ease of use as well as variability and resolution of results. Rubble count and digital results were significantly positively correlated; however, rubble count results were unable to consistently detect a 10% difference in bioerosion between samples. Volume displacement measurements of bioerosion were highly variable, unable to detect a significant difference in bioerosion between sites, and were not correlated with either rubble count or digital measurements of bioerosion. These results indicate that rubble count and displacement techniques may require a much larger sample size than digital methods to accurately detect differences in bioerosion between samples and sites. Based on the low variability of results within sites and the ability of the method to detect significant differences in bioerosion, digital techniques are recommended for quantifying internal bioerosion of coral.

INTRODUCTION

Bioerosion was first described by Neumann (1966) as the process of removing consolidated mineral or lithic substrate via the direct action of organisms. Today, our

concept of bioerosion, as it relates to corals, has expanded to recognize differences between external and internal bioerosion, as well as macrobioerosion and microbioerosion. This paper compares various methods of quantifying internal macrobioerosion of corals. Most macrobioerosion is a result of the boring and excavating activities of invertebrates including sipunculans, polychaetes, sponges, and lithophagic bivalves (Londono-Cruz, 2003; Pari *et al.*, 2002; Moreno-Forero, 1998). The abundance of these organisms and their associated rates of bioerosion can be significantly affected by various natural and anthropogenic factors. Some of the abiotic and biotic factors that have been found to influence local rates of bioerosion include: water depth (Perry, 1998; Highsmith *et al.*, 1983), density of coral skeleton (Reaka-Kudla *et al.*, 1996; Hutchings, 1986), intensity of grazing by fish and urchins (Hutchings *et al.*, 2005; Kiene and Hutchings, 1994), presence of algal gardens maintained by damselfish (Zubia, 2001; Sammarco and Carleton, 1986), eutrophication and rates of primary production (Hutchings *et al.*, 2005; Edinger and Risk, 1997), and sedimentation (Tribollet *et al.*, 2002). The overall influence of these factors on rates of bioerosion, however, are inconsistent and vary among sites.

As scientific efforts continue to focus on the sustainability of coral reefs and their inhabitants, our understanding of bioerosion and the development of appropriate methods for quantifying coral bioerosion are becoming increasingly important. Digital analysis of bioerosion has become a widely accepted approach, with the associated methods and results being well described and extensively published in the primary literature throughout the last 25 years (McDonald and Perry, 2003; Tribollet *et al.*, 2002; Reaka-Kudla *et al.*, 1996; Moran and Reaka, 1988; Highsmith *et al.*, 1983). Digital planimeters,

and more recently, image analysis software that calculates areas within images, have been used to measure internal bioerosion of corals on a variety of media including: x-radiographs, Xerox copies, and photographs of coral slabs or coral cross-sections. In attempts to identify an effective, less resource intensive method of measuring bioerosion, the present study assessed the effectiveness of using a rapid analytical technique described by Holmes *et al.* (2000), referred to herein as "rubble count", to determine whether the technique was more sensitive for detecting differences in bioerosion across sites than digital methods. I also examined the utility of determining percent bioerosion by comparing the volume displaced by coral samples to their solid volume, referred to herein as volume displacement.

The rubble count technique has to date, only been published by Holmes (2000) and Holmes *et al.* (2000). This method is thought to have advantages over digital techniques in that it does not require the financial resources, equipment, or technical expertise necessary for digital analyses, nor does it require the destruction of living coral. Unlike digital analyses, which quantify the volume of coral eroded, rubble count measurements are based on the presence or absence of boreholes in coral rubble, which are evidence of bioeroding activities. Volume displacement has been employed in bioerosion studies for the last thirty years in a variety of capacities. Volume based bioerosion measurements have been used to document changes in the external dimensions of carbonate samples, which are most often blocks cut from massive *Porites* spp. coral heads (Chazottes *et al.*, 2002; Hutchings *et al.*, 1992; Davies and Hutchings, 1983; White, 1980). Volume displacement has also occasionally been used in bioerosion studies to determine how the density of coral skeletons affects rates of bioerosion

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(Highsmith, 1981; White, 1980). Most studies, however, have used volume displacement measurements with samples of sand/sediment, coral rubble, and blocks of benthic substrate in conjunction with dissolution techniques developed by Brock and Brock (1977). Dissolving the coral or carbonate matrix liberates cryptofauna, allowing for measurements of the average number and biomass of macroborers per cm^3 of coral. Combining volume displacement with coral dissolution has allowed scientists to document the effects of nutrification resulting from sewage outfalls (Brock and Smith, 1983, Smith et al., 1981) and to describe the distribution and abundance of macrofaunal bioeroding species in various intertidal habitats (Zubia and Peyrot-Clausade, 2001; McCarthy et al., 1998; Bailey-Brock et al., 1980; White, 1980). In the present study, however, volume displacement is used in conjunction with coral dissolution, not to assess the biomass or types of cryptofauna living within the corals, but to approximate the volume of the coral matrix that has been lost to internal bioerosion.

Bioerosion, in the absence of equal or higher rates of calcium carbonate accretion, will eventually diminish the three-dimensional complexity of reefs by compromising the structural integrity of the coral. This could have negative repercussions on local fish and invertebrate populations by decreasing the abundance and diversity of available habitats, and may lead to an increase in shoreline erosion. Monitoring changes in rates of bioerosion can facilitate proper management of coastal areas and reef resources. By comparing the cost, ease of use, and resolution of results obtained from three different methods of estimating bioerosion, this paper may help managers identify the most efficient and effective technique for measuring bioerosion in the field.

METHODS

STUDY SITES

Five study sites were selected around the islands of Tutuila, Ofu, and Olosega, American Samoa on the basis of accessibility, water depth, exposure to prevailing trade winds and ocean swell, and presence of damselfish algal gardens (Figure 2-1). Reefs at these five sites are exposed to variety of natural and anthropogenic stressors. Utulei has the highest human population density of all the sites, has coastal industrial facilities, as well as a number of streams in the adjacent watershed. Airport Lagoon is directly adjacent to the international airport and one of the largest watersheds in American Samoa. Because the reef flat is in close proximity to a large channel and is subject to substantial wave action across the reef crest, this site is not expected to be substantially affected by terrigenous-based fresh water inputs. The reef at Alofau is adjacent to a village of moderate size and has a number of tributaries in the watershed that enter the ocean via a single stream at the center of this reef tract. Ofu reef is part of a national park and does not seem to experience frequent or intense anthropogenic stress of any kind. The fifth site, Olosega, is adjacent to a small village that lacks any major development. The influence of this village on the reef is expected to be minimal, but the localized prevalence of macroalgae in some areas suggests that effluent from septic systems may be leaching onto the reef.

Figure 2-1. (A) Map of the islands of Western and American Samoa, and distances to well known landmasses. (B) Map of the island of Tutuila with stars marking the three study sites- Airport Lagoon, Utulei, and Alofau. (C) The other two sites were on the south shores of the Manua Islands, Ofu and Olosega.

Blocks of *Porites spp.* corals are most often used as sampling units in studies of bioerosion and bioeroder recruitment (Hutchings and Peyrot-Clausade, 2002; Pari *et al.*, 2002; Hibino and van Woesik, 2000). The use of carbonate blocks, however, requires multi-year monitoring before a complete infaunal boring community develops. Unlike traditional bioerosion methods, rubble count requires the use of coral rubble, which can be collected from the reef flat and processed almost instantly. Because this study sought to use a single set of samples to compare rubble count and two other methods, coral rubble was selected as a sampling unit. Sampling techniques similar to those described by Perry (1998) were employed throughout the study. Twelve pieces of branching coral rubble (Figure 2-2) were collected from the back reef lagoons at each of the five study sites, for a total of 60 samples.

Figure 2-2. Photograph of a branch of coral rubble that was used to evaluate three methods for quantifying internal bioerosion. Coral rubble samples were on average 10.5 cm long.

Collection, preservation, processing and storage of samples were greatly facilitated by the use of ~0.05 mm mesh bags. Rolled upon themselves and secured with rubber bands, these bags were easily transported and their contents preserved, as they could be placed directly in a bath of formalin or alcohol while retaining the invertebrates associated with the sample. Prior to analyzing percent bioerosion, all samples were

photographed, weighed, measured, and their volume determined by water displacement with a 100 ml graduated cylinder. The density of each piece of coral rubble was calculated by dividing the weight of the rubble by its solid volume. The rubble pieces were then sectioned into 1 cm thick "disks" using a rock saw to cut across the longitudinal axis of the samples. The cross-section of each disk was digitally photographed with an Olympus C50-50 digital camera set to macro mode. Each sample was then analyzed using the three techniques described below: rubble count, volume displacement, and digital cross-sectional area.

MEASURING BIOEROSION

Rubble Count

To determine the relative amount that each sample had been bioeroded, five disks were randomly selected from the collection of disks cut from each sample (piece of coral rubble). Cross-sections of the five disks were examined and ranked as either a one or zero, for presence or absence of boreholes. These ranks were then summed for each piece of coral rubble, yielding a relative "score" of bioerosion (Equation 2-1). The score represents a count of the number of disks (zero to five) showing evidence of internal bioerosion, and is a relative measure of bioerosion intensity that can be used to compare bioerosion intensity among various samples and/or sites.

(Eqn. 2-1)

Bioerosion score $_{sample}$ = rank $_{disk\ 1}$ + rank $_{disk\ 2}$ + ...rank $_{disk\ 5}$

(rank = 1 or 0 for presence/absence of bore holes)

Displacement

The volume displacement technique yields a percent of volume eroded for each sample, which is obtained by dividing the volume of calcium carbonate ($CaCO_3$) eroded in each sample by the potential/hypothetical solid volume of that sample (Equation 2-2). The total volume of each sample was determined by water displacement prior to sectioning. Because samples typically contain a variety of boring invertebrates within the coral matrix, the volume of infauna, algae, and sediment associated with each sample had to be estimated to obtain an accurate determination of the volume of $CaCO_3$ actually eroded. This was accomplished by placing the coral disks in a bath of formalin and dilute nitric acid, which dissolved the coral matrix, leaving non-calcified materials behind (Brock and Brock, 1977). Throughout the dissolution process, the nitric acid solution was changed every other day, and infauna that had become liberated was separated and removed from the remaining coral skeleton. Once the coral was completely dissolved, the volume of invertebrates and other miscellaneous material was determined by water displacement using a 10 ml graduated cylinder. The volume of infauna and miscellaneous material recovered during the dissolution process was then subtracted from the initial volume of the intact branch, yielding the actual intact volume of $CaCO_3$ in each sample (Equation 2-3). The hypothetical "solid" volume of each sample is equal to the sum of the sample's disk volumes. Disk volume was obtained by multiplying the height of the disk by its total cross-sectional area. This method of determining "solid" volume allows for irregularities in dimensions, such as narrowing of branches at one end, or bends in the branch that could not easily be accounted for with standard cylinder-volume equations. Subtracting the volume of intact $CaCO_3$ from the sample's "solid" volume

yields the volume of $CaCO_3$ eroded (Equation 2-4), which is then divided by the hypothetical solid volume to obtain the fraction of that sample's volume that had been eroded (Equation 2-2), shown as percent bioerosion. The volume of coral lost during the sectioning process was not accounted for.

$$\% \text{ Bioerosion }_{sample} = \left[\frac{\text{volume of } CaCO_3 \text{ eroded}}{\text{hypothetical solid volume}} \right] \times 100 \qquad \textit{(Eqn. 2-2)}$$

$$\textit{(Eqn. 2-3)}$$
$$\textbf{Volume of intact } CaCO_3 = \text{total volume displaced } - \text{volume of infauna/misc. material}$$

$$\textit{(Eqn. 2-4)}$$
$$\textbf{Volume of } CaCO_3 \textbf{ eroded} = \text{hypothetical solid volume} - \text{volume of intact } CaCO_3$$

Digital

Unlike rubble count, which allows for random sectioning of coral rubble with a hand saw or hammer and chisel (see Holmes *et al.*, 2000), digital methods require cutting a series of very thin cross-sections across the longitudinal axis of the branch using a rock or tile saw. Digital photographs of the disk cross-sections (Figure 2-3) were examined and the percent of surface area eroded was determined using the image analysis software Coral Point Count with Excel extensions (CPCe). CPCe allows the user to import photos, properly scale images, and measure specified areas within images. Areas to be measured - either the entire cross-section or just the areas of the boreholes - were specified to the program by outlining them with the computer's cursor. To estimate the percent bioerosion of a given sample, the percent bioerosion of each disk was first determined.

Percent bioerosion for a disk was calculated by dividing the area eroded by the hypothetical "solid" area. Total area of disk eroded was determined by outlining each of the boreholes in a disk, then summing their areas. Hypothetical "solid" area of a disk is equivalent to the cross-sectional area that would exist in the absence of bioerosion. Once the percent bioerosion of every disk in a sample was known (Equation 2-5), these percentages were averaged to yield the percent bioerosion of the sample (Equation 2-6).

Figure 2-3. Digital photograph of a coral rubble disk. The total cross-sectional area and area of boreholes were measured using Coral Point Count with Excel extensions (CPCe). Each disk was approximately 1 cm thick.

(Eqn. 2-5)

$$\% \text{ Bioerosion }_{disk} = \left(\frac{\text{Area }_{borehole\ 1} + \text{Area }_{borehole\ 2} + \dots \text{Area }_{borehole\ n}}{\text{Potential Solid Area of Cross-section}} \right) \times 100$$

(Eqn. 2-6)

$$\% \text{ Bioerosion }_{sample} = \frac{\% \text{ Bioerosion }_{disk\ 1} + \% \text{ Bioerosion }_{disk\ 2} + \dots \% \text{ Bioerosion }_{disk\ n}}{n}$$

COMPARISON OF METHODS

In attempts to recommend the most efficient technique for measuring bioerosion, each method was ranked on a generic scale of one to three for time investment and on a similar scale of one to three for resource investment. For both scales, a rank of one was considered a minimal investment, two was moderate, and three was a substantial investment. Displacement and rubble count measurements of bioerosion were compared to digital results and evaluated for consistency and resolution. Questions posed to determine consistency and resolution of results included:

1. Are the digital and displacement results significantly different from each other?

2. Is the relative intensity of bioerosion at each site consistent across the three methods employed?

3. Are the bioerosion measurements attained using these methods positively correlated with each other?

4. When compared to digital area analyses, are rubble count and volume displacement measures of bioerosion precise enough to be considered useful techniques?

Rubble count yields a relative score, instead of a measure of the percent area or volume eroded, which prevented testing for significant differences between the rubble count results and results of digital or volume displacement methods. To determine whether rubble count, displacement, and digital results were comparable, either a Spearman rank correlation, or a Pearson's correlation was calculated for the following method combinations: digital and displacement, digital and rubble, and displacement and rubble. Consistency between methods was evaluated by comparing site-specific results (e.g., Did

each method indicate that site "x" was the most bioeroded?). A one-way Analysis of Variance (ANOVA) was used to test whether digital measurements of bioerosion were significantly different among sites. Outliers in displacement results and uneven spread in the rubble count scores required the use of non-parametric tests. Mood's Median was therefore used to test for significant differences in bioerosion between sites for these methods, and to test whether the results of digital and displacement techniques were significantly different from each other. To better describe the behavior of the variables measured and to satisfy assumptions regarding the normality of the data, digital and displacement measurement of bioerosion were natural log transformed.

RESULTS

TIME AND RESOURCE INVESTMENT

Differences in the amount of time and resources required to measure bioerosion using rubble count, displacement, and digital techniques are illustrated in (Figure 2-4). Rubble count, as expected, proved to be the quickest and easiest method to obtain relative measurements of bioerosion. Needing only a device to section coral rubble, 60 samples were easily scored in a few hours. The displacement technique required a significant time investment (each sample took an average of eight days to dissolve), while the chemicals and equipment needed to properly dissolve corals were considered a moderate resource investment. The digital method, the most prevalent method described in the literature and the standard for this study, required the greatest overall investment of both time and resources, requiring a rock-saw, digital camera, computer, image analysis software, and numerous hours to outline and measure the area of every borehole in each of the rubble cross-sections.

Figure 2-4. Relative ranks of investment required by three different methods of measuring internal bioerosion: rubble count, volume displacement, and digital area analysis. Each method was given a score of one (minimal), two (moderate), or three (substantial) for the time and resources required.

COMPARISON OF RESULTS

Digital vs. Rubble Count

Digital and rubble count results were significantly positively correlated (Spearman rank correlation: $r_s = 0.673$, p = 0.001) (Figure 2-5). Holmes *et al.* (2000) reported a similar positive correlation (r = 0.66) between rubble count (using coral rubble) and digital measurements of bioerosion from longitudinal slabs of massive *Porites* coral heads collected from the same area. In the present study, both digital and rubble count results found significant differences in bioerosion based on sampling location (**digital:** One-way ANOVA: F = 3.33, p = 0.011) (Table 2-1) (**rubble:** Mood's Median: $\chi^2 = 10.29$, p = 0.036). Site-based results, however, were not consistent between these methods, i.e., digital results indicated that samples from Utulei were the most eroded, while rubble count methods indicated that bioerosion was greatest at Olosega (Figure 2-6). Although the rubble count technique found a significant difference in

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bioerosion among the sampling areas, the resolution of these results was limited. Almost half the samples had a bioerosion score of five, which corresponded to samples that, when measured digitally, were between 5% and 30% bioeroded (Figure 2-5).

Figure 2-5. A comparison of measurements of internal bioerosion of coral rubble obtained via digital cross-sectional area analysis and by rubble count methods for 60 pieces of coral rubble. There is a significant positive relationship between percent bioerosion (digital results) and rubble count bioerosion score (Spearman rank: $r_s = 0.673$, $p = 0.001$).

Table 2-1. Results of a one-way Analysis of Variance, which found the average percent of bioerosion, measured digitally, was significantly different among five sites in American Samoa.

One-way ANOVA				
	Df	**MS**	**F**	**p-level**
Bioerosion (digital)	Natural log transformation			
Site	5	1.462	3.33	0.011
Error	54	0.44		

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Figure 2-6. Measurements of internal bioerosion of coral rubble determined using three methods: rubble count (purple), displacement (blue), and digital cross-sectional area (yellow). Rubble count results are presented as a score indicating the total number of cross-sections, out of five, showing evidence of bioerosion. Displacement and digital results are presented as a mean percent of bioerosion at each site. Site-specific results were not consistent across methods employed. Displacement and digital results indicated that samples from Utulei were the most bioeroded, while rubble count techniques found Olosega to have the highest percent bioerosion. Furthermore, only results from rubble count and digital measurements found significant differences in bioerosion between sites (**rubble**: Mood's Median: $\chi^2 =$ 10.29, p = 0.036; **digital**: one-way ANOVA: F = 3.32, p = 0.016). Data are mean ± standard error.

Digital vs. Displacement

Displacement measurements of bioerosion were significantly greater than digital results (Mood's median: $\chi^2 = 4.55$, p = 0.033). This is to be expected because the calcified parts of eroding organisms would be lost during the dissolution process and not accounted for in the infauna/miscellaneous volume measurement or in the final calculations of the volume of $CaCO_3$ eroded (Equations 2-2 and 2-3). Further analysis of displacement data, however, indicated that this overestimation was inconsistent, and that displacement results were not significantly correlated with digital results (Spearman rank correlation: $r_s = 0.130$) or with rubble count scores (Spearman rank correlation: $r_s =$

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0.058). Displacement measurements were highly variable and did not detect significant differences in bioerosion among sites (Mood's Median: χ^2 = 3.24, p = 0.518). Displacement and digital results were in agreement that bioerosion was greatest in samples from Utulei, but relative estimates of percent bioerosion were not consistent across the remaining sites (Figure 2-5).

DISCUSSION

Based on the low variability of results within and among sites and the overall ability of digital area analysis to detect significant differences in bioerosion, digital techniques appear to produce more reliable results than rubble count or displacement methods. Rubble count results did not provide adequate resolution to detect moderate differences in bioerosion, which limited the inferences that could be obtained from these results. In attempts to increase the resolution of rubble count results, two additional disks were examined from each sample, increasing the maximum potential bioerosion score from five to seven. The analysis of 120 additional disks did not further normalize the distribution of data, nor did it increase the statistical power or correlation with digital results. Results of this study, however, support findings of Holmes *et al.* (2000) that rubble count bioerosion estimates are significantly positively correlated with digital cross-sectional area analyses. In contrast to the methodology of Holmes *et al.* (2000), where the technique was compared to digital analyses of samples from a different coral species and growth form, methods and results presented here may provide a more reliable comparison of these methods because both digital and rubble count measurements were performed on the same set of samples.

Displacement results were highly variable and included a number of outliers that could not be accounted for. Such variability may be resolved in the future by using a greater sample size, and/or making initial volume measurements after the corals have been sectioned into disks. Each time a cut was made with the rock saw, the sample lost a portion of its length approximately equal to the width of the blade (*ca.*, 0.08 cm). Infauna, sediments, and other miscellaneous material would have been lost with these cuts as well, meaning that some of the materials that had occupied the boreholes during the initial volume displacement measurements were not recovered or accounted for. The volume displacement technique could also be improved upon by altering the manner in which the solid volume was determined. For example, foil can be wrapped around the sample to estimate surface area (Marsh, 1970). The potential/hypothetical solid volume of the sample can also be estimated using volume displacement and a wax coating. By dipping the sample in wax prior to immersion, water will be unable to enter boreholes in the coral, and the volume displaced should more nearly represent the solid volume of the coral sample.

Various scientists have reported correlations between rates of bioerosion and density of coral skeleton (e.g., Sammarco and Risk, 1990; Highsmith *et al.*, 1983). As with other abiotic and biotic factors influencing rates of bioerosion, the role of skeletal density varies with study site and coral species. Results from this study indicate that the relationship between coral density and rates of bioerosion can be significantly affected by the method used to measure bioerosion. Density of the coral skeleton was weakly negatively correlated with bioerosion for each method employed, with digital measurements showing the strongest negative correlation of bioerosion with coral density

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(Pearson's: r = -0.351, p < 0.001). This result may be influenced by the precision of each method as implemented with the current sample size, rather than reflecting inherent differences in the methods themselves.

As natural and anthropogenic stresses to reefs increase in both frequency and severity, the portion of degraded coral substrate available for colonization by macroborers will also increase. Bioerosion, which has previously been linked to increased eutrophication, decreased herbivore grazing, and decreased carbonate accretion, has the potential to provide a valuable tool for assessing the condition of reefs within and among sites. The development of accurate and efficient means for measuring bioerosion may contribute to rapid ecological assessments and aid in establishing baseline data regarding reef condition or local levels of nutrient enrichment. Although the rapid field technique, coral rubble count, produced bioerosion measurements that were significantly positively correlated with results of digital area analysis, the inability of rubble count to consistently detect a 10% difference in bioerosion in the present study suggests caution when using the rubble count technique to compare bioerosion between sites. Results of this study imply that rubble count and displacement techniques require a significantly larger sample size than digital methods to accurately detect differences in bioerosion among samples and sites. However, an increase in sample size does not greatly increase the processing time with rubble count techniques; therefore, future studies employing this method may find the rubble count technique to be more efficient and effective than this study presently demonstrates. Currently, digital area analysis appears to be the most accurate and reliable method for quantifying internal bioerosion of corals.

Chapter 3. ANTHROPOGENIC STRESS, DAMSELFISH TERRITORIES, AND BIOEROSION

ABSTRACT

Bioerosion, i.e., the biological degradation of carbonate materials, has the potential under eutrophic or other "disturbed" conditions, to substantially reduce the extent and three dimensional complexity of coral reefs. In addition to anthropogenic stress in the form of eutrophication, the presence of damselfish algal gardens has also been linked to local increases in rates of bioerosion. This study explored possible synergistic effects between anthropogenic stress, prevalence of damselfish algal gardens, and bioerosion. I also tested whether anthropogenic stress is significantly positively correlated with an increase in available habitat for damselfish, ultimately increasing the density of farming damselfish and overall rates of bioerosion. Using ratings of human influence assigned to watersheds by the America Samoa Environmental Protection Agency, sites with varying levels of anthropogenic stress were examined for differences in the density of farming damselfish (*Stegastes* spp.), the percent of reef occupied by damselfish algal gardens, and rates of bioerosion inside and outside gardens. *Stegastes* spp. density slightly increased as the level of anthropogenic stress increased; however, benthic habitat surveys did not demonstrate that increases in substrate available for algal recruitment (dead coral cover) were correlated with the density of farming damselfish or percent cover of damselfish algal gardens. Competitive interactions between the three species of *Stegastes* in American Samoa appear to influence the type of coral habitat in which each species is found, with territories of *S. lividus*, the largest and most dominant of the species, found mainly in the primary or preferred habitat of farming damselfish –

branching *Acropora* corals. Intensity of coral bioerosion was not positively correlated with levels of anthropogenic stress; however anthropogenic stress appears to influence the overall effects damselfish have on bioerosion of coral substrates within their territories. Bioerosion was significantly greater inside damselfish algal gardens at minimally stressed sites, yet greater outside algal gardens at intermediate and extensively stressed sites.

INTRODUCTION

Elements that influence the distribution and abundance of benthic marine species include resource availability, supply-side factors that affect recruitment, disturbance and physical/chemical stress, species interactions, and the current and historical interaction between these elements (McCook, 1999). Disturbances that limit coral abundance, or its three dimensional complexity, can result in a decline in reef species because populations of reef fish, algae, and invertebrates rely on these structures for habitat (Diaz-Pulido and McCook, 2002). Anthropogenic stressors are often thought to be more detrimental to benthic habitats than natural stressors, as they are often chronic, can occur in unnatural combinations with other stressors, and are usually of a greater intensity or magnitude (Sanders and Baron-Szabo, 2005). Eutrophication and overfishing are likely to occur simultaneously on many reefs (Hughes and Connell, 1999), which may produce a compounding effect with more serious detrimental effects on the overall abundance of coral and/or reef dwelling fishes.

Anthropogenic stress that results in decreased herbivore abundance and grazing and/or increased eutrophication promotes coral-to-algal phase shifts by enhancing the competitive ability of algae and inhibiting the recovery of coral following natural or

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anthropogenic disturbances (Diaz-Pulido and McCook, 2002). Eutrophication has been closely linked to rates of bioerosion (Carriero-Silva *et al.*, 2005; Zubia and Peyrot-Clausade, 2001; Rose and Risk, 1985; Smith *et al.*, 1981). Bioerosion, i.e., the biological degradation of coral and carbonate structures, significantly alters the three-dimensional complexity and longevity of coral reefs by decreasing topographic relief and increasing the susceptibility of reefs to physical damage through mechanical erosion or breakage (MacDonald and Perry, 2003). Bioerosion is a natural process that is evident throughout the geologic record. Bioeroding invertebrates, however, such as sponges, filamentous algae, bivalves and barnacles can effectively utilize nutrient pulses associated with eutrophication, leading to a proliferation of these species and a subsequent unnatural increase in bioeroding activities (Hallock, 1988; Scoffin, 1972). The study of factors that increase bioerosion is currently of particular interest because there is growing concern that climate change will substantially alter sea surface temperatures and the ocean's carbonate balance, which will slow coral accretion rates and lead to the global degradation of coral reefs (Craig, 2002).

In addition to eutrophication and other abiotic factors discussed above, the balance between accretion and bioerosion of coral substrates may be shifted by the activities of farming damselfish (*Stegastes* spp.), which establish and maintain territories with "gardens" of filamentous algae. In addition to physically removing coral recruits and clearing areas of coral to create open substrate for these gardens, damselfish can also move into and utilize coral colonies that have been bleached or recently killed. The proliferation of filamentous algae, which follows the establishment of an algal garden, is thought to restrict the recruitment of corals and crustose coralline algae and inhibit the

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growth and consolidation of reef material (Ceccarelli *et al.*, 2002). Damselfish territories can also increase bioerosion indirectly because the macroboring invertebrates responsible for internal bioerosion of coral can more easily penetrate the carbonate substrate of reefs once the live coral tissue has been replaced by filamentous algae (Glynn 1997). According to Hutchings *et al.* (2005), eutrophication and decreased grazing by herbivorous fish are major determinants of local rates of bioerosion. Damselfish aggressively defend their algal territories against other herbivorous fish, leading to a reduction in grazing activity within the territories (Potts, 1977). Consequently, Risk and Sammarco (1982) and Sammarco and Carleton (1986) have attributed increased rates of bioerosion inside damselfish territories to decreased grazing rates in territories as well, suggesting that decreased grazing activity reduces predation on coral-dwelling invertebrates, leading to a proliferation of macroborers and enhanced levels of bioeroding activities.

Under conditions that decrease coral calcification rates, bioerosion will eventually compromise the three dimensional structure and habitat complexity of reefs. Loss of physical complexity can have effects across various trophic levels and ultimately affect the biological complexity on reefs by: limiting the amount of habitat available for reef dwelling organisms, removing refuges from predation, and eventually reducing the abundance of prey species. Damselfish algal gardens are a prominent component of coral reefs around the world (Klumpp and Polunin, 1989; Sammarco *et al.*, 1986; Sammarco and Williams, 1982), and have been found to be positively associated with local increases in bioerosion (Hixon, 1983; Lobel, 1980). The abundance and distribution of damselfish algal gardens, however, has not been correlated with eutrophic conditions or with local

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anthropogenic activities.   The present study, therefore, sought to explore how disturbance, or localized levels of anthropogenic stress, affects damselfish habitat availability, and in turn, the distribution and abundance of farming damselfish (*Stegastes* spp.) in American Samoa. I hypothesized that increased anthropogenic stress would lead to an increase in the amount of habitat suitable for the recruitment of damselfish and the establishment of their algal gardens, and that the presence of these gardens, when coupled with anthropogenic stressors, would work synergistically to increase local rates of bioerosion.

METHODS

SITE DESCRIPTION

In attempts to sample reefs under varying degrees of anthropogenic influence, study sites were selected from two island groups in American Samoa - the Manua Islands and the main island of Tutuila. Two of the five study sites were located on reef flat or back reef lagoons on the south facing shores of the Manua Islands, Ofu and Olosega (Figure 2-1). The Manua Islands are a three-island chain, located approximately 100 km east of Tutuila.   There is no industrial development on any of these islands, and they contain only a few modest facilities that support a limited number of tourists annually.

The remaining three sites, Utulei, Airport Lagoon, and Alofau, are located on Tutuila, American Samoa's largest island. Tutuila serves as both the commercial and residential hub of the region and supports approximately 97% of American Samoa's total population (Buchan and DiDonato, 2004). Major industry on Tutuila includes two fish canneries, Chicken of the Sea and StarKist, which are located in Pago Pago harbor and process a combined total of approximately 1,000 tons of fish daily. Tutuila is a high

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island of moderate size (137 km^2), and reefs around it are subjected to significantly more freshwater and terrigenous input than the reefs of the Manua Islands. In addition to selecting sites based on different relative levels of anthropogenic stress, ease of access to the site, average water depth, exposure to prevailing trade winds and ocean swell, and presence of damselfish algal gardens were also considered.

MEASURING ANTHROPOGENIC STRESS

Two reports from the American Samoa Environmental Protection Agency (ASEPA) (Buchan and DiDonato, 2004; DiDonato 2004) were used to derive relative rankings of human influence for the study sites. These rankings are based on commercial and agricultural development or human population density in each watershed, as well as water quality in coastal areas supporting three designated uses: human consumption of seafood, healthy swimming conditions, and abundance and diversity of marine wildlife. As expected, the most densely populated and developed island of Tutuila contained two extensively influenced sites, Utulei and Airport Lagoon, and one intermediately influenced site - Alofau. Both sites on the Manua Islands, Ofu and Olosega, were considered minimally stressed. However, not all the designated uses have been analyzed for Olosega and Airport Lagoon, therefore, the ratings of human influence for these sites are based mainly on the extent of adjacent development and human population density (Table 3-1).

Table 3-1. Three relative measures of anthropogenic stress for five reef flats in American Samoa. The extent of development and human population density refer to lands in the watershed adjacent to the reef. The ratings for designated uses are specific to the coastal waters at each site. (-) indicates designated uses that have not yet been analyzed. Sources: DiDonato, 2004 and Buchan and DiDonato, 2004.

Various Measures of Anthropogenic Stress		SITES				
		TUTUILA			MANUA	
		Utulei	Airport	Alofau	Ofu	Olosega
Development Category		Extensive	Extensive	Intermediate	Minimal	Minimal
Human Population Density		2,647/mi^2	1164/mi^2	777/mi^2	162/mi^2	270/mi^2
Designated Uses	aquatic life	good	(-)	good	good	(-)
	Swimming	poor	poor	poor	fair	good
	Seafood consumption	poor	(-)	good	good	(-)

The densities of herbivorous damselfish, specifically *Stegastes nigricans*, *Stegastes albifasciatus*, and *Stegastes lividus*, were determined via visual surveys along 25 m x 2 m belt transects. To standardize survey effort, the total reef flat area was used to determine the number of transects to be conducted at a site, with a maximum of seven transects conducted at any given site. Transects were laid parallel to shore and were distributed randomly throughout each site. A one-way Analysis of Variance (ANOVA) was used to determine whether the density of *Stegastes* spp. was significantly greater in sites with an extensive rating. A two-sample t-test was used to determine whether the density of farming damselfish was significantly different between island groups.

Photoquadrats of the benthic substrate were taken at every meter along the length of the 25 m transects using an Olympus C50-50 digital camera. Pictures were taken approximately 1 m off the substrate and covered an area of 37 cm x 57 cm. Percent cover and composition of the benthos were determined using the image analysis software Coral Point Count with Excel extensions (CPCe). Thirty points were randomly distributed throughout the frame of each picture, and the substrate type under each point was

classified into general categories such as sand, sponge, rubble, pavement, and dead coral with algae. When possible, corals were identified to species and macroalgae was recorded to genus or division. The percent cover of each substrate type was averaged for each site. To determine whether anthropogenic stress or damselfish abundance was correlated with specific components of the benthos, substrate types were compared to the ASEPA ratings and damselfish density using a Spearman Rank and a Pearson's correlation, respectively.

Damselfish algal gardens encountered during or between belt transects were examined, and the species of coral and damselfish occupying the gardens were recorded. The size of each damselfish algal garden was determined by recording coordinates around the perimeter of each garden with a hand-held GPS unit. The coordinates were later downloaded into ArcView 3.0 and overlaid on geo-referenced maps. Points representing the perimeter of each algal garden were linked creating a number of polygons. The area of each polygon was calculated using the ArcView spatial analyst Animal Movement extension. The percent cover of damselfish algal gardens at a site was approximated by summing the areas of all algal gardens observed and dividing that sum by the total area of the reef flat surveyed. On average 27 km^2 of reef flat were surveyed at each site, covering an average of 15% of the total reef flat at each location. The size of each damselfish algal garden was natural log transformed and a one-way ANOVA was used to evaluate whether the intensity of anthropogenic stress significantly affected the size and percent cover of damselfish algal gardens in American Samoa.

BIOEROSION

Based on work by Sammarco and Risk (1990), Edinger and Risk (1996) concluded that reasonably accurate estimates of bioerosion intensity can be attained by measuring the percent of coral area eroded from cross-sections of massive coral heads or coral branches. Building from these methods, and based on the results of a concurrent study that compared techniques for measuring bioerosion (Chapter 2), digital measurements of area eroded from coral rubble cross-sections were used to assess intensity of bioerosion among sites and among the ASEPA rating categories. Of the 60 samples collected, half were from inside damselfish territories. The other half of the samples were from outside territories, yet within 3 meters of the boundary of an algal garden/territory. Prior to chemically fixing the coral rubble samples and the associated infauna, each piece of coral rubble was scrubbed with steel wool to remove filamentous algae and epifauna. Samples were later photographed, weighed, measured, and their volume determined by water displacement. The density of each sample was calculated by dividing the weight of the sample by its solid volume. Each piece of coral rubble was sectioned into 1 cm thick "disks" using a rock saw to cut across the longitudinal axis of the sample. The cross-section of each disk was then photographed with an Olympus C50-50 digital camera set to macro mode. Bioeroded areas within each cross-section were measured digitally using the "area" tools in the CPCe program, which allows the user to import photos, properly scale images, and measure specified areas within images. To estimate the extent of bioerosion for a given sample, the percent of each disk's cross-section that was bioeroded was first determined. Percent bioerosion was calculated by dividing the total area eroded by the total cross-sectional area of a disk that would exist in

the absence of bioerosion. Once the percent of bioerosion was known for each disk in a sample, the percentages were averaged to yield an overall percent bioerosion for the sample. A more detailed description of digital area analysis of internal bioerosion is presented in Chapter 2.

Values of percent bioerosion were natural log transformed to improve the normality of the data and better describe trends among sampling locations. A 2-sample t-test was used to examine the difference in bioerosion between the island groups, Tutuila and the Manua Islands. A General Linear Model (GLM) ANOVA was used to evaluate the influence of anthropogenic stress and damselfish algal gardens on bioerosion, and also to test the significance of an interaction between sampling location (inside versus outside algal gardens) and ASEPA ratings. A Spearman rank correlation was used to determine whether values of bioerosion were significantly positively correlated with intensity of anthropogenic stress.

RESULTS

DAMSELFISH TERRITORIES

The majority of damselfish territories encountered in American Samoa were colonies consisting of numerous adjacent damselfish algal gardens. The prevalence and expanse of these colonies led to substantial portions of the reef flat (up to 10% of the area surveyed) being occupied by damselfish territories. The percent of reef covered by damselfish algal gardens was widely different among sites (Figure 3-1); Utulei and Olosega had the smallest percentages of their total back reef area covered by algal gardens, 1.0% and 1.6% respectively. Percent cover of damselfish algal gardens did not appear to be influenced by levels of anthropogenic stress; ASEPA ratings of human

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influence were not significantly correlated with percent cover of algal gardens (Spearman rank correlation: $r_s < 0.01$).

Figure 3-1. Percent cover of damselfish (*Stegastes* spp.) algal gardens around Tutuila and the Manua Islands, American Samoa. Sites are listed in order, left to right, of decreasing intensity of anthropogenic stress. Red bars represent extensively stressed sites, the yellow bar is the intermediately stressed site, and the green bars are minimally stressed. Level of anthropogenic stress was not significantly correlated with the area of reef that had been converted to damselfish algal gardens (Spearman rank correlation: $r_s < 0.01$).

The median size of all damselfish algal gardens observed was 23.3 m^2, with the smallest and largest covering 0.5 m^2 and 872 m^2 of reef, respectively. The large size of many of the colonies did not allow for a census of the number of damselfish occupying each colony or a determination of the number of individual gardens within a colony. Colonies were therefore treated as a single large territory or garden, with the term "garden" being used throughout this document to include what may be a collection of numerous adjacent algal gardens. The average size of damselfish algal gardens was similar between the two island groups (2-sample t-test: $T = 1.00$, $p = 0.34$), and did not appear to be affected by anthropogenic stress. ASEPA ratings were not significantly

positively correlated with average garden size (Spearman rank correlation: $r_s = 0.109$), and garden size was not significantly different among the extensively, intermediately, and minimally rated sites (ANOVA: F = 0.78, p = 0.461) (Figure 3-2).

Figure 3-2. Size of damselfish algal gardens around Tutuila and the Manua Islands, American Samoa. Sites were categorized as either minimally, intermediately, or extensively influenced by humans based on water quality reports produced by the American Samoa Environmental Protection Agency (ASEPA). Average size of damselfish algal gardens was not significantly different among the different ratings of human influence (ANOVA: F = 0.78, p = 0.461). Size of damselfish algal gardens were natural log transformed; the boxplots represent maximum and minimum observations as well as the median of each sample.

Most of the algal gardens observed were occupied by either a mix of *Stegastes lividus* and *Stegastes nigricans*, or *S. nigricans* only. In mixed species colonies, a dominance hierarchy, similar to that described by Sammarco and Carleton (1986) and Itzkowitz (1977), was observed, with larger species occupying the center of the garden, while the smaller, less dominant species established themselves around the perimeter.

Effort was made to determine whether the species of damselfish inhabiting each garden influenced the size of the algal garden. Unfortunately, for some of the species and species combinations, the number of gardens observed was not sufficient for such an analysis with an appropriate level of power. The species inhabiting the algal gardens were noticeably different among sites. A mix of *S. lividus* and *S. nigricans* occupied the majority of algal gardens on Tutuila, while *S. lividus* was conspicuously rare on the Manua Island transects. *S. lividus* algal gardens were not observed on Ofu, and were only occasionally encountered on Olosega. According to Ceccarelli *et al.* (2006), removal of large herbivorous fishes of other species (e.g., by fishing) may lead to an increase in large territorial damselfish. Because *S. lividus* is the largest of the territorial damselfish species in American Samoa, the dominance by this species at the three sites on Tutuila may indicate that the abundance of herbivorous fish has been depressed on this island.

DAMSELFISH DENSITY

The density of *Stegastes* spp. varied among sites and between islands, with reef flats on Tutuila having a slightly higher average density of *Stegastes* spp. than that observed on the Manua Islands: 44.1 versus 30.2 fish/50 m^2 (2 sample t-test: t = 1.77, p = 0.088). Intensity of anthropogenic stress in adjacent watersheds did not appear to affect *Stegastes* spp. density. Although the extensively stressed sites had a greater density of damselfish than both the intermediate and minimally stressed sites (Figure 3-3), *Stegastes* spp. density was not positively correlated with ASEPA ratings of human influence (Spearman rank correlation: r$_s$ = 0.328), and did not differ significantly among the rating categories (ANOVA: F = 2.26, p = 0.124) (Figure 3-3).

Figure 3-3. Average number of *Stegastes* spp. per $50m^2$ of reef at five back reef/lagoons in American Samoa. Sites have been grouped according to ratings of human influence assigned by the American Samoa Environmental Protection Agency (ASEPA). The density of *Stegastes* spp. observed at extensively stressed sites is not significantly greater than the density of *Stegastes* spp. at the minimal and intermediate sites (ANOVA: $F = 2.26$, $p = 0.124$). Boxplots depicting the minimum, maximum, and median observations are shown.

The density of *Stegastes* spp. as a group tended to decrease as the percent cover of dead coral and coral covered with filamentous algae decreased, however, this relationship was not statistically significant (Pearson's correlation: $r = 0.243$, $p = 0.203$). When examined individually, however, each species of *Stegastes* was found to be positively associated with a different and specific benthic habitat type. *S. lividus* density was positively correlated with percent cover of live *Acropora* corals (Pearson's correlation: $r = 0.613$, $p < 0.001$), while density of *S. nigricans* and *S. albifasciatus* were positively correlated with percent cover of live *Porites* corals and coral pavement, respectively (Pearson's correlation: *S. nigricans*: $r = 0.552$, $p = 0.002$; *S. albifasciatus*: $r = 0.406$, $p = 0.029$) (Figure 3-4).

Figure 3-4. Characteristics of the benthic substrate and their relationship with the density of three species of *Stegastes* (fish/50m^2) at five back reef lagoons in American Samoa. Graph A depicts the percent cover of live *Acropora* corals, which was significantly positively correlated with the density of *S. lividus* (pink squares) (Pearson's correlation: r = 0.613, p < 0.001). Graph B depicts percent cover of live *Porites* corals, which was positively correlated with density of *S. nigricans* (green triangles) (Pearson's correlation: r = 0.552, p = 0.002). Graph C depicts the percent cover of coral pavement, which was weakly positively correlated with density of *S. albifasciatus* (blue diamonds) (Pearson's correlation: r = 0.406, p = 0.029). Trendlines have been drawn through each set of data points.

BIOEROSION

Based on the sites surveyed, coral substrates outside damselfish algal gardens in American Samoa are on average 11.2% bioeroded. This value is comparable to rates of bioerosion reported from other sites in the Pacific, and is substantially lower than rates reported from the Caribbean (Table 3-2). The relative effect of damselfish algal gardens on bioerosion in American Samoa appeared to be opposite for the two island groups, with more intense bioerosion occurring outside territories on Tutuila and inside territories on the Manua Islands (Figure 3-5). Intensity of human influence appeared to have some effect on overall rates of bioerosion. Bioerosion slightly increased as intensity of anthropogenic stress increased, but this trend was not statistically significant (Spearman rank correlation: r_s = 0.046) (Figure 3-6). The percent of coral bioeroded was not significantly different inside and outside damselfish territories, however; there appears to be a significant interaction between sampling location and intensity of anthropogenic stress. Bioerosion inside damselfish algal gardens tends to be less than outside algal gardens in extensively and intermediately stressed sites, while in minimally influenced sites, bioerosion is substantially greater inside the damselfish algal gardens (GLM-ANOVA: **ASEPA rating:** F = 2.99, p = 0.059; **location:** F = 0.29, p = 0.595; **ASEPA rating*location:** F = 4.16, p = 0.021) (Figure 3-7) (Table 3-3).

Table 3-2. Summary of various studies measuring bioerosion, including methods employed and location of study. Percent bioerosion was averaged for the Caribbean and for the Pacific to illustrate general trends in these areas. Bioerosion in the Atlantic Ocean is comparatively greater than that in the Pacific Ocean.

Author	Year	Study Site	Methods	% Area Bioeroded
Hein and Risk	1975	Florida		28%
Bak	1976	Curacao	coral block weight	25%
MacGeachy and Stern	1976	Barbados	*Montastrea* spp.	1.2 - 15%
Highsmith	1980	Florida and Barbados		15 - 28%
Highsmith *et al.*	1983	Belize	X-rays and planimeter on massive corals	4.8 - 7.9%
Sammarco *et al.*	1987	GBR	x-rays/photos	9 - 19%
Sammarco *et al.*	1987	GBR	dimension of blocks	3 - 5%
Moran and Reaka	1988	St. Croix, USVI	% of cross-section eroded (planimeter)	8.4 - 18.3%
Scott *et al.*	1988	Jamaica	coral block weight	65%
Sammarco and Risk	1990	GBR	live coral-slabbed / x-rays / digitizer	1.3 - 11%
Risk *et al.*	1995	GBR	cross-sections and digitizing board	0.33 - 23.6%
Risk *et al.*	1995	GBR	dead *Acropora* spp. bases x-section digitizing board	4 - 12%
Reaka-Kudla *et al.*	1996	Galapagos	limestone blocks; digitizing/photos	5% limestone; 61% Porites
Edinger and Risk	1996	GBR	Massive *Porites* spp.- x-rays; Branching *Acropora* spp.- photos- digitizing board	1.3 - 11%
Perry	1998	Jamaica	coral and coral rubble cross-sections	8.6% - 27.2%
Holmes	2000	Indonesia	x-rays/photos	0.8 - 9%
Londono-Cruz *et al.*	2003	Gorgona Is. South America	coral block weight	25.5% and 23.8%
MacDonald and Perry	2003	Jamaica	Digital analysis- slabbed recently dead corals	0.4 - 34.3%
Average Pacific Ocean				7.88%
Average Atlantic Ocean				24.49%

Figure 3-5. Average percent bioerosion outside (purple) and inside (blue) damselfish algal gardens at five study sites in American Samoa. Bioerosion differed among sites, with damselfish having an inconsistent effect on bioerosion. Bioerosion was greater inside damselfish algal gardens on the Manua Islands, while on Tutuila bioerosion was greater outside damselfish algal gardens. Sites are listed in order, from left to right, of decreasing intensity of anthropogenic stress. Bioerosion values have been natural log transformed; ± standard error bars are shown.

Figure 3-6. Percent bioerosion of branching coral rubble collected outside damselfish algal gardens around Tutuila and the Manua Islands, American Samoa. Sites were categorized as minimally, intermediately, and extensively stressed, based on water quality reports from the American Samoa Environmental Protection Agency (ASEPA). There was a trend for bioerosion to increase as intensity of anthropogenic stress increased (GLM-ANOVA: **ASEPA rating:** $F = 2.99$, $p = 0.059$). Values of percent bioerosion have been natural log transformed. Boxplots represent minimum, maximum, and median observations.

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Figure 3-7. Percent bioerosion inside and outside damselfish algal gardens at sites varying in intensity of human influence: extensive, intermediate, or minimal. Sampling location (in vs. out) did not significantly affect rates of bioerosion, while intensity of human influence appeared to have a minimal effect on local rates of bioerosion in American Samoa. There was good evidence for an interaction between sampling location and ASEPA rating, with bioerosion increasing inside damselfish algal gardens as the levels of anthropogenic stress decreased (GLM-ANOVA: **ASEPA rating:** F = 2.99, p = 0.059, **location:** F = 0.29, p = 0.595, **interaction (ASEPA rating*location):** F = 4.16, p = 0.021). Percent bioerosion values are natural log transformed. Box plots representing minimum and maximum observations and medians are shown above.
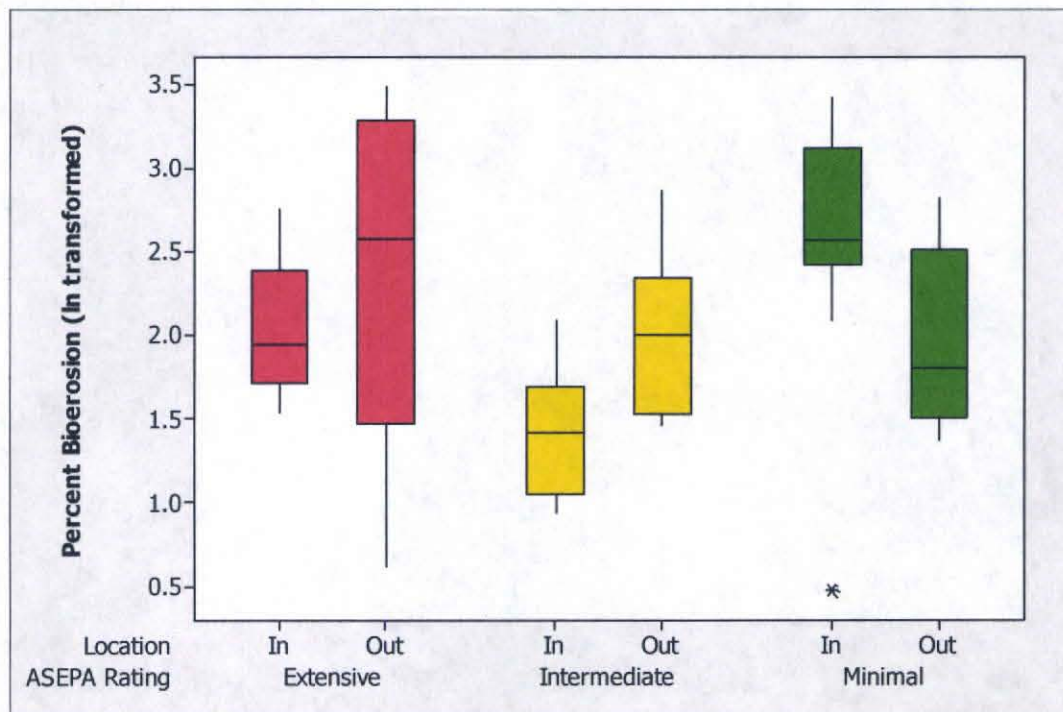
Table 3-3. Results of a General Linear Model Analysis of Variance, which found that coral bioerosion was slightly different among sites exposed to various intensities of anthropogenic stress. Relative levels of anthropogenic stress were determined by three water quality reports produced by the American Samoa Environmental Protection Agency (ASEPA). Bioerosion was not significantly different between sampling locations, inside versus outside damselfish algal gardens. There was an interaction between sampling location and anthropogenic stress, with minimally influenced sites exhibiting substantially more bioerosion inside damselfish algal gardens.

General Linear Model ANOVA				
	df	**MS**	**F**	**p-level**
Bioerosion Natural log transformation				
ASEPA Rating	2	1.357	2.99	0.059
Sampling Location	1	0.130	0.29	0.595
ASEPA Rating x Location	2	1.893	4.16	0.021
Error	54	0.455		

DISCUSSION

DAMSELFISH DENSITY AND TERRITORIES

According to Sammarco and Williams (1982) and Sale (1972), when habitat is in short supply, the size of damselfish algal gardens can be positively correlated with the number of fish occupying the territories. In the present study, the size of algal gardens did not increase as damselfish density increased, suggesting that these populations of *Stegastes* spp. may not currently be limited by habitat availability. However, it is also possible that the ratio between the size of damselfish algal gardens and damselfish density are affected by variation in the optimum density at which different damselfish species or species combinations thrive, and/or factors affecting the size of territories necessary to support the observed densities. Williams (1978) observed a scenario in which damselfish, when adjacent to or in close proximity of territories of conspecifics, increased the boundaries of their algal gardens, leading to an overall decrease in the number of damselfish per square meter. Jan *et al.* (2003) also illustrated how competitive interactions related to food abundance and frequency of intruder presence is related to territory size. According to Chabanet *et al.* (1995), eutrophication, which can cause a proliferation of algae, may alter the sizes of algal gardens by increasing the food resources of damselfish, which then changes the size of a garden a single fish will effectively defend and maintain. Additionally, structures (including some forms of macroalgae) that have increased three-dimensional complexity and surface area for growth of filamentous algae, can decrease the area of reef necessary to fulfill the dietary requirements of a damselfish (Ceccarelli *et al.*, 2005). Hence, the lack of a correlation between damselfish density and mean algal garden size does not necessarily indicate that

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damselfish in American Samoa are not habitat limited or would not respond to changes in habitat abundance.

Initially, I hypothesized that *Stegastes* spp. density would be dependent upon the abundance of substrate available for recruitment of filamentous algae and establishment of damselfish territories. I had assumed that the necessary substrate component was damaged or dead coral, and that increases in anthropogenic stress would increase the abundance of this substrate, thereby leading to an increase in the density of farming damselfish. Surprisingly, dead coral cover was not correlated with *Stegastes* spp. density. Instead, results indicated that different species of farming damselfish may have different habitat requirements or tolerances. I believe that the competitive hierarchy observed between the three *Stegastes* species in American Samoa is partially responsible for the different types of benthic substrate with which each species was found to be associated. Not surprisingly, the largest and most dominant species of the farming damselfish in American Samoa, *Stegastes lividus*, was found in the preferred/primary habitat, branching *Acropora* corals (Itzkowitz, 1979), while the smaller *S. nigricans* and *S. albifasciatus* were found occupying species of *Porites* corals and coral pavement. This finding is supported by Allen *et al.* (2001), in which staghorn corals, branching corals, and dead coral rubble and pavement are identified as usual habitat for these three species in the tropical Pacific. The ability of *Stegastes* spp. to utilize a variety of coral habitats may have contributed to the present inability to detect a significant difference in the density of farming damselfish or percent cover of damselfish algal gardens among sites differing in levels of anthropogenic stress.

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BIOEROSION

The overall rate of bioerosion (outside damselfish territories) in American Samoa is comparable to rates of bioerosion observed in other areas of the Pacific and in some areas of the Caribbean (Table 3-2). In general, bioerosion across sites followed a trend similar to that observed in previously published studies, i.e., bioerosion decreased as intensity of anthropogenic stress decreased, with the most extensively stressed site exhibiting the highest rate of bioerosion. This trend, however, was not statistically significant, and Olosega, a minimally stressed site, did not follow the expected pattern. Although human population density and coastal development are minimal at this site, Olosega is the most comparable (in terms of percent cover of algal gardens and amount of bioerosion) to our most extensively stressed site. As previously mentioned, the American Samoa EPA office has not yet evaluated all the designated uses for Olosega (Table 3-1), so the ASEPA rating of human influence for this site is not fully established. The present study was, in fact, the first attempt to systematically survey the benthic composition of the backreef at Olosega. During these surveys, it became obvious that the small village adjacent to this site may have a substantial influence on the local reef, possibly due to leaks in septic systems. Figure 3-8 is an example of a localized patch of macroalgae observed near a portion of Olosega's southwest shoreline. The size and distribution of this algae suggests that its presence is not the result of localized reductions in herbivory, but is most likely due to local increases in ambient nutrients that have given algae in this area a competitive advantage over corals. Because bioerosion has been linked to increases in nutrients and primary productivity on large and small spatial scales (Highsmith, 1980), and has also been shown to lead to the proliferation of bioeroding

invertebrates (Hallock, 1988; Rose and Risk, 1985), localized nitrification may be responsible for increased rates of bioerosion observed in this supposedly minimally stressed site, and for the lack of a significant correlation between anthropogenic stress and bioerosion.

Figure 3-8. Photograph of filamentous algae growing in a localized section of reef in front of Olosega village, American Samoa.

BIOEROSION AND DAMSELFISH TERRITORIES

Ambient levels of bioerosion vary around the world, and are known to be directly influenced by various oceanographic, anthropogenic, and biological factors, including the presence of damselfish algal gardens (Londono-Cruz, 2003; Rutzler, 1975). Previously published work regarding the effects of damselfish algal gardens on bioerosion indicates that bioerosion can be significantly greater inside gardens than in areas adjacent to, but outside gardens. This trend has been attributed to three factors: increased recruitment of boring macro-invertebrates in algal gardens (Hixon, 1983; Sammarco and Carleton, 1982; Lobel, 1980), increased protection from predation for both microborers and macroborers, and increased food supply for bioeroding invertebrates within algal gardens (Zubia and Peyrot-Clausade, 2001; Pari, 1998; Risk and Sammarco, 1982). This study, however,

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was unable to detect a significant difference in bioerosion inside and outside damselfish algal gardens. Ceccarelli (2002) and De Ruyter van Stevenick (1984) have illustrated that the effect of damselfish on their environment can be species specific, with the species of damselfish occupying the territory influencing the composition of algal species in that territory. It is possible that differences in the species of algae that make up the gardens alter the micro- and macroboring community to the extent that overall rates of bioerosion differ among *Stegastes* spp. territories in American Samoa and elsewhere.

The average amount of internal bioerosion occurring outside damselfish algal gardens in American Samoa is similar to that recorded in other areas of the central Pacific; therefore, the similarity in bioerosion observed inside and outside algal gardens may be due to a comparatively lower level of bioerosion inside American Samoa's damselfish algal gardens overall. Eutrophication, as mentioned throughout this paper, has been linked to increases in bioerosion in a variety of studies (Carriero-Silva *et al.*, 2005; Edinger and Risk, 1996; Rose and Risk, 1985; Smith *et al.*, 1981), and is often a result of local increases in development and human related activities. While data presented herein did not uncover a strong positive correlation between intensity of anthropogenic stress and bioerosion, the potential influence of differences in anthropogenic stress between American Samoa and that reported from other regions cannot be dismissed. As Figure 3-7 illustrates, bioerosion is only greater inside damselfish algal gardens at sites that are minimally influenced by humans and human development. This supports findings by Zubia and Peyrot-Clausade (2001), in which bioerosion by fauna inhabiting the tips of *Acropora* corals collected from *Stegastes*

nigricans territories was greater in an undisturbed site than in a site exposed to nutrient-rich groundwater.

Factors that may help explain this interaction include the age of the territories at each site and local sedimentation rates. Because the age of the coral and the amount of time it has been covered by algae are directly related to how long bioeroders have had access to the coral skeleton, older damselfish algal gardens would yield samples exhibiting higher amounts of bioerosion. If the level of anthropogenic stress is related to the longevity of coral colonies within territories, algal gardens at minimally stressed sites might be older than those in extensively and possibly intermediately stressed sites, leading to higher rates of bioerosion inside territories in areas with lower levels of anthropogenic stress. Tribollet *et al.* (2002) attributed decreased rates of bioerosion in inshore areas, compared to offshore sections of the Great Barrier Reef, Australia, to increased sediment loading at nearshore sites. Sedimentation rates may influence rates of bioerosion through a number of mechanisms including: decreasing water flow through corals and limiting food supply to sponges and other bioeroding species and/or by altering the species composition of the bioeroding community. The algal matrix found within damselfish algal gardens can trap sediments and particulate materials, increasing the local sediment load on substrates within the gardens. If the extensive and intermediately stressed sites examined in this study have higher sedimentation rates than the minimally influenced site, bioerosion of corals within damselfish algal gardens at the extensive and intermediate sites could be substantially reduced.

<u>CONCLUSIONS</u>

Damselfish algal gardens in American Samoa are dominated by the species *Stegastes nigricans* and do not differ significantly in size among sites. The percent cover of damselfish algal gardens and density of *Stegastes* spp. are not correlated with intensity of anthropogenic stress in American Samoa. Instead, the type of coral substrate present - *Acropora* spp., *Porites* spp., or coral pavement - influences the density of the particular species of farming damselfish present (e.g., *Stegastes lividus, S. albifacsiatus,* or *S. nigricans*). The effect that farming damselfish have on rates of bioerosion of coral substrates within their territories is influenced by the local intensity of anthropogenic stress, with bioerosion inside territories being highest at minimally stressed sites. Although farming damselfish have variable effects on internal coral bioerosion, rates of bioerosion inside and outside algal gardens are similar when samples from all sites around American Samoa are pooled. A trend was observed for bioerosion to increase with intensity of anthropogenic stress, suggesting that patterns of nearshore coastal land use may lead to increases in local rates of coral bioerosion.

CHAPTER 4: CONCLUSION

A number of factors have been identified that influence local rates of coral bioerosion, including algal gardens of farming damselfish, local abundance of herbivorous fish and grazing pressure, sedimentation rates, eutrophication, water depth, and current regimes. Because human activities may indirectly affect all these processes, local levels of anthropogenic stress were examined as a potential driver affecting the intensity of coral bioerosion inside and outside damselfish territories in American Samoa. In order to assess the influence that anthropogenic stress may have on local rates of internal coral bioerosion, it was necessary to identify a reliable and effective method for measuring bioerosion across and within sites. Three methods, digital area analysis, rubble count, and volume displacement, which vary in both the amount of time and resources they require, were evaluated for consistency and resolution of the results they produced.

Digital area analyses had lower inter- and intra-site variability, and were able to detect small-scale differences in bioerosion between samples. Consequently, this method was identified as the most effective and reliable technique currently available for measuring internal bioerosion of corals. As discussed in Chapter 2, comparisons of these methods would have been more informative had a larger sample size been used. The sample size employed in this study was too small to account for variability among samples and was unable to provide the level of precision necessary to make the displacement or rubble analysis techniques effective. Despite these limitations, this research showed that digital techniques, which are the most time and resource intensive,

are precise enough to achieve statistically significant results even with relatively small sample sizes. Furthermore, these results corroborated work published by Holmes *et al.* (2000), which indicated that digital area analysis and rubble count results are significantly positively correlated, and attempted to go one step further by comparing bioerosion measurements obtained with these methods, but using the same samples for each method.

Once an appropriate method for measuring bioerosion was identified, coral samples from various sites around American Samoa were examined to determine whether anthropogenic stress significantly increases local rates of internal bioerosion of coral, decreases live coral cover, and in turn is positively correlated with the abundance of farming damselfish and damselfish algal gardens. Unfortunately, oceanographic conditions and local terrestrial influences can affect water quality at small scales such that, despite current efforts to monitor water quality in American Samoa, the only reliable measurements of anthropogenic stress available for this study were qualitative and descriptive. This limitation influences the global context of this research because it prevents accurate conclusions regarding other mechanisms that may be influencing bioerosion among various sites and in published studies. Despite the absence of more specific data on intensity of anthropogenic stress at each site, this research produced evidence that human population density and amount of industrial development in coastal habitats may contribute to increases in coral bioerosion and may significantly influence the effect damselfish algal gardens have on coral bioerosion. The interaction between anthropogenic stress, farming damselfish and coral bioerosion is not an effect of damselfish abundance increasing with intensity of anthropogenic stress. Percent cover of

algal gardens and density of farming damselfish (*Stegastes* spp.) were not significantly different among extensively, intermediately, and minimally stressed sites. Instead, anthropogenic stress appears to influence rates of coral bioerosion inside damselfish algal gardens through some other means, possibly through increases in sediment load or by altering the longevity of the coral framework of the algal gardens.

While various components of the benthic substrate were quantified at each site, this study did not assess the density of fish species that may act as competitors with or predators of farming damselfish, and was unable to identify factors contributing to differences in the prevalence of damselfish and damselfish algal gardens among various reef tracts. Although *Stegastes* spp. live in and feed on algae covering what was once living coral, the density of farming damselfish (*Stegastes* spp.) was not correlated with the percent cover of dead coral substrate or percent cover of dead, algal covered coral. The initial hypothesis was that the availability of these habitat characteristics would be linked to levels of anthropogenic stress, and would possibly illustrate that farming damselfish can readily utilize, and are more abundant in, disturbed habitats. Instead, results from this study suggest that each species of farming damselfish either specializes in establishing algal gardens in certain types of coral, or occupies a secondary habitat type as a result of competitive interactions with congeners. This does not mean, however, that farming damselfish do not or cannot readily move into and establish algal gardens in areas where coral tissue has been killed or damaged. Instead, these results suggest that live coral cover is important for damselfish recruitment and that the effects of damselfish on the structural integrity of reefs not only have the potential to affect branching *Acropora* spp., but other types of coral substrates as well.

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As bioerosion becomes more commonly associated with eutrophication, overfishing, climate change, and overall reef health, there is increasing motivation to develop less time and resource intensive methods for measuring the rate and extent of bioerosion. In addition to identifying an appropriate method for measuring bioerosion, this research found that human activities in coastal environments may indirectly affect the structure of coral reef habitats by altering rates of coral bioerosion inside and outside damselfish algal gardens. Farming damselfish, like humans, can substantially alter their environment, and thereby influence the composition and abundance of species in the surrounding ecosystem. The effect of damselfish, however, is relative to what is occurring outside their algal gardens. While some published studies have concluded that farming damselfish increase coral bioerosion and may inhibit reef consolidation and coral cover by establishing and maintaining algal gardens, findings of the present study indicate that the effects of damselfish on coral bioerosion are mediated by human activities, and that anthropogenic stress, due to its ability to directly and indirectly alter rates of bioerosion, has a more substantial influence on the structural integrity and long-term persistence of coral reefs.

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