

DRAMATIC INCREASES IN THE MUSHROOM CORAL *LOBACTIS SCUTARIA*  
POPULATION IN KĀNE‘OHE BAY, HAWAI‘I OVER THE LAST 18 YEARS

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## Abstract

The coral reefs of Kāneʻohe Bay, Hawaiʻi have undergone significant changes in recent history. By the 1960s, vibrant coral reefs were transformed to an algae-dominated ecosystem as a result of dredging and increased nutrient input from wastewater discharge. Since the diversion of sewage from the southern bay in the late 1970s, coral populations have made a slow recovery despite periodic mortality from recent coral bleaching and freshwater flooding during heavy rainfall events. This study repeated surveys done in 2000 for the common mushroom coral *Lobactis scutaria*, previously referred to as *Fungia scutaria*. Unlike most coral species, *L. scutaria* is a solitary, free-living, non-colonial coral such that each coral is a single polyp which makes them easy to identify and count in the field. At 42 sites on patch reefs across Kāneʻohe Bay, two snorkelers surveyed *L. scutaria* density and colony size during 30 minute-timed swims at the same general locations of the 2000 study. Surveyed areas during the timed swims were recorded with GPS tracks and converted to total area surveyed for each patch reef site to calculate coral density. I found a significant increase in density of *L. scutaria* for all regions of the bay between 2000 and 2018 but coral size structure did not change significantly. The North region of Kāneʻohe Bay contained nearly twice the recruit density as the other regions and there was a positive relationship between sexual recruit density and adult density. In 2018, sexual recruits made up 9.2% of the population while asexual buds made up 3.8% of the population, showing a shift in reproductive modes from 2000 when sexual recruits were nearly absent and asexual buds constituted about 20% of the population. Sites on patch reefs under restoration by the Hawaiʻi Department of Land and Natural Resources that involved removal of invasive algae and sea urchin out-planting showed no difference in mushroom coral densities than control sites. This is probably due to a decrease in algae bay-wide and a recovery of coral on all reefs, not only

reefs that had restoration activities. These findings indicate a growing population of mushroom corals and recovering coral reef ecosystem in Kāneʻohe Bay, Hawaiʻi.

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## Introduction

An important question in coral reef conservation today is: How resilient are coral reefs? Numerous studies show they are fragile and on the brink of collapse (Jokiel and Brown 2004; Hoegh-Guldberg et al. 2007; Harvell et al. 2008) and yet others offer hope that they may be more tolerant, adaptive, and resilient than may have been feared (Bellwood et al. 2006; Baker et al. 2008; Birkeland et al. 2013; Coles et al. 2018). It is known that coral reefs react differently depending on the frequency, intensity, and duration of natural and anthropogenic stressors so management and restoration on a local basis, especially with an emphasis on improving recruitment, should be emphasized if coral reefs are going to survive the many challenges they face (Mumby and Steneck 2008).

In the Main Hawaiian Islands, coral cover, species richness, and diversity were overall steady between 1999-2012, with local variations offsetting each other (Rodgers et al. 2015). The coral reefs of Kāneʻohe Bay have experienced events both stressful and favorable for their well-being over that same time period and more recently. In 2002, a coral bleaching event hit Kāneʻohe Bay but most corals recovered, mortality was low and only the most sensitive species were affected (Jokiel and Brown 2004). In 2006, prolonged cloud cover led to a reduction in the green bubble alga, *Dictyosphaeria cavernosa*, abundance throughout the bay (Stimson and Conklin 2008). In 2008, the Hawaiʻi Department of Land and Natural Resources began restoration activities with an invasive algae removal program that combined physical removal with out-planting of the native urchin species *Tripneustes gratilla* (Neilson et al. 2018). Due to the currently low cover of invasive algae, physical removal is no longer necessary but urchin out-planting is continued. In July 2014, Kāneʻohe Bay experienced a large freshwater flooding event and in September 2014, unusually warm temperatures caused major bleaching throughout the

bay (Bahr et al. 2015a). In localized areas affected by both the freshwater inundation and heat-induced bleaching, mortality reached 60%. However, areas of the bay which were affected by the bleaching had only a 1% loss of coral cover. The following summer in 2015, the bay again experienced extremely warm temperatures resulting in bleaching and mortality of corals (Bahr et al. 2017). After two months the bay showed signs of recovery with an 16% loss due to mortality bay wide and the South Bay having the highest mortality at 28%.

Kāneʻohe Bay is a litmus test for the resiliency of coral reefs that have undergone significant changes in recent history due to dredging, high nutrient input, and invasive algae. The bay is located on the windward side of the island of Oʻahu with a large human population on shore. By the 1960s, once vibrant coral reefs had been transformed to an algae-dominated ecosystem as a result of dredging which caused both physical damage as well as massive sedimentation (Hunter and Evans 1995) and increased nutrient input from wastewater discharge in the Bay, which peaked in 1977 at over 8 million gallons of semi-treated sewage per day (Smith et al. 1981). By 1978, most sewage had been diverted and nutrient levels in the bay dropped within a year (Smith et al. 1981). Stimson (2015) showed that phosphates, ammonia, nitrates, and nitrites continued to decline until another short-term peak in 2006 due to exceptionally heavy spring rains. Before this drop, nutrients fed large algal blooms throughout the bay. In the 1970s, the native alga *D. cavernosa* covered 50 to 100% of some reefs (Stimson 2015). Four introduced species of algae also compete with corals in Kāneʻohe Bay. *Acanthopora spicifera* was accidentally brought to Hawaiʻi in the 1950's, from barge fouling in Pearl Harbor and quickly spread to all the main islands (Coles et al. 1999; Smith et al. 2002). *Gracilaria salicornia*, *Eucheuma sp.*, and *Kappaphycus sp.* were purposefully introduced to Kāneʻohe Bay in the 1970s for aquaculture research (Smith et al. 2004; Conklin and Smith 2005). *Eucheuma sp.*

*and Kappaphycus* are similar species which are often misidentified (Pickering et al. 2008) and they are commonly referred to now simply as the *Eucheuma/Kappaphycus* complex (Neilson et al. 2018). With the cessation of most nutrients from sewage input in 1978, invasive algae cover is now at the lowest point and coral cover is at its highest since the 1970s (Stimson 2018), in a rare example of a phase-shift reversal where an algae-dominated state returns to high coral cover (Stimson and Conklin 2008). Currently, the most common corals found in Kāneʻohe Bay are *Porites compressa*, followed by *Montipora capitata*, *Pocillopora damicornis*, and *Lobactis scutaria* (Sukhraj 2014). See Figure 10 for a timeline of recent environmental events in Kāneʻohe Bay.

*Lobactis scutaria*, previously known as *Fungia scutaria*, are solitary, free-living, non-colonial corals (Krupp 1983) which are particularly hardy, showing high tolerance to increased temperatures (Edmondson 1928; Jokiel and Coles 1977; Coles et al. 2018). Being unattached to the substrate, they can be susceptible to heavy wave action but are hydromechanically adapted to right themselves in certain conditions (Jokiel and Cowdin 1976). They are susceptible to being smothered by algae and fast growing coral species as they lie relatively flat on the reef surface but they are capable of traveling short distances by becoming neutrally buoyant by taking sea water into their tissues (Chadwick 1988).

*L. scutaria* is a gonochoric broadcast spawner in the summer months, however, previous to this survey sexual recruits were rare in Kāneʻohe Bay (Lacks 2000). Instead, *L. scutaria* appeared to rely on asexual budding (Krupp 1983; Lacks 2000). These buds grow abundantly from anthocaulus-like stalks derived usually from the aboral side of dead parent corallum with an average of 23 asexual buds per parent coralla (Krupp et al. 1992). Asexual buds are especially present after freshwater floods which are lethal to most corals (Jokiel et al. 1993) and it is

hypothesized that this is how Kāneʻohe Bay, an estuarine habitat that experiences occasional flooding events, has established a denser than usual population of mushroom corals (Krupp et al. 1992).

Four previous bay-wide surveys for *L. scutaria* have taken place in Kāneʻohe Bay. The first, a survey in 1967, determined the distribution of *L. scutaria* within the bay and located “areas of maximum density” (Bosch 1967). *L. scutaria* were located mainly in the central patch reefs of the bay and required a hard reef structure because they were never found in sand, muddy shore lines, or on the bay bottom. A second bay-wide survey in the early 1970s, used presence/absence surveys and concluded that *L. scutaria* was a relatively common coral in Kāneʻohe Bay, especially in “non-polluted areas” such as the North Bay reefs where ocean water is supplied regularly (Maragos 1972). During the spring of 2000, a third project surveyed 42 patch reef sites across the bay recording abundance counts, class size, color morphs, small-scale coral distribution (i.e. “clumping”), and if corals were located in “crevices” (Lacks 2000) and found that the North Bay had the highest density of *L. scutaria* corals. Finally, a comprehensive coral survey, including *L. scutaria*, of Kāneʻohe Bay was completed in 2009 (Sukhraj 2014) and found that there was a long but slow recovery of coral cover in the bay since 1970 with an average increase of 0.45% a year.

The objectives of this study were to reassess the *Lobactis scutaria* density, size-structure, and distribution in Kāneʻohe Bay as compared to the survey in 2000 (Lacks 2000). I also compared the 2018 survey results for reefs undergoing restoration with invasive algae removal and herbivorous urchin out-planting activities (Neilson et al. 2018) that have taken place since the 2000 survey to determine if there were differences in *L. scutaria* densities on reefs managed for alga growth and reefs which had not. The assessment of current and past management

practices is important to determine their effectiveness and practicality in the field and I expected to see a significant difference in *L. scutaria* densities on reefs managed for invasive algae.

## **Methods**

### **Site Description**

This study took place in Kāneʻohe Bay on the windward side of Oʻahu, Hawaiʻi. Kāneʻohe Bay represents one of the most intensely studied reef ecosystems in the world (Bahr et al. 2015b). It is also unique for being the largest embayment area in the main Hawaiian Islands (Hunter and Evans 1995). The bay contains approximately 70 inner patch reefs and an extensive fringing reef along the shoreline. The patch reef numbering system was established by Roy (1970) and is widely used in Kāneʻohe Bay research. The reefs are protected from heavy wave action by the barrier reef and the surrounding embayment (Franklin et al. 2013). There are two natural channels on either side of the barrier reef, one to the north and one to the south as well as a dredged channel that runs roughly north-south within the bay. The hydrology of the bay generally consists of ocean water entering over the central barrier reef and flushing water out through the north and south channels (Lowe et al. 2009). The patch reefs are generally oval in shape and rise sharply from the bay floor. Reef flats vary greatly in coral cover and mostly lie slightly above the average low tide line which causes the shallowest reef flats to have very low coral cover (Stimson 2018).

The watershed area for Kāneʻohe Bay covers 97 km<sup>2</sup> and nine perennial streams flow into the bay (Hunter and Evans 1995). The bay is often considered as having three main regions: South Bay, Central or Mid-Bay and North Bay (Bathen 1968). These three regions are distinct in many aspects. The South bay is generally defined as having the lowest water quality due to

restricted water flow and the highest human population on shore. Nutrient loads in the South bay peak after storm events, as run-off from on-shore activities leads to phytoplankton blooms but can return to normal levels in a matter of days (Ringuet and Mackenzie 2005; Drupp et al. 2011). The Central bay has higher water circulation and relatively low levels of nutrient input from land (Smith et al. 1981). The North bay is nearest to the open ocean which allows it to usually have the highest water quality. It generally has reefs with the highest coral cover. Kāneʻohe Bay has been extensively studied in the past which allows for comparisons with historic and current conditions to assess the long-term trends in coral reef health.

### **Survey Technique**

From May to November 2018, we surveyed 37 patch reefs with four sites on Coconut Island and three sites on Checker Reef for a total of 42 sites across the bay for the common mushroom coral *L. scutaria* (Figure 1). For consistency, we replicated the survey methods used by Lacks (2000). Sites were surveyed by two snorkelers for thirty minutes, for a total of 1 man-hour of survey at each site. Lacks provided a map of surveyed areas (2000) and to the best of our ability, we surveyed the same areas on each reef that were surveyed previously. On reefs which could not be completely surveyed in thirty minutes, surveys focused on areas of best suited habitat so that sand and rubble patches were not surveyed, as was done by Lacks (2000). The area surveyed was recorded on a map of each reef immediately after each survey was completed and later transcribed as a polygon in Google Earth software to calculate the surveyed area (m<sup>2</sup>). Lacks (2000) provided a map of the extent of her sites without giving a measure of the surveyed area for each site so these were also estimated by recreating the site polygons in Google Earth. In 2018, approximately 163,456 m<sup>2</sup> of reef were surveyed in 42 man-hours, averaging about 4,035

m<sup>2</sup> per site. Our estimation of total area surveyed in 2000 was 609,635 m<sup>2</sup> or 14,869 m<sup>2</sup> per site. Care was taken to not survey the same area twice or missing areas by having the surveyors start together and work outwards to opposite sides of the reef in a back and forth pattern and by using natural landmarks on the reef to position ourselves.

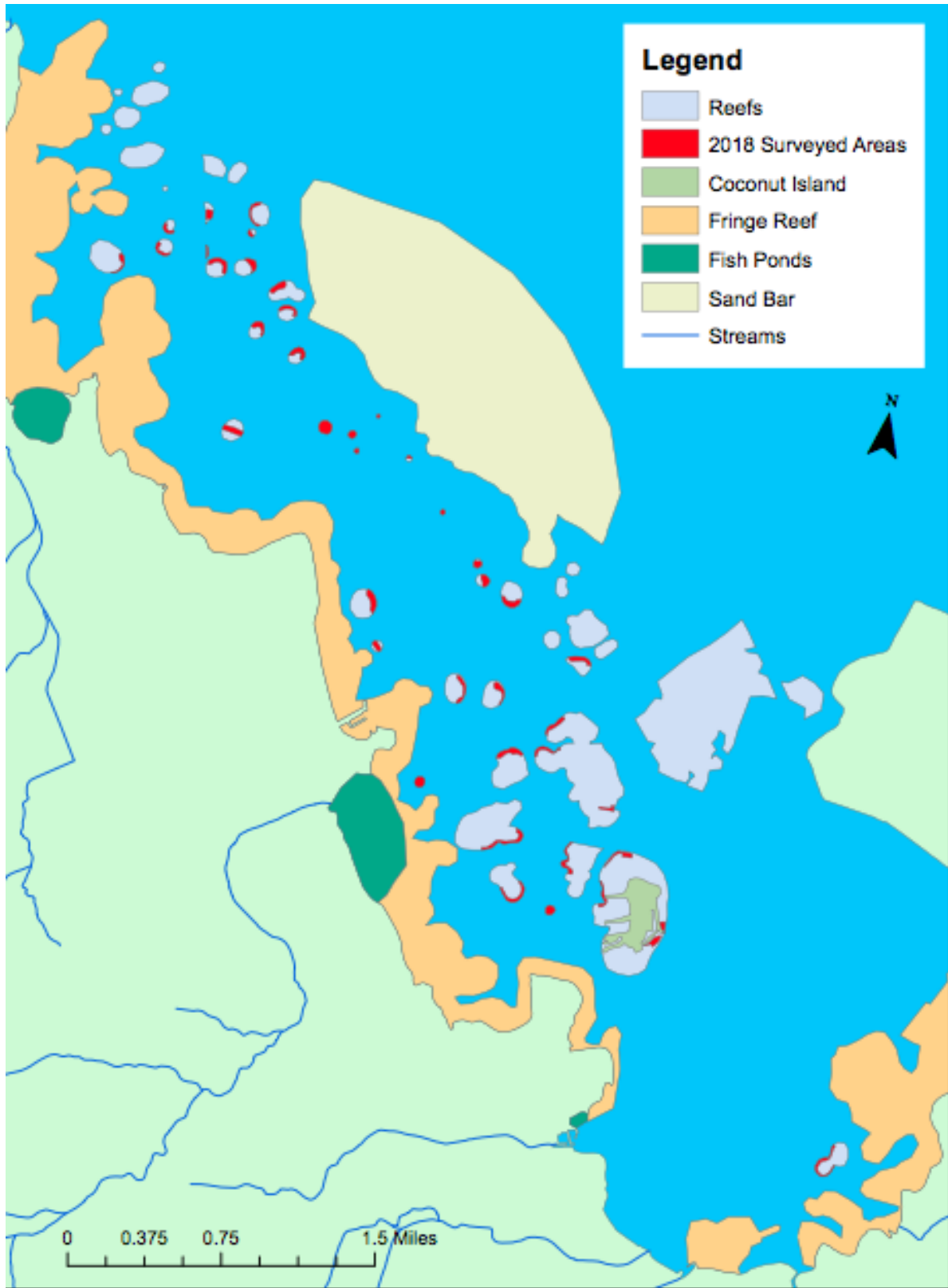
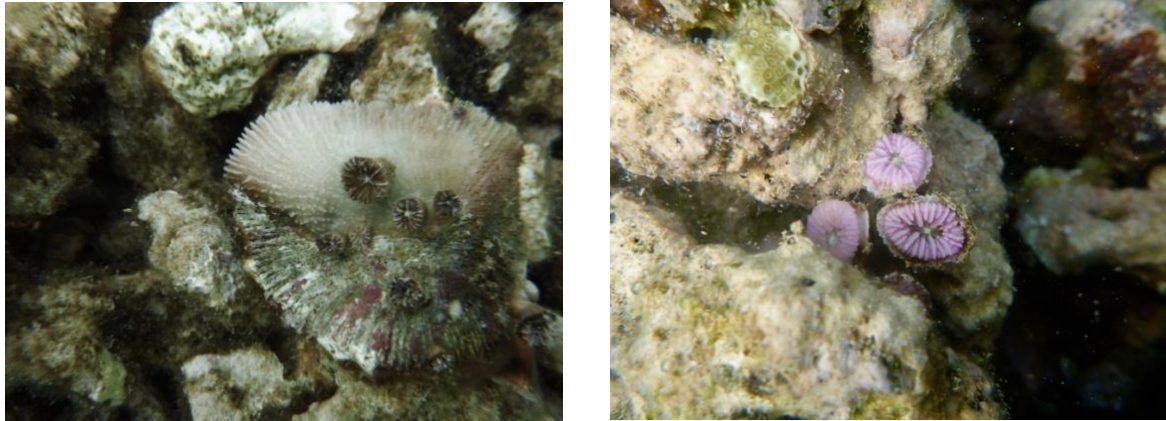


Figure 1. A map of Kāneʻohe Bay, Hawaiʻi with the 2018 surveyed areas highlighted in red.

Data collected during the surveys included the size class of each coral, color morph, whether the corals was located in a crevice or depression, and whether each coral was clumped with other *L. scutaria* individuals. These methods followed Lacks (2000) to allow comparisons between survey results. Size classes were binned as: extra small (0-5 cm maximum coral diameter), small (5-9 cm), medium (9-12 cm), and large (greater than 12 cm) in accordance with Lacks (2000). To efficiently classify individuals, surveyors used a measuring stick, pre-marked with the size classes. After noting a large number of sexual recruits in preliminary surveys, I distinguished the extra-small category into: sexual recruits (extra small corals, less than 5 cm that were attached individually on the reef floor and not to another *L. scutaria* coral), asexual buds (extra small corals clearly branching on a stalk from a parent coral) and simply extra small (any other extra small coral not clearly a sexual recruit or bud). See Figure 2 for examples of sexual recruits and asexual buds. For continuity, buds and sexual recruits were included as extra small individuals for comparisons with Lacks' results. The term "Adult" refers to all individuals in the small, medium, and large size classes although this may not accurately reflect sexual maturity. Color morphs were recorded by the color of the body, mouth and tentacles and a total of 33 different combinations were observed. Lacks (2000) defined a crevice as any depression in the reef that would disrupt the release of gametes which I took to mean any depression or hole in the reef more than 20 cm deep. Corals were classified as clumped if two or more corals were found within 10 cm of each other. See Figure 3 for an example of a surveyor with size-class measuring stick and equipment. A historical comparison of abundance classifications is given in Figure 4. These include Bosch (1967), Maragos (1972), Lacks (2000) and my results from the 2018 surveys. Bosch did not give value ranges for his abundance classes. Maragos rated sites simply

as abundant/present or few/absent. Lacks and Johannsen values ranges for abundance count per site are: Abundant (>250), Common (100-250), Few (10 – 99) and Few/None (<10).



*Figure 2.* The photo on the left shows a typical example of asexual budding in *Lobactis scutaria*. In this example, nine buds are growing from the aboral side of a dead parent corallum. The photo on the right shows three sexual recruits. Very young sexual recruits tended to have a pink hue and be firmly attached to the substrate. As they grow older, they grow up on a stalk, take a more adult-like form, and eventually break off.



*Figure 3.* Image of a surveyor using data sheets, clip-board and pre-marked measuring stick for efficient surveying

## Statistical Analysis

All counts by site given are merely the total number of individuals surveyed at that site and do not necessarily reflect an abundance or population count. Some patch reefs were able to be surveyed in their entirety but an abundance estimation was not intended. All densities are given as individuals per 100 m<sup>2</sup> and were calculated by dividing the area of each site (m<sup>2</sup>) by 100 and dividing number of individuals counted at each site by that value. When analyzing the densities between the two surveys, paired t-tests were used. Statistical analyses of regions were done using one-way ANOVA and Tukey-Kramer tests to compare pairwise comparisons for significant differences among regions. Analysis of management activities was done by comparing *L. scutaria* densities and recruit densities among three management practices with a one-way ANOVA with sites divided by management activities (Table 2). All statistical analyses were performed with Microsoft Excel 2016 and all graphs were created using R v3.3.1.

There are some limitations to analyzing population structure in coral species including their colonial nature and the non-correlation of size to age in many coral species due to branching forms and partial mortality (Bak and Meesters 1998). Delineation of population structure in mushroom corals, because of their solitary, non-colonial form, avoids these pitfalls. To collect data for the detailed population size structure, six transect surveys for *L. scutaria* were repeated, two for each abundance category (“abundant”, “common”, “few”) which had previously been categorized from the timed surveys. Instead of simply binning each coral into a size class, measurements to the nearest 0.1 cm were taken on a total of 209 individuals.

## Results

A total of 12,630 *L. scutaria* corals were counted at the 42 sites for an average of  $300.71 \pm 155.10$  (mean  $\pm$  SD) individual corals per one-man hour of surveying at each site. Average density of areas surveyed was 10.4 corals per 100 m<sup>2</sup> compared to Lacks' 2.5 corals per 100 m<sup>2</sup>. The average density of *L. scutaria* throughout the bay was more than four times higher in 2018 than 18 years ago (paired t-test,  $p < 0.000$ ). Using the abundance classification categories provided by Lacks (2000), 26 sites were classified as "abundant" from the 2018 surveys up from only 7 in the 2000 surveys. Eight reefs were currently classified as common and only 7 were classified as few. Whereas, in the previous surveys, 15 sites were classified as common and 19 were classified as few. Reef A, located in the far Southern region of the bay, was the only site in both surveys with no *L. scutaria* individuals.

There were 3,480 individuals or 28.0% of the population in the extra small size class, 3,424 individuals or 27.1% of the population were in the small size class, 2,627 individuals or 20.8 % of the population were in the medium size class and 3,099 individuals or 24.5% of the population were in the large size class (Figure 5). Using abundance counts, a chi-square test goodness-of-fit was performed to determine whether *Lobactis scutaria* were evenly distributed among the size classes. Individuals were not evenly distributed among the size classes,  $X^2 (3, N = 4) = 145.6, p = 0.5$ . Individuals were also not evenly distributed among the size classes in Lacks' (2000) results,  $X^2 (3, N = 4) = 323.8, p = 0.5$ . The size of corals from the ten transects with precise measurements showed the majority of individuals being in the smaller size classes (skewness = +0.258, mean = 8.33, mode = 3) which suggests a growing population (Figure 6). I found only 478 dead corals compared to 1935 dead corals found by Lacks in 2000. See Table 4. for raw survey data.

I classified each site as having abundant, common, or few *L. scutaria* based on survey counts (Figure 11) as was done by Lacks (2000). Figure 4 and Table 3 gives the abundance classifications in comparison to previous bay-wide surveys for *L. scutaria*.

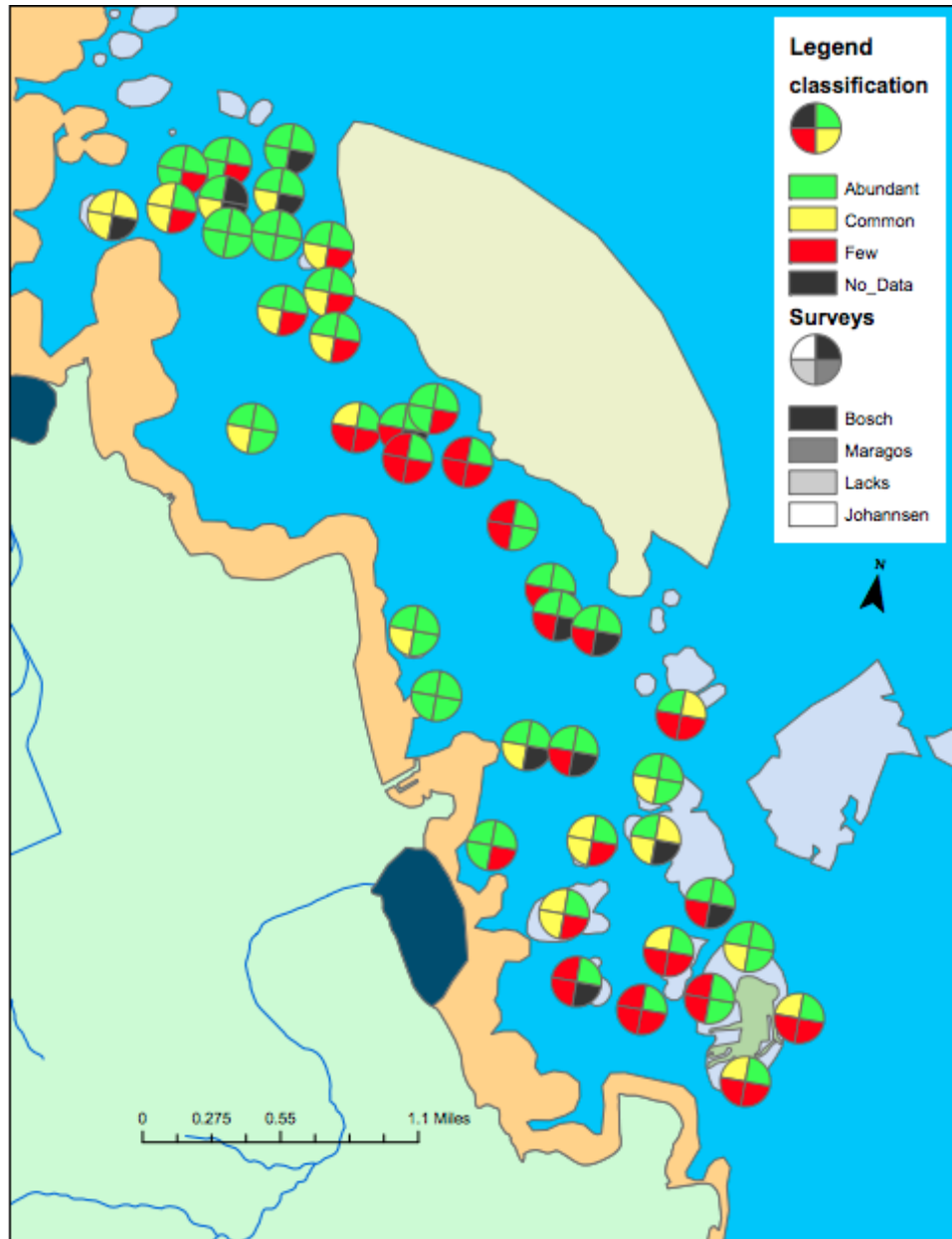


Figure 4. A comparison of survey abundance classifications of four bay-wide surveys for *Lobactis scutaria* in Kāneʻohe Bay: Bosch (1967), Maragos (1972), Lacks (2000), Johannsen (2018). Surveys are presented in chronological order, clock-wise around each chart, with Bosch’s survey classifications presented in the top right, Maragos bottom right, Lacks bottom left and Johannsen top left.

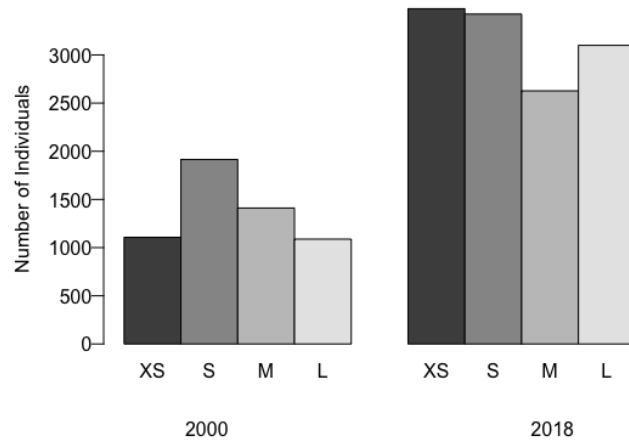


Figure 5. A comparison of the population size structures of *L. scutaria* surveyed from Kāne‘ohe Bay, Hawai‘i in 2000 and 2018 using abundance counts. Individuals were classified as extra small (<5 cm), small (5-9 cm), medium (9.1 – 12 cm) or large (>12 cm).

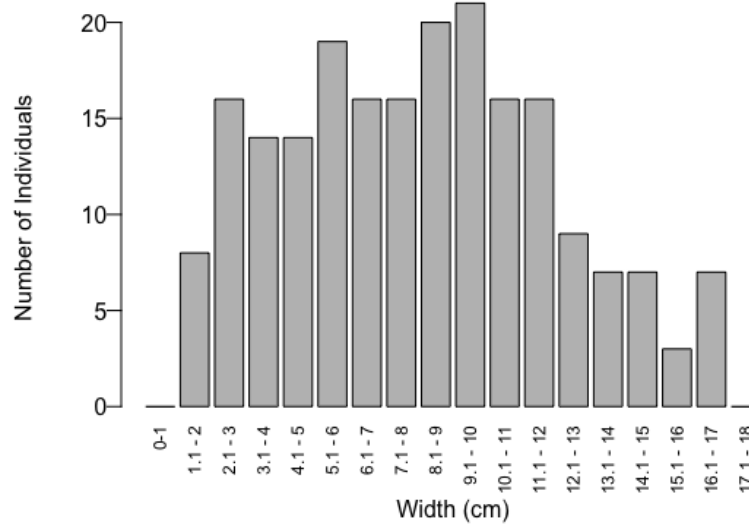


Figure 6. A detailed population size structure of *L. scutaria* surveyed in Kāne‘ohe Bay, Hawai‘i in October 2018. The population is slightly skewed (+0.258) with the majority of individuals being smaller than 10 cm coral diameter which suggests a growing population.

## Kāneʻohe Bay Regions

The physical characteristics of Kāneʻohe Bay divide it into three distinct regions. The average density of *Lobactis scutaria* in the South Bay (N=14 sites) was  $5.1 \pm 1.3$  (mean  $\pm$  SE) individuals per 100 m<sup>2</sup> compared to Lacks' average of  $0.8 \pm 0.4$  (mean  $\pm$  SE), an increase of 538%. The average density of the Mid-Bay (N=19) was  $8.2 \pm 0.9$  (mean  $\pm$  SE) per 100 m<sup>2</sup> compared to  $1.8 \pm 0.4$  (mean  $\pm$  SE) in 2000, a 356% increase. The average density for the North Bay (N=9) was  $23.3 \pm 10.0$  (mean  $\pm$  SE) as compared to  $6.1 \pm 0.2$  in 2000, a 282% increase (Figure 7).

*Table 1.* Comparisons of *L. scutaria* counts, density, change in density, and recruit density by region. Results are given as average per reef by region with  $\pm$  standard error. Densities are given as individuals per 100 m<sup>2</sup> and test results in all categories by region across the bay.

Average:	South	Mid	North	Total	Anova P-value
Count	217.0 $\pm$ 48.7	303.2 $\pm$ 38.1	425.8 $\pm$ 65.9	300.71 $\pm$ 29.31	0.032
Density	5.1 $\pm$ 1.3	8.2 $\pm$ 0.9	23.3 $\pm$ 10.1	10.4 $\pm$ 2.4	0.002
Change in density	4.4 $\pm$ 1.2	6.2 $\pm$ .9	17.2 $\pm$ 8.1	7.9 $\pm$ 1.9	0.032
Recruit density	0.48 $\pm$ 0.15	0.51 $\pm$ 0.12	2.47 $\pm$ 0.96	0.92 $\pm$ 0.25	0.002

Coral densities were significantly different by region for the 2018 survey ( $F(2,40) = 4.90$ ,  $p = 0.013$ ) with differences between all region pairs of the Bay (South-Mid, South-North, and Mid-North). Coral densities between the 2000 and 2018 surveys were significantly different by region ( $F(2,40) = 3.77$ ,  $p = 0.032$ ) with significant differences between all paired regions of the bay.

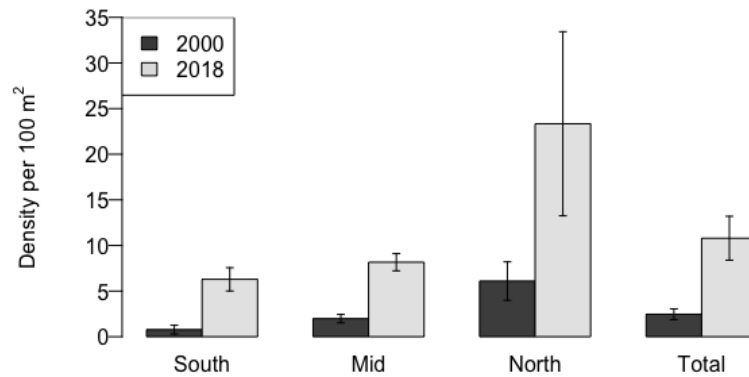


Figure 7. Average density with standard error of *L. scutaria* by region from surveys of Kāne‘ohe Bay in 2000 and 2018. This shows significant differences between surveys in all regions with the North Bay having the highest average density in both surveys. Total is the average by survey site bay wide.

### Restoration Activities

I found no significant difference in *L. scutaria* density on reefs which have not had any management action (N= 13), reefs which had urchins out-planted only (N= 8), and reefs which have had both urchin out-planting and invasive algae collected by the “Super-Sucker (N= 7) ( $F(2,25) = .24, p = 0.787$ ) (Table 2). Finally, there was also no significant difference in the sexual recruit density between control reefs, urchin out-planted reefs, and reefs with both urchins and algal removal by the “Super-sucker” ( $F(2,25) = 1.32, p = 0.28$ ).

Table 2. Comparisons by management on Central and North Bay reefs. We see no significant differences in *L. scutaria* densities or recruit densities on reefs with and without management.

No Management			Urchin Out-planting Only			Both Removal and Urchin Out-planting		
Reef	<i>L. scutaria</i> density	Recruit density	Reef	<i>L. scutaria</i> density	Recruit density	Reef	<i>L. scutaria</i> density	Recruit density
9	6.6	0.8	14	6.1	0.3	10	5.9	0.0
11	5.5	0.9	19	4.6	0.0	15	13.6	0.3
17	17.2	1.1	24	2.2	0.0	16	15.6	1.7
18	7.6	1.0	28	11.8	1.4	20	7.6	0.2
21	4.0	0.0	30	13.4	0.3	26	8.4	0.0
22	4.6	0.5	31	5.4	1.3	27	6.5	0.0
23	12.6	0.0	38	11.7	0.0	29	8.3	0.7
25	6.6	0.6	40	43.6	3.0			
32	97.8	8.9						
33	6.4	0.0						
34	5.2	0.8						
39	12.4	3.4						
41	14.2	4.5						
Average	15.4	1.7		12.3	0.8		9.4	0.4
SE	7.0	0.7		4.7	0.4		1.4	0.2

### Sexual Recruits

Lacks (2000) reported a total of 1,107 extra small corals and determined that 1,102 or 99.3% of them were asexual buds growing from dead parent corals. She noted that the other 5 corals could have “possibly settled on pieces of dead *Porites compressa*” meaning they were likely sexual recruits that had settled from planula larvae. In the 2018 surveys, sexual recruits were far more abundant totaling 1,160 individuals or about 9.2% of the total population. Asexual buds were also present but a total of only 485 buds were counted or about 3.8% of the total population. The South Bay averaged  $18.64 \pm 5.3$  (mean  $\pm$  SE) sexual recruits per reef with a density of  $0.47 \pm 0.1$  (mean  $\pm$  SE) recruits per 100 m<sup>2</sup>. Reefs in the Mid Bay averaged  $20.73 \pm 5.1$  (mean  $\pm$  SE) sexual recruits with a density of  $0.5 \pm 0.1$  (mean  $\pm$  SE) and the North Bay averaged  $48.11 \pm 19.44$  (mean  $\pm$  SE) sexual recruits per reef with an average density of  $2.5 \pm 0.9$  (mean  $\pm$  SE). Recruit densities

were significantly different by region ( $F(2,40) = 7.07$ ,  $p = 0.002$ ) with significant differences between the South to North and Mid to North regions but no significant difference between the South and Mid Bay regions.

An ordinary linear regression described a positive relationship between sexual recruit density and adult density ( $F(1,29) = 102.69$ ,  $p = 0.000$ ,  $R^2 = 0.779$ ) (Figure 8). There were also significant relationships between sexual recruit density and all size classes of adults (Figure 9). A significant positive relationship was found for recruit density to small adults ( $F(1,29) = 20.37$ ,  $p < 0.000$ ,  $R^2 = 0.413$ ) with a slope of 0.57. There was also a significant positive relationship between recruit density and medium adult density ( $F(1,29) = 46.99$ ,  $p < 0.000$ ,  $R^2 = 0.618$ ) with a slope of 0.65. Finally, there was a significant positive relationship between recruit density and large adult density ( $F(1,29) = 52.44$ ,  $p < 0.000$ ,  $R^2 = 0.644$ ) with a slope of 0.15.

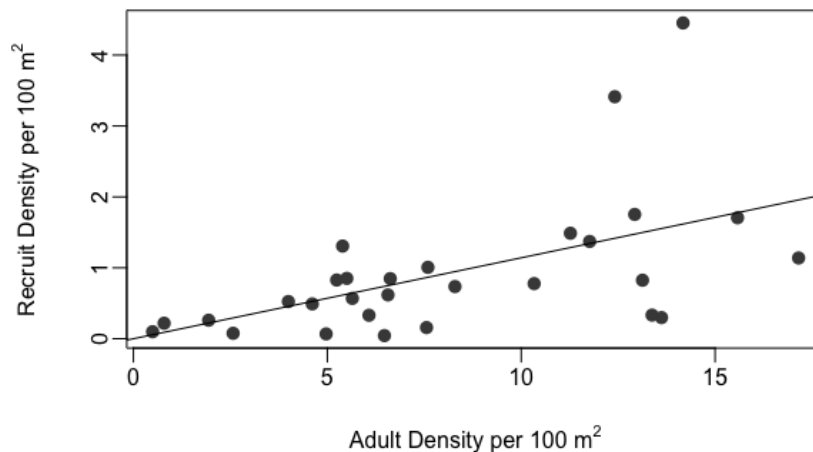


Figure 8. The recruit density to adult density relationship from *L. scutaria* surveys completed in Kāneʻohe Bay, Hawaiʻi, 2018. There was a significant correlation with an  $R^2$  value of 0.414,  $p < 0.000$ . Adults include all individuals in the small, medium and large size classes.

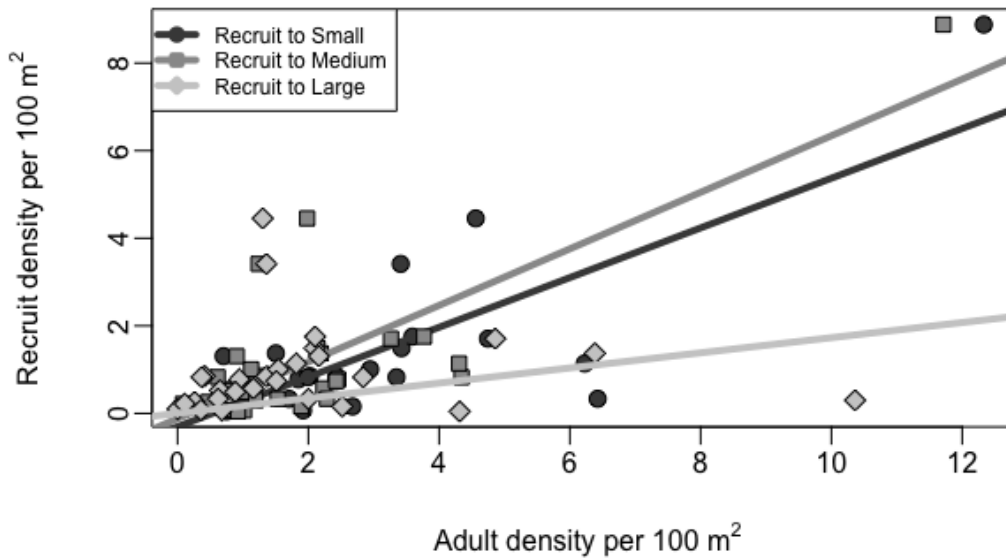


Figure 9. Correlation of recruit density to densities of adult size classes from surveys of *L. scutaria* in Kāneʻohe Bay, Hawaiʻi, 2018. All densities are given as individuals per 100 m<sup>2</sup>. There were significant positive correlations with recruit density to all three adult class sizes.

An ordinary linear regression was run to predict recruit density based on the percentage of clumped individuals (at least two individuals within 10 cm of each other) however no significant relationship was found ( $F(1,29) = 2.44, p = 0.129$ ). Also, an ordinary linear regression was run to predict asexual bud density by adult density but no significant relationship was found ( $F(1,19) = .758, p = 0.395$ ). Breaking this down further, there were no significant relationships found for asexual bud density to small adults ( $F(1,19) = 0.188, p = 0.670$ ), asexual buds to medium adults ( $F(1,29) = 0.399, p = 0.535$ ), or asexual buds to large adults ( $F(1,29) = 0.647, p = 0.431$ ).

## Discussion

The coral reefs of Kāneʻohe Bay have been affected by physical modification and sedimentation from dredging, freshwater kills, coral bleaching, and sewage-derived nutrient inputs. Yet, despite these stressors, coral reefs in the Bay have demonstrated resilience and increases in coral cover over the last 40 years (Stimson 2018). This study has shown a clear increase in the density of *L. scutaria* within Kāneʻohe Bay in the last 18 years. Rodgers et al. (2015) found that on average coral cover state-wide did not significantly change in the between 1999-2012 but change varied highly by site, with some locations seeing increases in coral cover while others saw decreases. So although this is a positive trend for the reefs of Kāneʻohe Bay, it cannot be extrapolated to reefs state-wide. Our findings were also corroborated by Stimson (2018) who also found that total coral cover in Kāneʻohe Bay had doubled from 2000 to 2015. He and others noted that this is a rare example of a reverse phase-shift, where corals reefs are overturned to algae dominated ecosystems but then shift back to coral dominated reefs (Hunter and Evans 1995; Bahr et al. 2015b, Stimson 2018).

In the abundance categorization and historical comparison map (Figure 4), some generalized patterns emerge. Most reefs in the North bay have had continued high abundance. The exception being the North Bay reefs nearest to shore. These reefs are most impacted by freshwater inundation during storm events (Bahr et al. 2015a). In the 2018 surveys, *L. scutaria* remains commonly abundant which indicates their slow recovery from the 2014 event. A surprising trend is the continued low abundance of some of the Central bay reefs. Stimson (2018) describes a lowering of the lowest low tide lines in the 1990s. This has caused these reefs to be exposed in extreme low tides and have very low coral cover on the reef flats. Finally, we see a general trend of continued low abundance in most of the South bay reefs.

## **Population size structure**

Analyzing population size structure in coral species can explain many characteristics of a population and is derived from both the growth of individual corals and the reproductive output of the population (Bak and Meesters 1998). Furthermore, population structures can inform us of the dynamics of environmental effects on these populations (Bak and Meesters 1999). Using four class sizes of *Lobactis scutaria* coral maximum diameter, the population size structures were unevenly distributed but showed no clear trend. The detailed size assessment showed a slightly positively skewed population bay-wide. A higher percentage of juvenile and small corals, as shown by a skew value of +0.25 indicates an expanding population as more individuals are being produced than are dying. Although this more detailed population size structure supports our survey results, that the population grew bay-wide in the last 18 years, to match our dramatic increases from the survey results, we would expect an even more highly skewed population. It is possible that small and extra small corals were simply missed in our surveys. Hendricks et al. (2012) showed that size correlated with detectability for the noble pen shell (*Pinna nobilis*) in surveys from the Mediterranean Sea and that smaller individuals were more likely to be missed by surveyors. If this occurred during our surveys, we could be under representing the number of sexual recruits, buds and other small individuals when in reality their actual numbers were even higher.

## **Effectiveness of management actions vs natural decline of algae**

It is widely seen that algae have a negative impact on coral species in general (Nugues et al. 2004; Smith et al. 2006). However, this survey found no difference in densities of *L. scutaria* on

reefs actively treated for invasive algae as compared to reefs which were not treated. Although, management efforts did in fact decrease the amount of invasive algae on reefs as compared to control reefs (Neilson et al. 2018), the lack of apparent impact on *L. scutaria* densities is likely due to the overall decrease of invasive algae bay wide. This dramatic decrease resulted from the diversion of semi-treated sewage from the bay in 1978 and a natural decline after a long period of rain and clouds in 2006 (Stimson and Conklin 2008). It is also possible that grazing by the green sea turtle contributed to this decline and that the present low levels of invasive algae seen today are a result of the sea turtle population expanding in the Hawaiian islands (Balazs and Chaloupka 2004) and shifting their diet to include more invasive algae species (Rodgers et al. 2015; Russell and Balazs 2015; Bahr et al. 2018). It would have been difficult to predict that this dramatic decline would happen naturally as there are few examples of this occurring at reef sites around the world. Without this natural decline, there may have been an even more pronounced decrease in algae cover on managed reefs compared to controls and possibly a link to the increase in *L. scutaria* densities would have been observed.

## **Sexual recruitment**

This survey found a surprising number of sexual recruits given prior survey results. Of the 1,107 extra small individuals counted in the 1999 surveys, only 5 were classified as potential sexual recruits (Lacks 2000). In 2018, I documented 1,160 sexual recruits which made up about 9.2% of all the individuals counted. It was unexpected to find this number of sexual recruits because they had not been previously observed to be abundant in Kāneʻohe Bay (Krupp 1983; Krupp et al. 1992; Lacks 2000; Kolinski and Cox 2007).

Coral recruitment is an important topic in coral reef conservation today. As reefs continue to experience bleaching events and environment degradation, their recovery will determine long term success (Baker et al. 2008). Sexual recruitment is an important part of this recovery process (Gilmour 2002; Price 2010; Hughes and Tanner 2013) but it is complicated and unpredictable. Algae can limit recruitment of coral larvae (McCook et al. 2001). Specific crustose coralline algae (CCA) species are required to induce settlement in some coral species (Harrington et al. 2004; Price 2010).

Considering all of these factors, the low numbers of sexual recruits observed on prior surveys in Kāneʻohe Bay may be attributed to the poor environmental conditions in past decades. The significant correlation of recruits to adult density indicates that there is a relationship between adults and the settlement of recruits in *L. scutaria*. It is known that space is a limiting factor in coral reefs, particularly for sexual recruits (Fairfull and Harriott 1999). In the 2018 surveys, it was clear that even in the North Bay reefs, which contained the highest coral cover in the bay, there was still ample space for recruitment, possibly due to the recent bleaching events. Because of this, as the population continues to increase, an even greater number of sexual recruits should be expected.

Despite warnings of global threats to coral reefs, there has been a clear increase in the abundance and density of *L. scutaria* in Kāneʻohe Bay, Hawaiʻi. In the immediate future, I anticipate that this increasing trend will continue but it is unclear for how long. With the diminished nutrient input into the bay and the invasive algae outbreaks kept in check through natural herbivory and management, the remaining major threats to the corals in the bay are freshwater floods and bleaching events caused by elevated seawater temperatures from global climate change. Kāneʻohe Bay has experienced bleaching events in 1996, 2014 and 2015 but

these events did not have long lasting effects as mortality was relatively low (Jokiel and Brown 2004; Bahr et al. 2015a; Stimson 2018) and there is some evidence that corals will be able to adapt to warmer temperatures (Coles et al. 2018).

Appendix

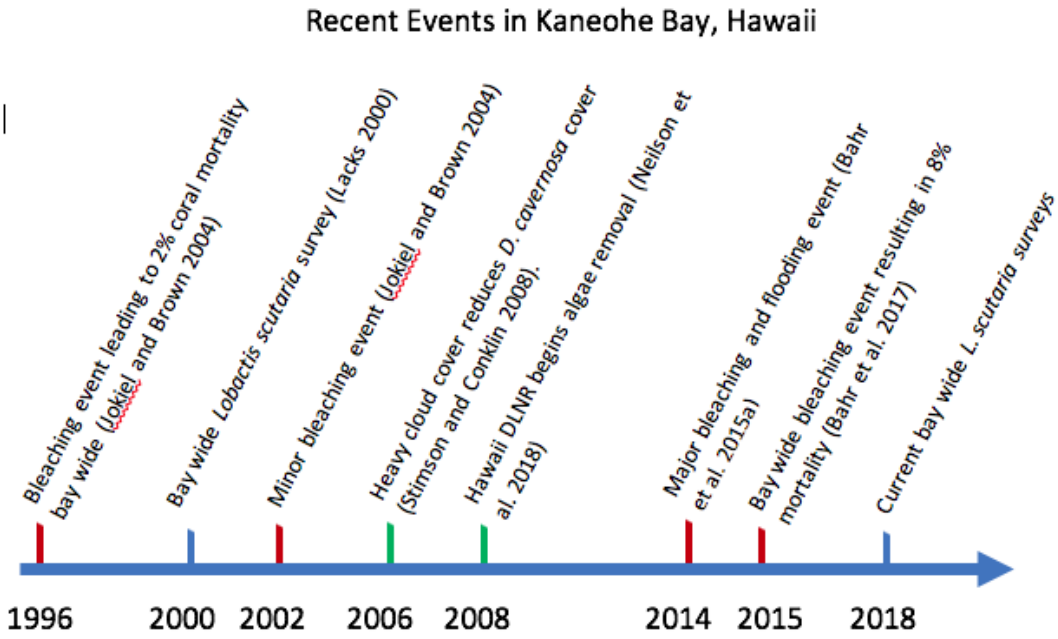


Figure 10. A timeline of recent events affecting the coral reef ecosystems of Kāne‘ohe Bay, with recent surveys for *L. scutaria* included for reference.

Table 1. Comparison of previous *L. scutaria* survey results. A = Abundant, C = Common, F = Few, N = None, H = High Abundance, L = Low Abundance, - = No data.

Reef	Bosch 1963 Rating	Maragos 1972 Rating	Lacks 2000 Rating	Johannsen 2018 Rating	Lacks 2000 Abundance	Johannsen 2018 Abundance
A	-	-	N	N	0	0
Coconut N	A	H	F	A	63	258
Coconut E	A	L	F	C	32	160
Coconut S	A	L	F	C	32	119
Cocunt W	A	H	R	F	8	20
Checker N	A	H	C	A	176	500
Checker S	A	-	F	A	44	541
Checker W	C	-	C	A	100	295
2	A	L	F	F	48	29
3	A	L	F	C	33	127
4	A	-	F	F	51	76
5	A	L	C	C	119	201
6	A	L	A	A	326	492
7	A	L	C	C	132	220
9	A	-	F	A	98	297
10	A	-	C	A	147	288
11	C	L	F	A	28	291
14	A	-	F	A	44	349
15	A	-	F	A	36	548
16	A	-	F	A	53	420
17	A	H	A	A	366	482
18	A	H	C	A	175	513
19	A	H	F	F	24	45
20	A	L	F	F	23	48
21	A	L	F	F	14	20
22	A	L	F	F	59	47
23	A	-	F	A	46	311
24	A	L	F	C	93	165
25	A	H	C	A	181	393
26	A	L	C	A	122	386
27	A	L	C	A	146	294
28	A	L	C	A	141	446
29	A	L	C	A	124	417
30	A	H	A	A	397	562
31	A	H	A	A	303	322
32	-	-	C	A	172	793
33	A	L	C	C	127	206
34	C	-	C	C	204	171
38	A	L	A	A	286	309
39	A	L	A	A	357	411
40	A	-	C	A	218	536
41	A	-	A	A	374	522

Table 4. Raw survey data from 42 sites in Kāneʻohe Bay, Hawaiʻi. Data was collected summer and fall of 2018 in a timed survey (1-man hour).

Reef	Abundance	Density (100 m <sup>2</sup> )	Recruits	Buds	XS	S	M	L	Crevices	Clumped	Dead	Area surveyed (m <sup>2</sup> )
A	0	0.00	0	0	0	0	0	0	0	0	0	6006
Coconut N	258	5.65	26	8	20	49	102	53	258	239	2	4570
Coconut E	160	4.00	21	29	22	31	31	26	159	143	41	4004
Coconut S	119	1.94	16	3	19	36	29	16	119	85	5	6132
Cocunt W	20	0.50	4	8	2	4	2	0	20	18	13	4040
Checker N	500	11.27	66	18	76	152	95	93	491	477	12	4437
Checker S	541	13.13	34	41	32	138	179	117	537	505	29	4121
Checker W	295	12.93	40	0	39	82	86	48	293	265	15	2282
2	29	0.79	8	0	4	10	3	4	26	25	0	3662
3	127	2.46	0	0	37	25	36	29	115	112	0	5169
4	76	1.29	0	31	12	15	9	9	76	66	22	5892
5	201	2.57	6	22	11	67	67	28	201	181	34	7818
6	492	10.33	37	107	98	88	117	45	491	475	18	4761
7	220	4.97	3	13	44	85	45	30	164	203	10	4427
9	297	6.62	38	8	24	109	57	61	201	278	7	4484
10	288	5.89	0	0	43	71	118	56	186	278	1	4891
11	291	5.50	45	0	53	107	64	22	275	287	0	5288
14	349	6.07	19	0	29	98	88	115	211	321	14	5745
15	548	13.62	12	0	27	44	48	417	30	533	3	4024
16	420	15.58	46	0	27	128	88	131	415	397	24	2696
17	482	17.15	32	17	86	175	121	51	482	445	4	2810
18	513	7.59	68	5	61	199	76	104	512	483	10	6755
19	45	4.62	0	0	7	13	9	16	43	37	0	975
20	48	7.56	1	0	2	17	12	16	48	31	18	635
21	20	4.00	0	10	0	4	4	2	9	15	10	500
22	47	4.61	5	0	11	12	10	9	42	33	1	1019
23	311	12.64	0	0	116	48	82	65	284	242	11	2461
24	165	2.19	0	0	57	43	29	36	124	139	66	7546
25	393	6.56	37	4	80	141	77	54	379	325	6	5987
26	386	8.36	0	68	55	70	67	126	365	378	8	4615
27	294	6.47	2	0	20	34	42	196	210	278	0	4542
28	446	11.76	52	0	12	57	83	242	425	436	0	3791
29	417	8.29	37	4	56	122	122	76	408	384	8	5029
30	562	13.37	14	4	152	270	96	26	411	523	3	4202
31	322	5.39	78	0	19	42	54	129	213	311	0	5969
32	793	97.78	72	0	100	100	95	426	429	751	12	811
33	206	6.35	0	0	83	60	48	15	171	170	13	3243
34	171	5.24	27	22	25	65	20	12	170	151	9	3262
38	309	11.71	0	0	41	99	109	60	210	224	15	2638
39	411	12.41	113	37	62	113	41	45	397	406	19	3311
40	536	43.61	37	0	128	233	93	45	419	481	10	1229
41	522	14.17	164	26	43	168	73	48	520	507	5	3683
Totals	12630	NA	1160	485	1835	3424	2627	3099	NA	NA	478	169462

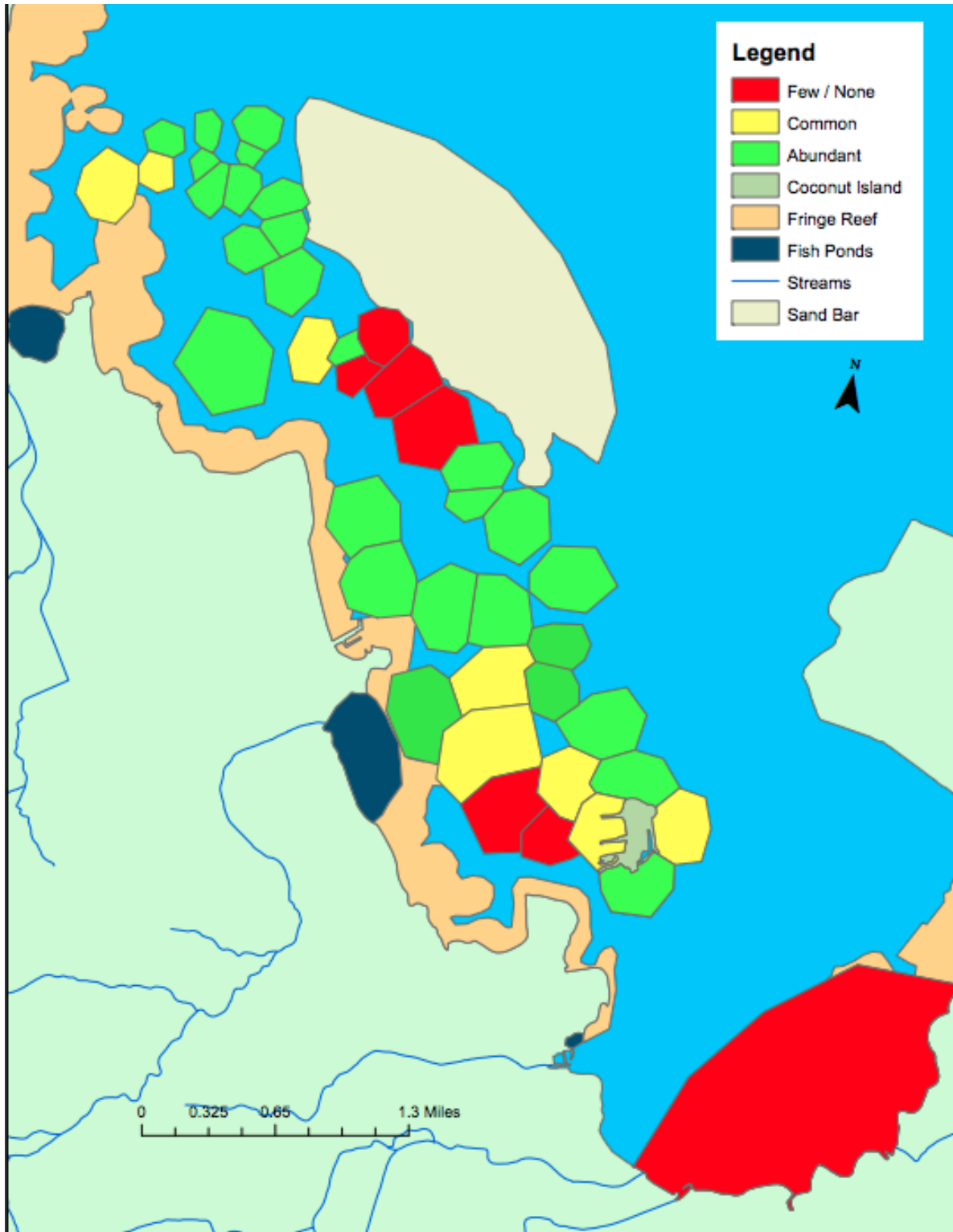


Figure 11. Abundance classifications of *Lobactis scutaria* for each site from 2018 surveys. Irregular polygons represent survey sites (exaggerated in scale for easier visualization) with abundance categories of “few/none” (red polygons), “common” (yellow), and “abundant” (green).

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