An ecological comparison of turf algae between two sites on West Maui that differ in anthropogenic impacts.

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Abstract

Kahekili Beach on the northwest coast of Maui, Hawaiʻi has experienced multiple blooms of native and non-native algae over the past 30 years. These blooms have been associated with run-off from agriculture, coastal development, golf courses, and the Lahaina Wastewater Reclamation Facility injection wells which are now known as the source for substantial wastewater delivery to the coast. Multiple studies have examined the macro-algae, fish and invertebrate communities associated with the wastewater seeps in the nearshore water at Kahekili. However, the turf algae community has never been characterized. Turfs are a functional group made up of small multi-species assemblages of algae that are hard to identify in the field. They are important as a major source of primary production and they can also trap sediments, smother corals and compete with other benthic species for space. For this study, plugs with turf algae were taken from dead *Porites* spp. coral heads at Kahekili Beach and Olowalu as a comparison site with relatively oligotrophic water. Plugs were examined for turf height, sediment load, percent cover and identification to the lowest possible taxon. Herbivore fish data were obtained from the State of Hawaiʻi Division of Aquatic Resources to assess whether herbivore biomass would influence differences in the turf community between sites. At both sites turf height was positively correlated with higher sediment loads, however at Kahekili, turf was taller near-shore at the seep area compared to Olowalu, where turf was higher in deeper water off shore. Olowalu had higher species richness and near the seeps at Kahekili, many of the plugs had only cyanobacteria. Herbivore biomass for grazers and browsers was similar at both sites but scraper biomass was higher at Kahekili. These results indicated that the submarine groundwater coming from the LWRF is impacting the turf community at Kahekili by reducing species richness, promoting growth of cyanobacteria, and allowing turf to grow taller and trap more sediment.

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Chapter 1

Coral reefs are among the most diverse and productive ecosystems on Earth. They are comprised of varied associations of plants and animals that thrive in oligotrophic tropical waters (e.g. Odum and Odum 1955, Connell et al. 1978, Littler and Littler 1984). Reefs provide many ecosystem goods and services such as food, recreation, protection from storms and high surf, links to other ecosystems, cultural values, medicine, and intrinsic beauty (Moberg and Folke 1999). Coral reefs worldwide are estimated to provide goods and services worth over $75 billion annually and over $1.6 billion from reef tourism activities alone (Pandolfi et al. 2005).

In 1955, Odum and Odum published the results from a 1954 expedition to the relatively unimpacted coral reefs at Eniwetok Atoll and provided an invaluable baseline for future research. The authors observed that the natural state of reefs is not always dominated by coral. As is characteristic of stable ecosystems, aquatic and terrestrial, there is a predominance of living plant biomass on coral reefs. Even though corals and fish are more conspicuous, small filaments of red, green, and brown algae as well as hidden macroalgae make up a large portion of the overall biomass on healthy coral reefs. Besides the visible algae, zooxanthellae and endolithic algae live within live corals. The high productivity of coral reefs is aided by the high surface area of organisms for metabolic activities, continous water movement, nitrogen fixing cyanobacteria and associated micro-organisms, and recycling of nutrients and organic matter (Odum and Odum 1955). Littler and Littler (1984) proposed that the term biotic reefs may be a more accurate term than coral reefs because corals are not always the dominant substrate and fast growing filamentous algae play a large role in productivity in many reef locations.

On reefs, turf algae are widespread and are a major source of primary production (Odum and Odum 1955, Littler and Littler 1984, Polovina 1984, Adey and Goertemiller 1987, Fong and

Paul 2011). Polovina (1984) constructed a mathematical ecosystem model, ECOPATH, to estimate standing stock and production of an entire reef at French Frigate Shoals, a remote reef in the Northwestern Hawaiian Islands. Benthic algae were the primary input for energy into this reef ecosystem model (Polovina 1984).

Today, many stressors affect biotic reefs globally. This review addresses turf algae in relation to reef ecology, sedimentation, herbivory, excess nutrients, and phase shifts in a changing climate with a focus on issues in Hawaiʻi, specifically on Maui.

Definition of turf and background

Marine algae as a whole are easily categorized in functional groups because of similar ecologies, but these plants are, at best, distantly related phylogenetically. Algae are ancient, diverse, and include members from two Kingdoms and at least four phyla including the prokaryotic Cyanobacteria, eukaryotic Chlorophyta, Rhodophyta, Ochrophyta and Miozoa (Lee 1999, Guiry and Guiry 2019). These plants are the primary producers on reefs, and provide reef structure, sand production, and nutrient recycling (Hay 1981, Polovina 1984).

There are four major functional groups of photosynthetic benthic organisms on reefs:corals with their symbionts, crustose coralline algae (CCA), macro-algae and turf algae (Littler and Littler 1984). While the species in most of these groups can be identified in the field, turf algae are more difficult because their small size requires a microscope or genetic assays for genus and species identification.

Algal turfs have a high surface area/volume ratio and are therefore able to take up nutrients in the water efficiently, grow quickly (Adey and Goertemiller 1987), and recover from grazing in as little as four days (Bonaldo and Bellwood 2011). An advantage of the turf growth form is persistance in areas with high herbivore abundance. Even though uprights may be eaten, the prostrate axes or crusts can regrow from basal remnants (Hay 1981, Littler and Littler 2013a). Often, nitrogen fixing cyanobacteria among the turf can enhance the growth of other species (Fong and Paul 2011).

The term “turf” has had several definitions over the last four decades. Hay (1981) defined turf as algae with upright branches taller than 0.5 cm that are packed so tightly that each axis is in contact with its neighbor(s). Algae taller than 0.5 cm that have a single attachment site and don't grow in tight clumps were not considered turf by Hay. Filamentous plants smaller than 0.5 cm that trap sediment were classified as algal mats and algae with a single attachment site and not growing in tight clumps were considered individuals. Thin, flat forms that adhere to the substrate were crusts. Hay concluded that these terms may not always be useful because of morphological plasticity found in algae. In addition, some species alternate between forms in different stages of their life history (Hay 1981).

In contrast, Klumpp and McKinnon (1992) described turf as “the multispecific and inconspicuous association of unicellular, and short (<1 cm), simple filamentous algae”. They used the term epilithic algal community (EAC) for the turf algae and included crustose coralline algae (CCA) (Klumpp and McKinnon 1992).

Crossman et al. (2001) described EAC as “a complex assemblage of filamentous and crustose algae, detritus- including dead organic matter (algae, fish feces and coral mucus), inorganic material, microbes, microalgae (diatoms, dinoflagellates and cyanobacteria) and associated meiofauna”. Because detritus can provide from 10 - 78% of the organic matter in the EAC, Wilson et al. (2003) suggested epilithic algal matrix (EAM) as a more fitting name to include living and non-living resources. Many have assumed that grazing fish are primarily eating algae, but some of the fish are selectively feeding on detritus (Crossman et al. 2001, Choat et al. 2002), non-living organic matter such as fish feces that settle from the water column. This category can often include living microbes such as bacteria, protozoans, algae, and fungi. The amount of detritus held in a turf species can depend on the height of the alga and its morphology. Additionally, mucus-like material in some algae can trap more sediment and detritus (Bowen 1987). Microbes may be one of the main sources of nutrients in detritus (Wilson et al. 2003).

In 2013, turf were commonly defined as "multispecies assemblages of diminutive, mostly filamentous algae that are from about 1 mm to 2 cm tall" (Littler and Littler 2013). They usually exist as assemblages and can be the small stages of macroalgae, fast growing filamentous species, cyanobacteria, diatoms, detritus and sediments. Turf assemblages have high diversity and often a high seasonal turnover. These plants can trap sediments, smother corals and compete with all other benthic species for space. Damselfish cultivate diverse turfs with high biomass (Hixon and Brostoff 1996, Littler and Littler 2013a).

Connell et al. (2014) reviewed the definitions of turfs from 109 papers published from 2005 – 2010 to encourage researchers to provide a more effective description with a common basis for comparison. "Turf" has commonly been used as a convenient catagory for multi-species, short algae that are hard to identify in the field. In many cases the term "turf" is used to describe short, densely branched algae that are a part of a community (Birrell et al. 2005, Clausing et al. 2014, Kelly et al. 2017). These broad descriptions might be suitable in studies focusing on other components of the benthic habitat, but when the study is specifically about turf, there is a need to provide more details such as species names so that meaningful comparisons can be made among studies and areas. Connell and colleagues suggested some parameters that need to be examined for turf such as species composition, height, morphology, growth form, reproduction, density, association with sediments, cover, and temporal persistance (Connell et al. 2014). Following Connell and colleagues, this study will consider turf as short, single or multi-species assemblages of algae. Specifically, turf height, percent cover, association with sediment and species composition are examined to better understand the turf community at experimental sites on West Maui, Hawai‘i.

Turf species richness studies

More than 200 algal species qualify as turf in Hawai‘i. Most are small, filamentous species, but some can be alternate phases of macroalgae or juveniles of macroalgae (Abbott 1999, Huisman et al. 2007). Few studies have examined species richness or even attempted species identification of turfs in Hawai‘i (Smith 1992, Stuercke and McDermid 2004, Smith et al. 2010). Researchers working on Maui reefs have grouped turf into functional groups (Kelly et al. 2016) or classified all short algae as turf (Vermeij et al. 2010a, Ross et al. 2012, Sparks et al. 2016, Williams et al. 2016, Kelly et al. 2017). To correctly identify most of the species in the turf, they need to be intact, examined microscopically, fertile, and not heavily grazed (Abbott, 1999).

Harris et al. (2015) examined the turf community at multiple spatial scales in the Maldives. In a hierarchical sampling design, the authors documented variability in cover, canopy height, species richness and composition. The least amount of variability in assemblage composition was on the largest scale of kilometers, possibly from well-mixed oceanographic conditions. In contrast, the highest variablity was on a scale of centimeters (Harris et al. 2015).

Some of the work conducted in Hawai‘i has examined turfs to species level, not just a functional group aspect. Stuercke and McDermid (2004) examined species composition at two sites on the opposing sides of the island of Hawaiʻi. Turf samples collected over 12 months represented 102 species. Thirty-eight species were new records for the island of Hawaiʻi, and many of the new records were among the most abundant species found (Stuercke and McDermid 2004). An earlier study quantitatively sampled intertidal algae on Oʻahu and Hawaiʻi Island, documenting over 100 species (Smith 1992). Sixty species identified were considered turf (Smith 1992). A third study assembled a species list of 105 species from a settlement study in 10m water depth at Puako, Hawaiʻi, identifying 59 genera among red, green and brown algae as well as three cyanobacteria (Smith et al. 2001). In all, 92 of the species were reported as turf.

Traditionally, reef ecologists have placed algae in functional groups as assemblages rather than separate individuals (Hay 1981). Littler and Arnold (1982) proposed placing algae into functional groups based on productivity using net photosynthesis as an indicator. The groupings followed previous research that showed forms with higher surface area to volume ratios outproduced species with lower surface to volume ratios (Littler and Arnold 1982). Steneck and Dethier (1994) further refined those categories by characterizing seven functional groups ranging from single cell microalgae to crustose algae. These groups are designated by plant size, anatomy and complexity (Steneck and Dethier 1994).

It is important to know the species composition in marine habitats for many reasons. Genetic diversity is important for maintaining ecosystem health (Connell et al. 1978, Wilson 1992). Herbivore feeding preferences may be more important in maintaining algal diversity than physical habitat (Lubchenco 1978, Littler et al. 1983, Hixon and Brostoff 1996, Hay 1997) and some algal species may be able to outcompete coral (McCook 2001, Jompa and McCook 2003a, Barott et al. 2012).

Crustose coralline algae

Crustose coralline algae (CCA) are important members of marine environments worldwide with the highest diversity found in tropical reefs (Littler and Littler 2013b). As members of the Division Rhodophyta (red algae), CCA appear pink because of the white, calcite-calcium carbonate deposits between their cell walls. They are of great importance on reefs because they form the wave resistant algal ridge in the surf zone (Littler and Littler 1984; 2013b), occur on all hard substrates, and even grow on other marine organisms from the upper intertidal zone to depths of 295 meters, which makes them the deepest known plant life on earth. There are more than 1,600 described living species of CCA and possibly many more to be discovered (Littler and Littler 2013b). CCA can be fast growing, early colonizers, but most are slow growers that can tolerate nutrient limitation. These plants have many ecological survival strategies, including chemical defenses and hard structures that resist grazing pressure (Klumpp and McKinnon 1992). Crusts provide micro-habitats for small invertebrates and chemically attract coral larvae settling on their surfaces (Harrington et al. 2004). Sea urchins, parrotfishes, surgeonfishes, limpets, and chitons feed on CCA (Littler and Littler 2013b). Crustose corallines may also prevent settlement of fast-growing opportunistic seaweeds (Gomez-Lemos and Diaz-Pulido 2017). In Hawaiʻi, Vermeij et al. (2011) showed that CCA can lower growth and recruitment success of the green alga *Ulva lactuca*. In experiments on the Great Barrier Reef, Gomez-Lemos and Diaz-Pulido (2017) found evidence of allelopathy, microbial inhibition, and epithallial tissue sloughing against settlement of spores of *Padina boergesenii*. These defenses and growth strategies enable CCA to compete for space on the reef.

The Relative Dominance Conceptual Framework.

Littler and Littler (1984) introduced the Relative-Dominance Paradigm (RDP) to predict the dominant reef biota under different environmental conditions (Figure 1). The authors recognized four space-occupying groups of sessile organisms: corals, coralline algae, frondose macro-algae, and microfilamentous algae. They all compete for space and light, and each one can dominate under its preferred conditions. The interactions of environmental and biological factors can determine the outcome of competition for space on a reef. Environmental conditions such as nutrient levels are considered to be bottom-up controls and biological factors such as herbivory are top-down controls. Corals were predicted to dominate when algae are under intense herbivory and algae were predicted to dominate with elevated nutrient levels. With low nutrient levels and low to moderate herbivore grazing, turfs were predicted to dominate. With high nutrient levels and high herbivory, coralline algae were predicted to dominate. Corals and coralline algae build the $CaCO_3$ reef framework and provide complexity to support the diverse reef community (Littler and Littler 1984), yet other species are important as food for upper trophic levels (Polovina 1984).

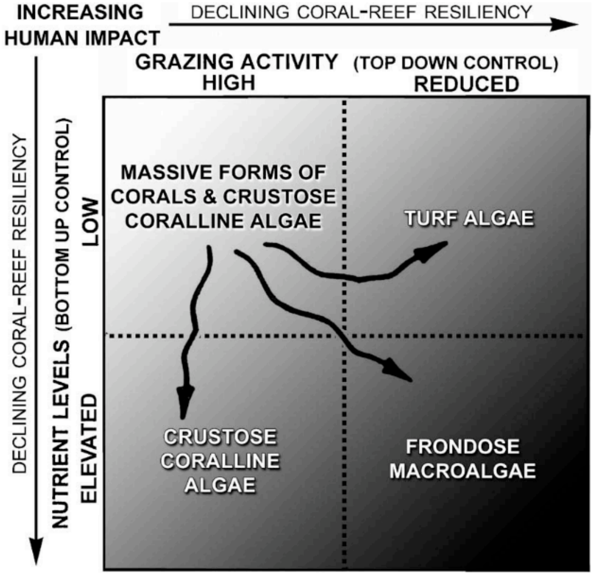

Figure 1. Diagram of the Relative Dominance Model showing four groups of sessile reef organisms. Dominance of each group is a function of long term levels of nutrients and herbivore biomass. Herbivores are considered to be the most important controller of standing algal stocks on undisturbed reefs (Littler and Littler 1984, Littler et al. 2006).

Smith et al. (2010) first tested the relative dominance model in a field experiment with cages and fertilizer on a reef at Puakō, Hawai‘i. This experiment was run over a period of 18 months. In plots with cages and no fertilization, filamentous turf dominated. However in cages with fertilizer, mixed asemblages of fleshy turf and macroalgae were the dominant components. After 420 days, the cages were removed and turf algae were quickly consumed. This work demonstrated a significant response in the algal community to increased nutrient levels and decreased herbivory over a short amount of time. Importantly, this tells us that phase shifts can happen quickly with the right conditions, even in those regions with almost 100% coral cover as was the case at Puakō (Smith et al. 2001; 2010). The results of this experiment provided relevant experimental evidence to support the relative dominance paradigm as a conceptual model (Littler and Littler 1984).

Littler et al. (2005) revisited the RDP with a complex, two year investigation on the Belize Barrier Reef. The site is a well-developed reef system with healthy coral growth and naturally low nutrient levels. Numerous studies have been conducted at this location for over a quarter of a century, so the authors had detailed information on both biotic and enviromental factors. When nutrients are elevated on reefs that naturally have low nutrient levels, and herbivory is low, turf and macro-algae growth will increase. Even high levels of herbivory will not prevent algal growth when nutrient levels are increased. The combination of low nutrients and high herbivory may facilitate the growth of crustose coralline algae and coral. In addition, this and other studies suggest that elevated nutrient levels not only promote the growth of algae, but they can inhibit the settlement and growth of reef building corals (Littler et al. 2006).

Competition between turf algae and coral

Intense intra- and interspecific competition drives algal communities, as all algae and corals compete for space on the reef (Lirman 2001, McCook et al. 2001, Jompa and McCook 2003a, Barott et al. 2012, Ferrari et al. 2012, Littler and Littler 2013a, Bonaldo and Hay 2014, Cetz-Navarro et al. 2015). As a functional form, turfs are especially successful on heavily fished reefs with reduced herbivory. Turf can also outcompete corals at the initial stages by inhibiting coral larval settlement when turf is covering all available hard substrate (Birrell et al. 2005, 2008, Diaz-Pulido et al. 2010).

As herbivory decreases on over-fished reefs, algae can become dominant in areas that once had coral. Bonaldo and Hay (2014) studied the frequency and extent of coral-seaweed contact in three no-take Marine Protected Areas and three adjacent unprotected areas in Fiji. In an experimental manipulation, allelopathic algae species *Chlorodesmis fastigiata* and *Galaxaura filamentosa* were transplanted next to five coral species in the field. The following species of corals were chosen because they were common and included a range of taxonomic groups: *Acropora aspera, Montipora digitata, Pocillopora damicornis, Porites cylindrica,* and *Porites lobata*. Their results suggested that *C. fastigiata* and *G. filamentosa* can rapidly damage corals and damage is more extensive in unprotected areas where the grazing pressures are lessened. The authors also pointed out that a canopy of non-allelopathic species such as *Sargassum* and *Turbinaria*, may help protect corals from intense solar radiation during bleaching events (Bonaldo and Hay 2014).

It is often assumed that algae have a competitive edge over corals. However, different species or functional groups of algae may have different effects on corals. Jompa and McCook (2003b) compared the effects of *Anotrichium tenue* with mixed species turfs on massive *Porites* spp. corals on the Great Barrier Reef. Observations and monitoring showed that most of the live coral tissue died when it was overgrown by *A. tenue*. There was a pattern in which the alga colonized live coral tissue usually at the boundary between dead coral skeleton and mixed algal turfs. The filaments of *A. tenue* trapped sediment which may have enhanced damage to the coral tissue. *A. tenue* filaments disappeared from the dead coral and appeared to colonize adjacent live coral tissue. The dead coral tissue was then colonized by cyanobacteria and within one to two months, the massive *Porites* coral heads were covered by mixed-species filamentous algal turfs. The same patterns were seen on other growth forms of corals including foliose *Turbinaria* spp.*,* encrusting to foliose *Montipora* spp., and branching *Porites annae* corals*.* The authors suggested that the alga produces allelochemical substances because mixed algal turfs without *A. tenue* were relatively harmless to corals. However, they did not test this (Jompa and McCook 2003b). *Corallophila huysmansii,* a turf algae, was found to over-grow and kill *Porites cylindrica* (Jompa and McCook 2003a). In experimental manipulations, algal species *C. huysmanii*, *Hypnea pannosa,* and *Chlorodesmis* spp. were placed next to healthy *Porites* coral colonies. *Hypnea* and *Chlorodesmis* had minimal effect on the coral while *C. huysmansii* caused considerable damage to live coral tissue (Jompa and McCook 2003a). These examples reinforce the need to look at algal species individually rather than only as functional groups.

Smith et al. (2006) found that corals growing in close proximity to turf algae had higher rates of bacterial infection. Algae released dissolved organic carbon (DOC) which gave the bacteria an increased substrate to grow on. The bacteria created a hypoxic zone which in turn killed the coral. The study showed that with the use of the antibiotic ampicillin, coral mortality was prevented. The authors suggested that this effect is concentration dependent and would be more pronounced in areas with high DOC. While algae contributes to DOC levels, waste water influx into the reef could also increase DOC levels (Smith et al. 2006).

Sediment impacts and interactions with algae

Sediments are a natural part of reefs. Examples of reef-produced sediments are carbonate particles from coral, coralline algae, foraminifers and urchin tests. They can also be siliceous sediment particles from sponges and diatoms. Land-based sediment comes from erosion and can be fine to coarse silt (Purcell 2000). Sediment accumulation in turf is patchy with many factors that vary at multiple spatial scales (Airoldi and Virgilio 1998).

Sedimentation from coastal runoff has degraded coral reefs globally (Fabricius 2005). Sediment directly smothers corals and traps nutrients, thereby facilitating algal growth (Rogers 1990, Purcell 2000, Stimson and Larned 2000, Nugues and Roberts 2003, Fabricius 2005). Benthic nutrient sources within sediment may include excretion by macrofauna and meiofauna, groundwater discharge, nitrogen fixation by cyanobacteria, and other organic matter in the sediment (Wilson et al. 2003). Sediments can retain nutrients and act like slow-release fertilizer that can nourish algae even when the nutrients in the water column are low (Stimson and Larned 2000).

Algae can facilitate trapping of sediments. In a quantitative study of sediment trapping by macroalgae on the south shore of Molokaʻi, Hawaiʻi, Stamski and Field (2006) found that while there was on average over 75% carbonate sand on the bottom, the sediment in macroalgae was on average 59% fine-grained terriginous sediment, suggesting a strong role for algal morphology trapping fine-grained sediment from land. In areas where sediment was trapped by macroalgae, the algae percent cover was higher. During calm conditions, the fine sediment was held by algae, but when waves and currents picked up the sediment was re-suspended. Algae can become a sediment sink if the particles stick to algae, but they can also become a source when the algae dies or wave and current action cause them to become re-suspended. Either way, algae can increase the residence time of sediment with sediment re-suspended multiple times (Stamski and Field 2006). Purcell (2000) found a positive correlation with sediment load in small branching turfs but a negative correlation between sediment and CCA. Turf height varied in different reef zones with varying amounts of water motion (Purcell 2000). In areas of low flow, sedimentation becomes a significant factor in turf algae winning the competion with corals for space on the reef (Gowan et al. 2014).

Nugues and Roberts (2003) observed that reef areas with increased sediment also had high biomass of turfs. This effect increased with proximity to a rivermouth with its increased sediment loads. The authors studied 198 coral colonies of *Colpophyllia natans* and *Siderastrea* spp. and found that once corals were covered with sediment, mixed turf algae overgrew the coral. Without sediment, algae had minimal impact compared to sediment and algae acting together (Nugues and Roberts 2003). Sediment also covers hard substrate and prevents coral larvae from settling (Jokiel et al. 2014).

Bellwood et al. (2008) examined effects of natural sediment loads in turf algae on rates of herbivory of those algae on the Great Barrier Reef. To test if sediment would inhibit herbivory, turf consumption by fish was quantified in an area with natural sediment and in experimental plots where sediment had been removed. Remote video documented fish feeding and quantified changes in standing stock of algae with sediment and after removal of sediment. They found a rapid 3.8 fold increase in feeding rates in the treatment plots where the sediment had been removed. Further, within four hours of sediment removal, algal length was reduced by approximately 64%. The authors observed that parrotfish *Scarus* spp. and *Chlorurus* spp. are predominantly detritus feeders and prefer to feed in areas where inorganic sediments form a smaller proportion of particulate matter in the EAM. Their research showed that with sediment removed, the resident algal species were highly palatable to a wide range of herbivores. Many studies have looked at anthropogenic sediment, but this study examined the carbonate sediment that is produced on a reef. Parrotfish and surgeonfish in the genus *Ctenochaetus* are key to removal of these sediments from the system. If sediments affect rates of herbivory and algae can trap more sediment, this may create a positive feedback loop that could lead to a stable state of sediment rich turf (Bellwood et al. 2008). This experiment demonstrated the potential effects of natural reef-based sediment loads to synergistically add to turf production.

Herbivore impacts and interactions with algae

Healthy tropical reefs have high grazing levels by abundant and diverse herbivorous fishes (Randall 1961) and sea urchins (Ogden and Lobel 1978). Herbivory can determine the abundance and distribution of seaweeds (Littler and Littler 1984, Smith et al. 2001, 2010) and support co-evolution of additional algal traits such as toughness, chemical, and morphological defenses (Hay 1997). Primary productivity by algae on reefs is naturally high and kept in balance by the top-down actions of herbivores (Grigg et al. 1984). Many studies have shown that algal turfs thrive and expand when grazers are removed (Littler and Littler 1984, 2005, Hughes 1994, Smith et al. 2010). As predicted by the relative dominance model, we can expect that the removal of herbivorous fishes will release top-down controls and can give algae more of a competitive edge for space on a reef (McCook et al. 2001).

There are differences in feeding mechanisms among herbivores (Hamilton et al. 2014, Kelly et al. 2016). Browsers bite or tear benthic algae, and grazers mainly eat detritus either by rasping or sucking (Ogden and Lobel 1978). Parrotfishes are classified as scrapers and are important for opening up hard substrate for recruitment by corals (Green and Bellwood 2009). Tebbett et al. (2017) sampled fish species *in situ* and in aquariums to determine feeding preferences. Two surgeonfish, *Acanthurus nigrofuscus* and *Ctenochaetus striatus*, were apparantly both feeding on turf. However, *C. striatus* with its comb-like teeth was not good at tearing off turf, and fed mostly on detritus and sediment within the turf as a grazer. In comparison, *A. nigrofuscus* with spatulate teeth capable of tearing algae was primarily browsing on the algae in the turf. Both species fed on some early successional turfs that were smaller and more easily removed. The authors were able to confirm observations by examining the gut contents of the fish (Tebbett et al. 2017). Categorizing organisms into functional groups helps managers understand their ecology within the ecosystem. These relationships become especially important in ecosystem-based management.

Nutrients impacts and interactions with algae

Szmant (2002) evaluated numerous reports on the effects of nutrient enrichment and other stressors on coral reefs such as sediment, turbidity, storms, physical damage, disease, and over-fishing. While there is evidence that high levels of nutrients relax nutrient limitations, if intense herbivory is present, then effects of nutrient enrichment may not be measurable by excess algal growth (Szmant 2002). However, as predicted by the RDP, in experiments with nutrient addition and caging, the treatments inside cages had more algae biomass than treatments outside cages that were open to herbivores (Smith et al. 2001, Thacker et al. 2001, Gil et al. 2016).

Even though coral reefs exist in oligotrophic tropical latitudes, high islands often have natural nutrients from upwelling, streams, and submarine groundwater discharge, which can result in substantial water column productivity (Smith et al. 2001, McManus and Polsenberg 2004, Gove et al. 2016). In the test of the relative dominance paradigm at Puakō, Hawaiʻi, only ~ 4-6 μM of nitrogen was added to the reef, but the algal communities changed dramatically in response to that small input (Smith et al. 2001). Those data also suggest that many plants are nutrient limited on Hawaiian reefs (Smith et al. 2001).

Kāneʻohe Bay is a classic example of anthropogenic nutrients and algae. After the sewage was re-routed outside the bay in 1977, the water clarity improved but *Dictyosphaeria cavernosa* (green bubble algae) continued to grow as its morphology allowed the plant to sequester nutrients diffusing from underlying sediments (Stimson and Larned 2000). Because coral reefs typically require high water flow, sewage and nutrient pollution seem to be more problematic in harbors, bays, and other areas with reduced water circulation (Szmant 2002). At regional scales, areas with high nutrient levels may also have increased levels of terrestrial runoff, making it hard to distinguish the effects of nutrients from the effects of freshwater input, sediment and other pollutants (Fabricius 2005).

With changing environmental conditions, benthic cyanobacterial mats (BCMs) are becoming dominant components on reefs worldwide (de Bakker et al. 2017). They are favored in nutrient rich, over-fished and warmer reefs. They can inhibit coral larvae from settling (Kuffner et al. 2006) and produce toxins that may deter herbivorous fish (Nagle and Paul 1999). Brocke et al. (2018) investigated cyanobacterial diversity and nitrogen fixation rates of multiple BCMs on the coral reefs of Curacao. They collected and incubated cyanobacterial patches from the reef and identified them by morphological and molecular analyses. All of the species collected fixed nitrogen and rates were 3-10 times higher during daylight. Additionally, the species found were part of the turf community in previous studies, indicating that changing environmental conditions favored existing species (Brocke et al. 2018).

In West Maui, the historical record for nutrients in near-shore water generally shows high but varying levels of input. For instance, Soicher and Peterson (1997) concluded that in 1990 wastewater injection appears to have been the greatest contributer to groundwater nitrate in the Lahaina region with an estimated 82,000 kg/yr injected into the groundwater. Agricultural practices associated with sugar cane production were a close second (68,000 kg/yr) and pineapple ranked third (12,000 kg/yr) (Soicher and Peterson 1997). Later, Laws et al. (2004) found a mean concentration of 8.2 μM for total dissolved nitrogen at North Beach (Kahekili), approximately 100 meters south of the injection well south seep group that was sampled in future studies. It is interesting to note that roughly 100 meters off shore, nutrient and turbidity levels were on par with open ocean conditions, suggesting nutrients were land based (Laws et al. 2004).

Stressors on coral reefs

Worldwide, reefs are facing multiple stressors such as climate change, unsustainable fishing practices, and land-based pollution. It is estimated that 22% of reefs worldwide are classified as threatened from land-based pollution and soil erosion (Fabricius 2005). Over the last few decades, coral reefs have been transitioning from coral-dominated to algae-dominated ecosystems world wide (Done 1992, Hughes 1994, Mccook 1999, Bellwood et al. 2004, Smith et al. 2006, 2016, Hughes et al. 2007, Bruno, et al., 2009, Vermeij et al. 2010).

It is often assumed that seasonal weather patterns do not vary as much in the tropics compared to other regions around the globe and that tropical ecosystems should have generally stable conditions that would allow high levels of complexity and biodiversity (Littler and Littler 2005). Even though the tropics do not experience great changes in temperature throughout the year, there are natural causes of disturbance on reefs such as seasonal storms and changes in day length. In a study that spanned 38 years, Connell et al. (2004) observed that reefs were not stable but dynamic systems.

By 2017, human induced warming of air and sea surface combined, reached about 1.0°C above pre-industrial levels and temperatures are currently increasing at approximately 0.2°C per decade (IPCC, 2018). This warming is leading to sea level rise and more intense storms which increases land-based sediments on reefs. Greenhouse gasses are also changing the chemistry of the oceans, turning them more acidic. Rising sea level will affect where waves break, potentially causing increased shoreline erosion and increased sediments on reefs (Storlazzi et al. 2004). Temperatures of only 2° C above normal will cause Hawaiian corals to bleach on a regular basis. Hawaiʻi has already experienced widespread, large-scale coral bleaching events in 1996, 2002 (Jokiel and Brown 2004), and more recently in 2014, 2015 (Sparks et al. 2016, Williams et al. 2016), and 2016 (Pers. Obs.). Another state-wide bleaching event is currently underway (August/September 2019).

Jamaican reefs have been studied since the 1950s and changes have been documented as a result of large disturbance events such as hurricanes. Despite chronic overfishing, the effects on the reef were not obvious for many years. For example, the decline of fish predators on sea urchins resulted in an increase in urchin abundance. The urchins were maintaining algae at low levels and masking the impacts of fishing to the coral reef ecosystem. From 1982-1984, a species-specific pathogen caused a massive die-off of *Diadema antillarum* urchins. Due to the relaxation of herbivory pressure, there was a massive algal bloom and resulting phase shift from a coral dominated ecosystem to an ecosystem dominated by algal species of *Sargassum, Lobophora, Dictyota*, and *Halimeda*. Even the most abundant and robust coral *Montastrea annularis* declined to 0-2% cover by 1993 (Hughes 1994).

In many cases, there isn't an absolute or even relative baseline of what is normal and healthy for most reefs. In many "baseline surveys" algae were most likely underestimated (Odum and Odum 1955, Polovina 1984). There were few studies before the 1970s, but even by then, many anthropogenic changes such as over-fishing in the Caribbean were already taking place. Remote Pacific reefs may be better indicators of pre-anthropogenic conditions, but they still have global stressors such as ocean warming (Bruno et al. 2014). National Oceanic and Atmospheric Administration–Coral Reef Ecosystem Division (NOAA–CRED) surveys of 46 remote Pacific reefs found that macroalgal cover ranged from 10 - 30% and averaged 22% on atolls as remote and relatively pristine as Johnston, Wake, Kingman, Palmyra, and the Northwest Hawaiian Islands (Bruno et al. 2014). They explained that their study only looked at macroalgae because turf is rarely quantified accurately (Bruno et al. 2014).

There is a common perception that coral reefs should be predominately coral but that is not always the case. Vroom et al. (2006) also examined data from (NOAA-CRED) studies of remote reefs. An average of 7.1 - 32.7% live coral cover was reported from "healthy" reefs. At French Frigate Shoals in the Northwest Hawaiian Islands all but one of the 94 surveyed sites had more algae than coral. In 69% of the sites, turf occupied more space than coral (Vroom et al. 2006). This may seem surprising because these areas are so remote and far from anthropogenic stresses. Klump and McKinnon (1992) examined the community structure, biomass, photosynthesis-irradiance relationship, and primary productivity of the EAC on the Great Barrier Reef (GBR) over different seasons and habitats. They estimated that the EAC covers up to 80%

on reef flats and up to 50% on reef slopes throughout the GBR and contributes much to reef productivity (Klumpp and McKinnon 1992). Although localized areas on reefs may be coral dominated, various zones support different dominant organisms. Crustose coralline algae and *Halimeda* spp. are often the most important organisms for reef accretion and can be confirmed by coring studies (Vroom 2011). Ultimately, the pre-anthropogenic state of reefs is highly variable and region specific due to differences along environmental gradients between reef zones, even on the same island. Corals typically dominate in many of the relatively pristine locations, but as documented in the CRED surveys a wide range of coral reef ecosystems exist. This is an important perspective because it tells us that without algae, there would be no tropical reef ecosystem. However, algae remain an understudied part of the reef.

In the 21st century, the balance of disturbance and recovery seems to be shifting more towards disturbance. Coral reefs undergo phase shifts where algae replaces coral as the dominant cover on the benthos. At some point, certain reefs reach tipping points. If the community is not resilient, it is unable to recover to the pre-disturbance state and the result may be an alterative stable state which is algae dominated (Done 1992, McCook 1999, Miller 2015). These alternative stable states may be from global impacts such as climate change or local impacts such as over-fishing, sedimentation and nutrient influx, which can give algae a competitive edge over coral (McCook et al. 2001).

West Maui, an area in distress

A consequence of disturbance is that it creates opportunities for new species to take hold (Miller 2015). In some cases, the disturbance is human-induced such as the introduction of the alien invasive *Hypnea musciformis*, to Kāneʻohe Bay on Oʻahu in 1974 (Smith et al. 2002). By

1978, that alga had spread to Maui and by the late 1980s it formed massive blooms on the shallow reef flats around the island. Most of the blooms were in areas with higher than normal levels of nutrients from cesspools and agricultural run-off (Hodgson 1994). At the height of the *H. musciformis* blooms, the rotting seaweed on the beach smelled so foul that property values and occupancy in hotels and condos dropped. The Maui economy lost an estimated $20 million a year during the 1990s and 2000s when the blooms were at their peak (Van Beukering and Cesar 2004, Waddell et al. 2005).

There have been several algae blooms along West Maui since the mid-1980s. Some blooms were from alien invasives, but there were also massive blooms of *Cladophora sericea*, which is a native that can form seasonal blooms when nitrogen or phosphorus levels are high (Smith et al. 2005). Sources of excess nutrients to nearshore waters in West Maui include the Lahaina Wastewater Treatment Facility (LWTF) effluent that is pumped into injection wells, cesspools, septic tanks, golf courses, and landscaping. In the past, sugar and pineapple plantations most likely contributed, but the Pioneer Mill sugar plantation closed in 1999 and Maui Land and Pine stopped harvesting pineapple in 2009 (Glenn et al. 2012). Most of the lands have been left fallow since the last harvests or repurposed into housing.

Sources of nutrients entering into the ocean can be difficult to detect because waves, currents and mixing of water can dilute elevated nutrient levels. The ratio of the stable isotope of $\delta^{15}N$ and $\delta^{14}N$ can distinguish between sources of nitrogen. Dailer et al. (2010) collected multiple algal species from intertidal waters island-wide and used $\delta^{15}N$ values within the algal tissues to determine whether elevated N values were from sewage or other sources. The highest $\delta^{15}N$ values were at two sites near Kahekili Beach Park north of Lahaina, suggesting that wastewater was flowing from a nearby wastewater treatment facility through the groundwater and seeping out onto the reef. Further, these were the highest $\delta^{15}N$ values ever reported in the scientific literature (Dailer et al. 2010). In another study, Dailer et al. (2012) placed small cages containing algae at different depths for a 3-dimensional bioassay of nutrients on the reef at Kahekili. Because the water coming out of the seeps is low salinity it is less dense and floats above the denser ambient salt water. This experiment detected significantly higher levels of $\delta^{15}N$ values in algae grown near the surface over the freshwater seeps (Dailer et al. 2012). The normal currents along this shoreline flow from North to South (Storlazzi et al. 2006, Storlazzi and Field 2008). As expected, there were increased $\delta^{15}N$ values to the south of the plumes (Dailer et al. 2012).

Hunt and Rosa (2009) used a multiple *in situ* tracer approach to detect plumes from the sewage treatment plants at Kihei and Lahaina, both on the island of Maui. They were able to map out plumes using parameters such as salinity, pH, DO, and contaminants such as fabric brighteners and caffeine, which would not normally be found in seawater. The authors found that the most detectable tracers were pharmaceuticals, organic waste indicator compounds, and highly elevated $\delta^{15}N$ values in water samples and in algal tissue. They measured the dissolved inorganic nitrogen (DIN = NO_2 + NO_3 +NH_4) concentrations at 3 submarine springs at Kahekili with concentrations between 51.7 to 62.1 µM as compared to 1.6 to 3.2 µM in the water column (Hunt and Rosa 2009). In a more recent study, fluorescein and rhodamine dyes were added to the effluent in the injection wells at the Lahaina Wastewater Reclamation Facility (LWRF) (Glenn et al. 2012). Only one dye was detected from warm, brackish submarine springs within 3 - 25 meters from shore at Kahekili Beach. It took a minimum of 84 days and an average of over seven months to reach the ocean. Groundwater coming from the seeps in June 2011 had NO_3- + NO_2- values ranging from 13.6 to 28.7µM. For this study, they used Honokowai Beach Park, Wahikuli

Wayside Park, and Olowalu as comparison sites. Because Honokowai was about 1.8 km north of the LWRF, it was a possible place of effluent emergence if the flow was to the north. Wahikuli was used because it was close to the submarine springs location. Olowalu was chosen to represent water with minimal anthropogenic impact because agricultural operations ceased in 1999 and little development has transpired since. The site is about 12 miles south of the LWRF. All of the locations showed little to no freshwater influx and no evidence of tracer dye (Glenn et al. 2012). (Murray et al. 2019) took cores from two *Porites lobata* coral heads within an active seep area from the LWRF and one from about 150 m to the south to detect changes in δ^{15}N values sources to the reef system at Kahekili Beach Park. From these cores the authors constructed a temporal record of δ^{15}N in the water at each of the sites. δ^{15}N values in the coral cores at the seep increased rapidly from less than 8 to over 16 ‰ in one year beginning in 1996. The increase in δ^{15}N corresponded to the use of biological nutrient removal by heterotrophic denitrification that was initiated in 1995 to treat wastewater at the LWRF prior to injection. From October 2011 to May 2014 an EPA mandate required the effluent from LWRF to be chlorinated prior to injection (Murray et al. 2019). Chlorination was thought to suppress denitrifying microbes metabolism which could result in an a return to high levels of DIN discharge (EPA 2004). In July 2013, mean DIN concentrations from vent groundwater at Kahekili was reported at 72.6 µM ± 15 SE (Swarzenski et al. 2017). Full UV disinfection has been in use since May 2014 (Murray et al. 2019). However, conventional secondary biological treatment and full UV disinfection do not completely remove the nitrogen and phosphorus and may convert the organic forms into mineral forms which makes them more usable for algae growth (EPA 2004). Prouty et al. (1018) sampled nutrients and carbonate chemistry every four hours during two 3-day periods from 16-24 March 2016 at the vents at Kahekili. They reported nitrate concentrations near the seeps that ranged from 0.45 to over 70 µM, with an average nitrate concentration of 117 ± 0.09 SE µM measured directly from the discharging seep water. (Prouty et al. 2018). In March 2016 the average seawater nitrate $\delta^{15}N$ value at the seeps was over + 70 ‰ (Murray et al. 2019).

A lawsuit initiated by Hawaiʻi Wildlife Fund, the Sierra Club, Surfrider Foundation and West Maui Preservation Association was filed against the county of Maui in April, 2012 for violations of the Federal Water Pollution Control Act, (the Clean Water Act). In 2014, the County of Maui was found to be in violation of the Clean Water Act. The county appealed this decision to the 9th district court and lost in February, 2018. The county appealed to the U.S. Supreme Court and in February 2019 the U.S. Supreme Court accepted that case. On September 20, 2019 the Maui County Council voted to settle the case and not take it to the U.S. Supreme Court.

Kahekili Herbivore Fisheries Management Area (KHFMA) was established in 2009 in response to algae blooms in the Kahekili area. The premise was that increasing herbivore abundance could help control the overgrowth of algae. The KHFMA encompasses about three kilometers of coastline from Hanakaʻōʻō Beach to the southern end of Honokowai Beach Park. (*State of Hawaii Kahekili HAR* 2009). This stretch of coastline is known as Kaʻanapali Beach and has several resorts that are built close to the shore. This area is heavily used by tourists and residents for snorkeling, scuba diving, fishing and other water sports because it is easily accessible (Williams et al. 2016). At Kahekili Beach Park, coral cover declined from about 55% in 1994 to about 35% in 2006 (CRAMP data E. Brown, pers, comm.). In response, the State of Hawaiʻi, Division of Aquatic Resources (DAR) proposed a fishery management area to increase herbivore biomass with a goal of keeping algae biomass at healthy levels. The KHFMA was established in 2009 and now it is illegal to fish for parrotfishes (Scaridae) surgeonfishes (Acanthuridae), chubs (Kyphosidae) and sea urchins (Echinoidea) but legal to catch other fishes (State of Hawaii, Kahekeli HAR 2009) in the KHFMA.

Williams et al. (2016) conducted intensive fish and benthic surveys at KHFMA and comparative sites starting 19 months before the adoption of the new fishing rules and continued six years after to assess the efficacy of the fishery management area. Since the KHFMA was established, biomass of some species of parrotfish and surgeonfish has increased significantly. In addition, there was a five-fold increase in CCA cover. There was a mass coral bleaching in 2015 and as a result, many of the corals died. This made it difficult to determine if the KHFMA has been beneficial to corals since the study was published. Additionally, many of these reef fish (especially the surgeonfish) have long life spans so it will take more time to assess this management strategy (Williams et al. 2016).

Williams et al. (2016) noted, however, that turf were the dominant algae with little macroalgae. They observed a wide variety of algal turf communities from sparse heavily grazed turfs to thick mixed turf assemblages. The authors commented "Since these different types of turf communities likely have different ecological roles on the reef, in hindsight it would have been desirable to distinguish between different turf types" (Williams et al. 2016). This statement highlights the need for more detailed study of turfs.

Donovan et al. (2018) gathered data from seven monitoring programs of fish and benthic assemblages in the main Hawaiian Islands to describe spatial variation and ecological patterns in species composition and diversity over time. A majority (97%) of the data were from the years between 2000 and 2013. They characterized five reef regimes in the main Hawaiian islands as:

1. Low coral cover and fish biomass (especially predators); benthos dominated by turf algae.

2. High fish biomass (mostly grazers/scrapers); benthos dominated by turf algae.
3. Moderately high fish biomass in all fish functional groups, high coral and turf algae with no macroalgae.
4. Moderately high fish biomass in all functional groups, benthos with high coral cover and a combination of turf algae, macroalgae and other.
5. Moderate fish biomass in all functional groups with lower predator biomass, highest coral cover, high CCA and comparatively low turf algae.

After two years in regime 4, Kahekili transitioned to 1 and recovered to 5 after fish biomass increased with the establishment of the KHFMA. These data support the findings in other studies that having a healthy supply of herbivores can support reef resilience and lead to a healthier reef ecosystem (Donovan et al. 2018).

What parameters are typically used to define a healthy reef and how does turf algae fit into the picture? Currently there is some consensus with high species diversity, high fish biomass, presence of apex predators, low disease, and the ability to accrete calcium carbonate faster than erosion as parameters that most researchers would agree on (Vroom 2011). The predictions of the relative dominance model can be seen as general tendencies, but there are many environmental factors to consider for the effective management of reefs (Littler and Littler 1984). It is important to adopt an ecosystem based approach that takes into consideration all organisms and not just focus on select groups, such as corals, as indicators of a healthy reef. It is time to take a better look at the turfs because they are major components of healthy reefs and necessary for the primary production of complex reef food webs (Odum and Odum 1955, Littler and Littler 1984, Polovina 1984a, Adey and Goertemiller 1987).

In 2011, the U.S. Coral Reef Task Force (USCRTF) adopted a resolution to take action to address the state of coral reef management and science. The USCRTF partnered with the National Ocean Policy (NOP), National Ocean Council (NOC), State of Hawaiʻi, and local agencies to identify priority watersheds for management and restoration. Kaʻanapali was one of three watersheds in the U.S. chosen for restoration because the reef had declined since monitoring was initiated, but was not completely dead and management efforts such as the KHFMA were already in place. The major goals were to address sustainable land practices to reduce pollution, restore regional terrestrial and aquatic ecosystems, and increase resiliency and adaptation to climate change (coralreef.gov). Adopting a Native Hawaiian management approach by starting at the top of the mountain and extending to the reefs (ridge to reef; *māuka* to *mākai*), working groups identified needs and formulated local action strategies between 2011 and 2014.

The priority watershed designation coupled with algal blooms, effluent from the sewage treatment plant, and declining reef health at Kahekili Beach have focused considerable research effort in the study area. A long-term monitoring partnership between the University of Hawaiʻi Coral Reef and Monitoring Program and the State of Hawaiiʻi, DAR conducts annual surveys of benthic communities and fish assemblages. The University of Hawaiʻi (UH), U.S. Geological Survey (USGS), DAR, and the State of Hawaiʻi Department of Health (DOH) have been mapping and monitoring the sewage effluent seeps since 2008 (Smith et al. 2005, Hunt and Rosa 2009, Dailer et al. 2010, 2012, Glenn et al. 2012, Swarzenski et al. 2017, Prouty et al. 2018, Murray et al. 2019). Ross et al. (2012) mapped out a large area of the reef at Kahekili to characterize the reef into zones related to the health of corals. They documented large "dead zones" with high turf algae cover (Ross et al. 2012).

Researchers studying this area have concluded that herbivores are mainly eating turf algae and they are doing so at higher levels than one might expect relative to the amount of turf available (Kelly et al. 2016). With the protection of herbivores at Kahekili, the gap between turf and macroalgal production and turf and macroalgal growth has been shrinking. Kelly et al. (2017) reported that turf algae covered 41.2% of the reef at Kahekili, but little is known about how they grow and what species thrive there (Kelly et al. 2017). Even after six years of intense surveys at Kahekili, Williams et al. (2016) noted that turf algae occupies a large part of the reef, and it would be desirable to characterize the benthic algal community more carefully (Williams et al. 2016). In addition, Connell and colleagues suggested some of the parameters that need to be examined in relation to studies on turf algae are species composition, density, height, association with sediments and cover (Connell et al. 2014).

Consequently, this thesis seeks to characterize the turf community at Kahekili Beach and add to the existing knowledge concerning the impact around the submarine groundwater seeps. I hypothesize that the turf canopy height, cover and species composition of the turf community will be different at the location where the seeps release water from the LWRF than at locations that do not have sewage seeps. To test this hypothesis, I will examine the turf canopy height, sediment retention in relation to turf canopy height, percent turf cover, and community composition of turfs growing on dead *Porites lobata* heads at Kahekili Beach. Olowalu, a control site for other studies at Kahekili (Glenn et al. 2012), was chosen as a comparison because the site resembles the reef at Kahekili in terms of depth and other environmental conditions, but has minimal anthropogenic impact.

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Chapter Two

Introduction

The Northwest coast of Maui is a popular tourist destination known for its sandy beaches and fringing reef. From historical data, Kahekili Beach in Kaʻanapali has experienced changing conditions associated with run-off from agriculture, coastal development, golf courses, and the Lahaina Wastewater Reclamation Facility (LWRF) injection wells, which are now known as the source for substantial wastewater delivery to coastal regions (Soicher and Peterson 1997; Dailer et al. 2010; Glenn et al 2012). A positive flow path from the injection wells to Kahekili Beach was unequivocally established when fluorescein and rhodamine dyes were added to the effluent stream in two of the wells. One dye was detected emerging from warm, brackish submarine springs within 3 - 25 meters from shore at Kahekili Beach. It took a minimum of 84 days and an average of over seven months to reach the ocean (Glenn et al. 2012).

At Kahekili Beach, there have been multiple blooms of native and non-native algae over the past 30 years (Hodgson 1994, Smith et al. 2005); coral cover has declined from about 55% in 1994 to about 30% in 2017 (CRAMP, unpublished data). These events and corresponding changes in the reef ecosystem have stimulated studies to understand causal mechanisms. Dailer et al. (2012b) demonstrated that invasive algae have faster growth rates under conditions of elevated nutrients found in wastewater. Laws et al. (2004) found a mean concentration of 8.2 µM for total dissolved nitrogen (TDN) at North Beach (Kahekili), approximately 10 meters from the shoreline and 100 meters south of the then unknown seeps, the only sites where samples were taken for this study. While 8 µM is not generally considered excessive, TDN concentrations were consistently below the HIDOH standards (7.86 µM) at distances of 40 m or more off shore, suggesting nutrients were land-based and became diluted with distance from shore (Laws et al. 2004). Further, in the Puakō, Hawaiʻi test of the relative dominance paradigm, turf communities grew dramatically with only a reduction in herbivore grazing (Smith et al. 2001). Even small increments of change in physical and biological parameters can cause change in reefs (Smith et al. 2001; 2010).

The Kahekili Herbivore Fishery Management Area (KHFMA) was established in 2008 and is the first Fishery Management Area (FMA) of its kind in Hawaiʻi. The KHFMA was designed to increase herbivore abundance in hopes that this would also reduce periodic algal blooms that have occured along that coastline. The KHFMA regulations allow fishing for many species, but the take of any herbivorous surgeonfishes (Acanthuridae), parrotfishes (Labridae, tribe: Scaridae), chubs (Kyphosidae), and sea urchins (Echinoidea) is prohibited.

Since the establishment of the KHFMA, the injection wells have changed management routines (Glenn et al. 2012). Prior to October 2011, the LWRF did not treat for bacteria, allowing substantial de-nitrification to occur as the plume moved to the coast (Glenn et al. 2012). In that interval, nitrate concentrations via seeps to the reef were as low as 5 µM and macro-algae biomass dropped to background levels (Fackrell et al. 2016; per obs). From October 2011 to May 2014, an EPA mandate required the effluent at LWRF be chlorinated prior to injection (Murray et al. 2019). Chlorination was expected to suppress pathogens as well as denitrifying microbes, which would result in a return to high levels of DIN discharge (EPA 2004). In July 2013, mean DIN concentrations from seep groundwater at Kahekili were reported at 72.6 µM ± 15 SE (Swarzenski et al. 2017). Full UV bacterial disinfection has been in use since May 2014 (Murray et al. 2019). However, conventional secondary biological treatment and full UV disinfection do not completely remove the nitrogen and phosphorus and may convert the organic forms into mineral forms which makes them more usable for algae growth (EPA 2004). When Prouty et al. (2018) sampled nutrients and carbonate chemistry every four hours during two 3-day periods from 16-24 March 2016 at the seeps at Kahekili, nitrate concentrations near the seeps ranged from 0.45 to over 70 µM, with an average nitrate concentration of 117 µM ± 0.09 SE measured directly from the discharging seep water (Prouty et al. 2018). In March 2016, δ^{15}N values for water at the seeps was over 70 ‰ (Murray et al. 2019), consistent with spatial patterns and δ^{15}N values reported by Dailer et al. (2012a).

Recent studies have reported large areas of the reef where corals have died and turf algae have become dominant (Ross et al. 2012, Williams et al. 2016). The term "turf" has commonly been used as a convenient category for multi-species assemblages of algae that are from about 1 mm to 2 cm tall and hard to identify in the field (Littler and Littler 2013). On tropical reefs, turfs are widespread, diverse, and are a major source of primary production (Odum and Odum 1955, Hatcher and Larkum 1983, Littler and Littler 1984, Polovina 1984, Adey and Goertemiller 1987, Smith 1992, Abbott 1999, Stuercke and McDermid 2004, Smith et al. 2010, Fong and Paul 2011, Connell et al. 2014, Harris et al. 2015, Kelly et al. 2017). Because turfs have a high surface-area to volume ratio, they can thrive in relatively low nutrient regimes as in oligotrophic water (Adey and Goertemiller 1987). Turf occur naturally in high abundance on many reefs; even on remote tropical reefs that have no local anthropogenic influences (Polovina 1984, Vroom et al. 2006). In addition to their role as primary producers, these small plants can trap sediments, smother corals, and compete with other benthic species for space.

Littler and Littler (1984) introduced the Relative-Dominance Paradigm (RDP) to predict the dominant reef biota under different environmental conditions. The authors recognized four space-occupying groups of sessile organisms: corals, coralline algae, frondose macro-algae, and filamentous turf algae. They all compete for space and light under conditions of extreme nutrient limitation, yet each group can dominate under a combination of conditions. Environmental conditions such as nutrient levels are considered to be bottom-up controls and biological factors such as herbivory are top-down controls. Corals are predicted to dominate when algae are under intense herbivory, and frondose macro-algae can dominate with elevated nutrient levels and reduced herbivory. With low nutrient levels and low to moderate herbivore grazing, turfs are predicted to dominate and with high nutrient levels and high herbivory, coralline algae are predicted to dominate. Even in a state of having one functional form dominant, other groups are still cryptically present on reefs, allowing for rapid transitions from one state to another as regulating factors change (Smith et al. 2001).

In healthy reefs, herbivores exert top down control and can eat most of the algae that are accessible, above coral fingers and reef texture (Grigg et al. 1984, Littler et al. 2006, Smith et al. 2010 and others). Typically, this condition results in coral-dominance. Phase shifts from coral-dominated to algal-dominated reefs can occur when anthropogenic stressors such as warming water associated with climate change negatively impacts competitive coral-algal interactions and/or excess nutrients and sediment from land stimulate algal growth (Done 1992, McManus and Polsenberg 2004, Hughes et al. 2007, Bruno et al. 2009, Fung et al. 2011). Reefs near human population centers often experience higher levels of nutrients from sewage and fertilizers as well as land-based sediments (Hunter and Evans 1995, Laws et al. 1999, Stimson and Larned 2000, Fabricius 2005, Dailer et al. 2012a, Houk et al. 2014, Risk 2014, Abaya et al. 2018, Lapointe et al. 2019). Nutrient enrichment can impact the competitive balance between herbivory pressure and algae (Hatcher and Larkum 1983, Jompa and McCook 2002, Littler et al. 2009, Smith et al. 2001; 2010). Sediments can impact reefs with direct smothering of coral (Rogers 1990, Nugues and Roberts 2003, Fabricius 2005) and some herbivores are deterred from eating sediment-laden turf (Bellwood et al. 2008, Clausing et al. 2014, Gordon et al. 2016). In addition, sediments can increase nutrient levels (Stimson and Larned 2000) and be repeatedly re-suspended with water motion (Storlazzi et al. 2004, Stamski and Field 2006, Ogston and Field 2010).

This study will examine turf algal communities associated with the KHFMA and contrast them to turf communities at Olowalu, a non-managed site approximately 12 miles south of the KFMA boundary. These sites were chosen because of the differences in multiple anthropogenic stressors that impact the two areas.

Past studies (e.g., Smith et al. 2005, Dailer et al. 2012b, Williams et al. 2016, Kelly et al. 2017) have focused on macroalgae from the perspective of the RDP, but as coral reefs become more stressed, the importance of knowing about turf grows. This study aims to add to the knowledge and highlight the diversity of turf algae on reefs.

Specifically, these are the questions:

1. What are the common turf species in shallow reef regions and do turf communities vary between sites with different anthropogenic impacts?
2. Will the turf height differ between two sites? Is there a relationship between turf height and sediment load?
3. Will percent cover of turf vary between sites?
4. Is there a difference in the biomass of fish herbivore functional groups between sites that may be influencing turf species richness, turf height, and cover?

Methods

Site selection

Sub-surface groundwater seeps at Kahekili Beach Park have been well documented (Hunt and Rosa 2009, Dailer et al. 2010, 2012a, Glenn et al. 2012, Fackrell et al. 2016, Swarzenski et al. 2017, Prouty et al. 2018) to carry nutrients from the LWRF to the adjacent near-shore reef (Figures 2.1 and 2.2). In order to compare how an algal turf community would differ across reefs with different land use practices and management regimes, samples were collected at two sites. Olowalu (Figure 2.3) was chosen as an alternate site to Kahekili because it has a similar sun exposure, depth, and coral community but minimal anthropogenic nutrient input. Sugar cane was grown on West Maui above both sites from the late 1800s to 1999 (Engott and Vana 2007). Since the sugar mill closed in 1999, the land has become fallow. Today, there are a few houses in the area and the highway runs along the shore. Seawater from this site has low values for nitrogen and phosphorus (Dailer et al. 2010, 2012b, Glenn et al. 2012). Olowalu is on the dry side of the West Maui Mountains, but when it rains, there are several nearby streams that deposit land-based sediment onto the reef (pers. obs.). The wave climate at Olowalu is typically influenced from southerly swells during the summer in contrast to northwest swells in the winter at Kahekili (Moberly and Chamberlain, 1964). Olowalu is subject to the standard State of Hawaiʻi rules and regulations for areas with open access to fishing.

Sample collection

Turf samples were taken at Kahekili Beach Park on 15 June 2016 and Olowalu on 17 June 2016. A summer sampling time was chosen for optimal turf algae growth and the short sampling interval minimized temporal variation. All of the samples were taken from the horizontal surface of dead *Porites* spp. coral heads under the State of Hawaiʻi permit # DLNR SAP 2016-54.

At Kahekili, samples were collected starting at a visible freshwater seep (N 20°56.314, W 156°41.575) about 10 meters from the shoreline at the south seep location documented by Glenn et al. 2012 and others. Warm fresh water was flowing freely from the seeps at the time of collection. In addition, gas bubbles were seen rising from the substrate in the proximity of the seeps. Divers created a grid pattern at 10 m intervals, in which the first sample was collected at the seep and subsequent samples were taken at successive 10 m offshore or down current from the seep at a depth range from 1.8 - 3.7 m (Figure 2.4). A total of 12 dead coral heads were sampled and at each coral head, five 1.33 cm^2 area plugs were taken of turf algae. Four of the plugs were used as subsamples (N=96). The fifth plug from each coral head was taken to the Maui Ocean Center and allowed to grow out to help clarify taxonomic composition. Plugs were taken using a 1.3 cm diam grommet punch and mallet to a depth less than 1 cm into the calcium carbonate dead coral skeleton. Plugs were situated approximately 10 cm apart for each coral, as in Harris et al. (2015). Care was taken to not damage live coral and to retain all sediment in the turf samples. Each plug was placed immediately into a separate marked and sealable vial. All plugs were preserved in 10% formalin to await further analysis. At Olowalu, a similar grid was established approximately 10 m from shore at N 20°48.552, W 156°36.388 with water depths ranging from 0.6 to 4.6 m.

Lab analyses

To examine taxonomic composition, each plug was examined under a dissecting scope and turf algae were removed with forceps and placed in 0.1% solution of HCl for five minutes to dissolve calcium carbonate in calcified turf and bits of coral that adhered to the holdfasts. Next, samples were stained using a 1% solution of aniline blue and placed on a slide with a 30% solution of Karo syrup and sterile seawater to make permanent slides (Tsuda and Abbott 1985). Slides were examined to identify turf algal specimens to the lowest possible taxon. The total number of algal taxa per plug were recorded for each sample. Permanent slides, photographs, and detailed drawings were made to create an archival taxonomic reference. The majority of specimens were identified to genus because they lacked identifying features for species level identification (Figure 2.5). Abbott (1999), Abbott and Huisman (2004) as well as (Huisman et al. 2007) were used for identification. The fifth plugs from the grow-out at Maui Ocean Center were not used in the analysis because their open system water flow introduced other species of algae.

Turf height was measured under a microscope at six haphazardly chosen places on each plug using a digital caliper (DCLA-0605 High Quality Electronic Digital Vernier Caliper, Vinca Clockwise Tools with accuracy of ± 0.02mm; repeatability ± 0.01mm and resolution of 0.01mm). Data were recorded to the nearest 0.5 mm.

To examine sediment load on preserved plugs, a small paint brush and rinse bottle with artificial seawater (Instant Ocean, 34 ‰ salinity) were used to remove all sediment while viewing each plug under a dissecting scope. sediments were then filtered onto preweighed #1 Whatman filter paper circles (Mettler Toledo AG104 digital analytical balance) and rinsed with DI water to remove salt. Filters with sediment samples were dried at 60 ^{o}C for one week and then reweighed for dry weight of sediment in grams for each turf sample.

Percent cover of turf algae was determined from preserved (N=96) samples. Plugs were photographed with a Canon EOS Rebel T5i camera on a LMscope macroscope camera stand with 12x microscopic lens attachment (Micro Tech Lab, Graz, Austria). Photogrid (2003(c) C.

Bird Photogrid) was used to superimpose 50 points onto each image and the points were identified as bare skeleton, crustose coralline algae, or turf algae. Percent cover of these categories was determined by dividing the number of points for each substrate category by the total number of points on the projected image.

Data Analysis

Non-metric multi-dimensional scaling (nMDS) analysis coupled with a Similarity percentage (SIMPER) test were conducted using PRIMER v. 7 (Clarke & Gorley 2001) to examine differences in algal turf community composition between Kahekili and Olowalu. The data matrix consisted of presence/absence data by unique taxon for each turf plug within a colony. Site was used as a categorical factor. A Bray-Curtis similarity matrix was created from the presence/absence data matrix prior to conducting the nMDS.

A species accumulation plot in PRIMER v. 7 (Clarke & Gorley 2001) was used to estimate the number of samples needed to characterize the taxonomic composition of the turf assemblages at each site. Six S extrapolators (Chao 1, Chao 2, Jacknife 1, Jacknife 2, Bootstrap, and Michaelis-Menton) were selected to compare the asymptotes of each species accumulation curve (*S)*. The Michaelis-Menton (MM) is the only parametric model and returns the predicted asymptote of the hyperbola fitted to the cumulative *S* curve.

A general linear mixed model in the R statistical software (ver. 3.5.1, *lmer* in the *lmerTest* package) was used to examine differences in turf height (mm) between sites (Kahekili, Olowalu) with depth (m) and sediment (g /cm^2) as continuous covariate predictors (R Core Team 2018). Distance from the start point of the sampling grid was not used in the model because exploratory plots and preliminary models revealed a strong correlation between depth and distance at each site. The random factor examined the effect of depth between colonies nested in site. Turf height data were square-root transformed to meet the assumptions of normality (Zar 1999). The fixed effect or effect of interest in the model was site – Kahekili and Olowalu. Raw data were plotted for ease of interpretation. The p-values for the t-statistic at $\alpha = 0.05$ were based on a Satterthwaite approximation for denominator degrees of freedom.

Differences in percent turf algae cover between sites were examined using a general linear mixed model in the R statistical software (ver. 3.5.1, *lmer* in the *lmerTest* package). A logit transformation was used for percent turf algae cover to meet the assumptions of normality because the range of values was >20% and <80% (Starcevich 2013). The p-values for the t-statistic at $\alpha = 0.05$ were based on a Satterthwaite approximation for denominator degrees of freedom.

Fish herbivore biomass data for these sites in 2016 were obtained from the State of Hawai‘i, Division of Aquatic Resources (DAR) to examine differences between sites in herbivore functional groups and how they might impact algal turf communities. Three functional groups were used, grazers that mainly eat turf (e.g., *Acanthurus* spp., *Zebrasoma* spp.), scrapers that clear the substrate (e.g., *Scarus* spp., *Chlorurus* spp.), and browsers that mainly eat macroalgae (e.g., *Naso* spp., *Kyphosus* spp., *Calotomus* spp.). A detailed description of the DAR fish survey methodology is available in Sparks et al. (2015). A factorial ANOVA generalized linear model in Statistica (TIBCO Software, 2018) was used to examine differences in fish herbivore biomass (g/m^2) of the three functional groups (browsers, scrapers, grazers) between Kahekili and Olowalu. Site and functional group were treated as fixed factors with fish herbivore biomass as the dependent variable. The error distribution was modeled using a gamma distribution with an identity link function.

Results

Thirty-five taxa from four phyla were identified from a total area of 124.4 cm^2 across both locations (Table 1). Twenty four taxa were identified from Kahekili samples (0.39 taxa/cm^2) and 31 were identified from Olowalu samples (0.50 taxa/cm^2). There were nine distinctly different specimens that did not have enough material to place them at genus level; they were numbered and listed as unknowns 1-9. The most abundant taxon was *Sphacelaria* spp. (Phaeophyceae) followed by *Gelidiopsis* spp. (Rhodophyta), and *Gelidiella* spp. (Rhodophyta), as well as multiple unidentified Cyanobacteria. Many others were rare and only found on a few samples. The largest number of taxa found on a single plug (1.33 cm^2) at Kahekili was 13 and 17 at Olowalu. Cyanobacterial mats and no other visible algae were found for eleven plugs at Kahekili but only one plug at Olowalu. The species accumulation plots reached an asymptote at between 25-30 total species at Kahekili depending on the estimator used (Figure 2.7). The MM estimator predicted an asymptote of 25.5 total species at Kahekili. At Olowalu, an asymptote was not as apparent suggesting more samples were needed to fully characterize the turf assemblage. The MM estimator predicted an asymptote of 33.8 total species at Olowalu, which was almost half the number of species that the Chao 1 and Chao 2 estimators predicted (Figure 2.7).

At Kahekili, 34 of 48 plugs had cyanobacteria and those photosynthetic bacteria contributed substantially to the similarity among samples within the site (46.9% similarity). *Sphacelaria* spp. was the second most common taxon and was present in 32 of 48 samples at Kahekili.

At Olowalu, average similarity of 36.9% was calculated for all samples. *Sphacelaria* spp. was the most common taxon (present on 40 of 48 samples) and contributed 41.3% to the similarity among samples. *Gelidiopsis* spp. was the second most common and was present on 26 samples.

There was an average dissimilarity of 66.7% between the two sites with cyanobacteria (10%) contributing the most to the difference followed by *Gelidiopsis* spp. (9.42%; Table 2). There was substantial amount of overlap at the two sites in terms of taxonomic composition (Figure 2.6).

There were no statistically significant differences in turf height between Kahekili (1.19 mm ± 0.15 SE) and Olowalu (2.33 mm ± 0.23 SE). At both sites, turf height varied as a function of water depth, although this factor was not statistically distinct for the two sites ($t = 1.94$, $p = 0.057$; Figure 2.8). At Kahekili, turf algae were taller near-shore and within the seep area but shorter with increasing depth. At Olowalu, the opposite pattern was detected; turf heights were shorter in shallow areas near-shore and taller in deeper water off-shore.

At both locations, more sediment was present with greater turf height ($t = 2.78$, $p = <0.01$; Figure 2.9). Turf samples from across the Kahekili sampling grid tended to have lower average sediment loading ($0.057\ g/cm^2 \pm 0.007$ SE) than found for comparable samples at Olowalu ($0.067\ g/cm^2 \pm 0.008$ SE) but this was not statistically different. However, when considering depth, turf height and sediment load at Kahekili decreased moving away from shore with increasing depth. The opposite relationship with depth was seen for turf height and sediment load at Olowalu ($t = -2.55$, $p = 0.01$).

Samples from Kahekili had significantly higher percent cover of turf as a mean (83.9% ± 1.9 SE) than did plugs taken from Olowalu (82.0% ± 2.1 SE), when all depths were pooled ($t = 2.67$, $p < 0.01$; Figure 2.10). There was a significant relationship between depth and percent cover; however these relationships were not consistent between sites. Samples taken from

Kahekili had greater cover in deeper water rather than shallow. In marked contrast, sample plugs from Olowalu revealed that coverage by turf was greater in shallower water ($t = -2.76$, $p < 0.01$). At both sites, if turf cover was greater, then canopy height was shorter. This opposite relationship was also seen in the association between cover and sediment accumulation. Sediment load had a positive relationship with turf height, but a negative relationship with turf cover (Figures 2.9, 2.11).

Overall, mean fish herbivore biomass was higher at Kahekili (12.4 g/m^2 ± 1.7 SE) than Olowalu (9.6 g/m^2 ± 0.7 SE) but was not statistically significant (estimate = 1.4, $W = 3.7$, $p = 0.055$). Examining functional groups indicated that mean biomass for scrapers from both sites was significantly higher than browser biomass at both sites (estimate = -6.7, $W = 77.0$, $p < 0.0$), but a significant interaction term (estimate = -1.8, $W = 5.8$, $p = 0.16$) indicated that scraper biomass was relatively higher at Kahekili (20.8 g/m^2 ± 2.4 SE) than at Olowalu (14.6 g m^2 ± 1.4 SE; Figure 2.12). Even though mean scraper biomass was slightly higher than grazer biomass, this was not a significant difference (estimate = 0.06, $W = 0.0$, $p = 0.95$) and the relationship was consistent between sites (estimate = 0.15, $W = 0.0$, $p = 0.88$).

Discussion

Olowalu – a relatively healthy West Maui reef.

The most common algae in Olowalu's shallow reef region included *Sphacelaria* spp., multiple cyanobacteria species, *Gelidiella* spp., *Gelidiella* spp., *Herposiphonia* spp. and *Polysiphonia* spp. Turf height varied from 0.5 mm- 5.8 mm at this site with turf growing taller in deeper water between 3-4 meters deep. There was also a significant relationship between turf height and sediment load (0.01 – 0.26 g/cm^2) where taller turf in deeper water samples retained more sediment. This was expected because in shallower water close to shore, waves and water motion tend to remove sediments and re-suspend them in the water column but in deeper water, with less water motion the sediment is easily trapped in the algae (Purcell 2000, Stamski and Field 2006, Gowan et al. 2014). Turf percent cover had an opposite relationship with turf height and sediment load; where height and sediment were higher, turf percent cover was lower. Although Olowalu is known to have a low nutrient loading, Olowalu is not a pristine site. It has stress from sediment and fishing pressure as shown by fish scraper biomass such as parrotfish, which were significantly lower at Olowalu that at Kahekili. However, the turfs were highly grazed and many of the samples showed evidence of regrowth from nibbled tips. The scrapers do not nibble the tips; they tend to scrape down to the substrate (Green and Bellwood 2009). Given the similar herbivore biomass for grazers that preferentially eat turf, and the fact that turfs are fast growing, herbivory was probably not a significant factor in the small differences for turf height and cover between sites.

Olowalu has been selected by other studies as a reference or control location for the Lahaina impact regions (Dailer et al. 2010, Glenn et al. 2012, Van Houtan et al. 2014). This relatively healthy reef also had fewer cyanobacteria and higher species richness for turf algae, principal food for small mouthed grazers, another data set confirming this site as relatively healthy.

Kahekili – a highly managed but still impacted reef.

The most common taxa in the shallow reef regions at Kahekili were cyanobacteria followed by *Sphacelaria* sp., *Gelidiopsis* spp., *Herposiphonia* spp., and *Polysiphonia* spp. Turf height varied from 0.5 mm - 4.6 mm at this site with taller turfs (0 - 4.5 mm) and more sediment (0.01 – 0.22 g/cm^2) found in the shallow water near the seeps. Turf height and sediment load were both negatively correlated with turf percent cover; samples with higher percent cover had shorter turfs and less sediment. Fish herbivore biomass for grazers and browsers were slightly higher at Kahekili compared with comparable data for Olowalu, however, scraper biomass was significantly higher at Kahekili. Scrapers (parrotfish) are beneficial for coral recruitment as they tend to scrape down to the substrate, which opens up area for coral larvae to settle (Mumby et al. 2007).

In marked contrast to Olowalu, this research showed a lower richness of turf species and frequent cyanobacteria mats from plugs taken at Kahekili near the seeps. In a review of over 800 papers, Johnston and Roberts (2009) found that in the majority of published reports, there were significant negative effects of pollution on species richness in marine communities. Cyanobacteria can grow quickly, especially if phosphate limitations are relaxed, outcompete eukaryotes for space, and inhibit coral larvae from settling (Kuffner et al. 2006). Some cyanobacteria produce toxins that may deter herbivorous fish (Nagle and Paul 1999).

Further, turfs were taller and trapped more sediment in proximity to the groundwater seeps at Kahekili in shallow water with typically higher water motion. In contrast, Purcell (2000) reports a positive correlation with greater sediment load and taller turfs in reef zones with less water motion. One explanation for this discrepancy is that groundwater precipitates may be adding to the sediment load near the seeps (Sotka and Hay 2009). Additionally, the higher phosphorus levels around the seeps could be augmenting cyanobacteria growth. The State of Hawaiʻi Clean Water Branch reported total phosphorus (P) concentrations in the seeps at Kahekili exceeded the Water Quality Standards (WQS) by more than 20 times from 2012 -2015 but they report concentrations in nearshore water away from the seeps remained low and did not have an apparent effect on nearshore water quality (Clean Water Branch, DoH, State of Hawaiʻi

2016). These water quality data and algal identifications raise the issue that seep P could relieve P-limitations for cyanobacteria at Kahekili. Further research is needed to examine these observations.

As put forth by the Relative Dominance Paradigm, turf algal production can be high with growth regulated by top-down herbivory (e.g. Grigg et al. 1984, Littler et al. 2006, Smith et al. 2010). If herbivore biomass is reduced, as in Olowalu, competitive balances shift among three algal states and corals to re-establish a new equilibrium, an alternate stable state on that reef (Hatcher and Larkum 1983, Jompa and McCook 2002). Critically, levels of herbivore biomass and herbivory in the waters around the Main Hawaiian Islands are lower than healthy ecosystems (Friedlander and DeMartini 2002) even in the best-case scenarios, as we see for the KHFMA (Willliams et al. 2016).

The RDP further predicts that in areas with high nutrients and low herbivory pressures, macro-algae will dominate. With high herbivory, crustose coralline algae (CCA) are predicted to increase in cover. We have seen periodic macro-algal blooms at Kahekili, but since the establishment of the KHFMA contemporaneously with changes in LWTF practices, the resulting increased biomass of herbivores was balanced by lowered nutrient inputs that should lead to a dominant mixed turf assemblages; this outcome has been reported by Williams et al. (2016). Results from this study could indicate that even though herbivore biomass is increasing, more herbivory is needed to keep up with turf algae production. This may be in part because nutrient levels vary with EPA mandates.

There have been many studies at Kahekili over the past 25 years to examine the effects of macroalgae blooms and evidence of elevated nutrient addition via tainted submarine groundwater discharge. None of the studies at Kahekili have characterized turf algae beyond the category “turf”. Identifying turf algae to the species level is not easy. Many algal species are positively identified by their reproductive structures, so they need to be mature and not be heavily grazed. The samples for this study were taken from the flat tops of dead coral heads in prime areas for herbivores to nibble the tips off. *Polysiphonia/Herposiphonia* were especially challenging and they were in many of the samples. There are over 50 species in this complex of closely related genera (Abbott 1999) and it is likely that there were many different species in our samples. For future studies to identify turf to species level, DNA barcoding analysis may be helpful (Sherwood and Presting 2007, Conklin et al. 2009, Sherwood et al. 2010). The sample plugs for this study were small and a better representation of turf species richness might be made with larger samples and taken from areas where herbivores cannot reach. Placement of cages around experiemental areas to increase turf availability can also clarify the taxonomic composition for the turf community (Smith et al. 2001; 2010). In addition, algae could be grown out in aquariums in closed systems where they could regrow tips or reach their reproductive stages for positive identification. Finally, to better characterize the dynamics of these turf communities at Kahekili and Olowalu, future research should also include contemporaneous water sampling and turf sampling during multiple seasons, such as wet and dry seasons, to account for fluctuations in nutrient loading. Adding other pairs of sites, associated with Maui‘s municipal wastewater treatment plants as well as agricultural and cesspool inputs (Amato et al. 2016) could elucidate the relative importance of various nutrient sources on turf communities.

Management insights

In response to chronically elevated nutrient levels and periodic algae blooms at Kahekili, the KHFMA was established to allow an increase in the herbivore biomass to exert top down control of algae. Fish herbivore biomass is increasing and with potentially lower nutrients due to the decline in agricultural sources, macroalgae biomass is also decreasing, however turf algae are now the dominant substrate (Williams et al. 2016). Submarine groundwater seeps continue to discharge nutrient-rich, warm, acidic, low salinity water onto the reef, which is especially impactful at low tides. Land-based sediment also continues to enter the ocean and become re-suspended when the surf is up. At least three interacting parameters have been realized from this work: algal distribution is set by plant physiology, 2) algal distribution is influenced by herbivory (Burkepile and Hay 2008), and 3) sediment trapped in turf can make those plants less palatable to herbivores (Goatley et al. 2012, Clausing et al. 2014, Gordon et al. 2016). Thus, sediment trapped in turfs can affect rates of herbivory. If algae are not grazed and can then trap more sediment , this may create a positive feedback loop that could lead to a stable state of sediment rich turf (Bellwood et al. 2008), few coral larvae recruits, and fewer fish in the browser category.

Coastal reefs are facing multiple stressors from climate change, unsustainable fishing practices and land-based pollution. Over the last few decades, reefs have been transitioning from coral-dominated to algae-dominated ecosystems world wide (McCook 1999). Even with the top down control of increasing herbivore biomass such as we see with the KHFMA at Kahekili, algal turfs have become the dominant substrate with bottom up nutrient enrichment (Smith et al. 2010, Ross et al. 2012, Williams et al. 2016). The relatively healthy reefs at Olowalu have also experienced decline in coral cover in recent years (Hau et al. 2015).

By 2017, human induced warming of air and sea surface combined, reached about 1.0°C above pre-industrial levels and temperatures are currently increasing at approximately 0.2°C per decade (IPCC, 2018). This warming is leading to sea level rise and more intense storms which increases land-based sediments on reefs. Greenhouse gasses have already changed the chemistry of the oceans, turning them more acidic. Rising sea level will affect where waves break, potentially causing increased shoreline erosion, increasing sediments on reefs (Storlazzi et al. 2004).

Temperatures of only 2° C above normal have caused Hawaiian corals to bleach, which can lead to overgrowth by turfs (Jokiel 2004). Hawaiʻi has already experienced widespread, large-scale coral bleaching events in 1996, 2002 (Jokiel and Brown 2004), more recently in 2014, 2015 (Sparks et al. 2016, Williams et al. 2016), 2016 (pers. obs.) with another state-wide bleaching underway (Summer and Fall 2019). Coral can out-compete turf with healthy levels of herbivory, but when coral is stressed or dies, algae and cyanobacteria will grow over dead coral, reducing the chances that coral communities will recover (McCook 2001, Jompa and McCook 2003, Diaz-Pulido et al. 2010). To increase resilience on reefs, managers need to reduce nutrient and sediment input to reefs and implement fishing regulations that will ensure that herbivores can do their job. More no-take marine reserves or marine managed areas should be established in appropriate areas and enforcement needs to be funded (Friedlander et al. 2007, Green and Bellwood 2009, Fenner 2012). Kahekili Herbivore Fish Management Area is a remarkable location to test these ideas.

There have been many years and studies documenting the decline of reefs. Now is the time to act to protect these diverse and ecologically important ecosystems for the future. The predictions of the relative dominance model can be seen as general trends, but there are many environmental factors to consider for the effective management of reefs (Littler and Littler 1984). Because the turf community is fast growing and is sensitive to influences from nutrients, studying turf could give managers an early warning to changes in reef health. The turf community is a critical link between elevated nutrients and fish herbivore biomass. In areas with increased nutrient input, such as we see at Kahekili, it is imperative to have a healthy, diverse population of herbivores.

Summary

Near the seeps at Kahekili, cyanobacteria dominated a species-poor area in contrast to the turf community at Olowalu. At both sites, turf height and sediment load were positively correlated. However, turf height and sediment load had an opposite relationship with depth between the two sites. At Kahekili, turf height and sediment load were higher in shallower water near the seep even though higher water motion should carry sediment away as was the case at Olowalu. These results suggest that the elevated nutrients override the influence of water motion and herbivory at this site, illustrating the importance of bottom-up controls. Percent cover had an opposite relationship with turf height and sediment load at both locations. Where turf was taller, percent cover was lower. Scrapers (parrotfish) were the only herbivore functional group that had statistically higher biomass at Kahekili even with the KHFMA in place. Results of this study indicated that the submarine groundwater coming from the LWRF is impacting the turf community at Kahekili by reducing species richness, promoting growth of cyanobacteria, and allowing turf to grow taller and trap more sediment.

Figures:

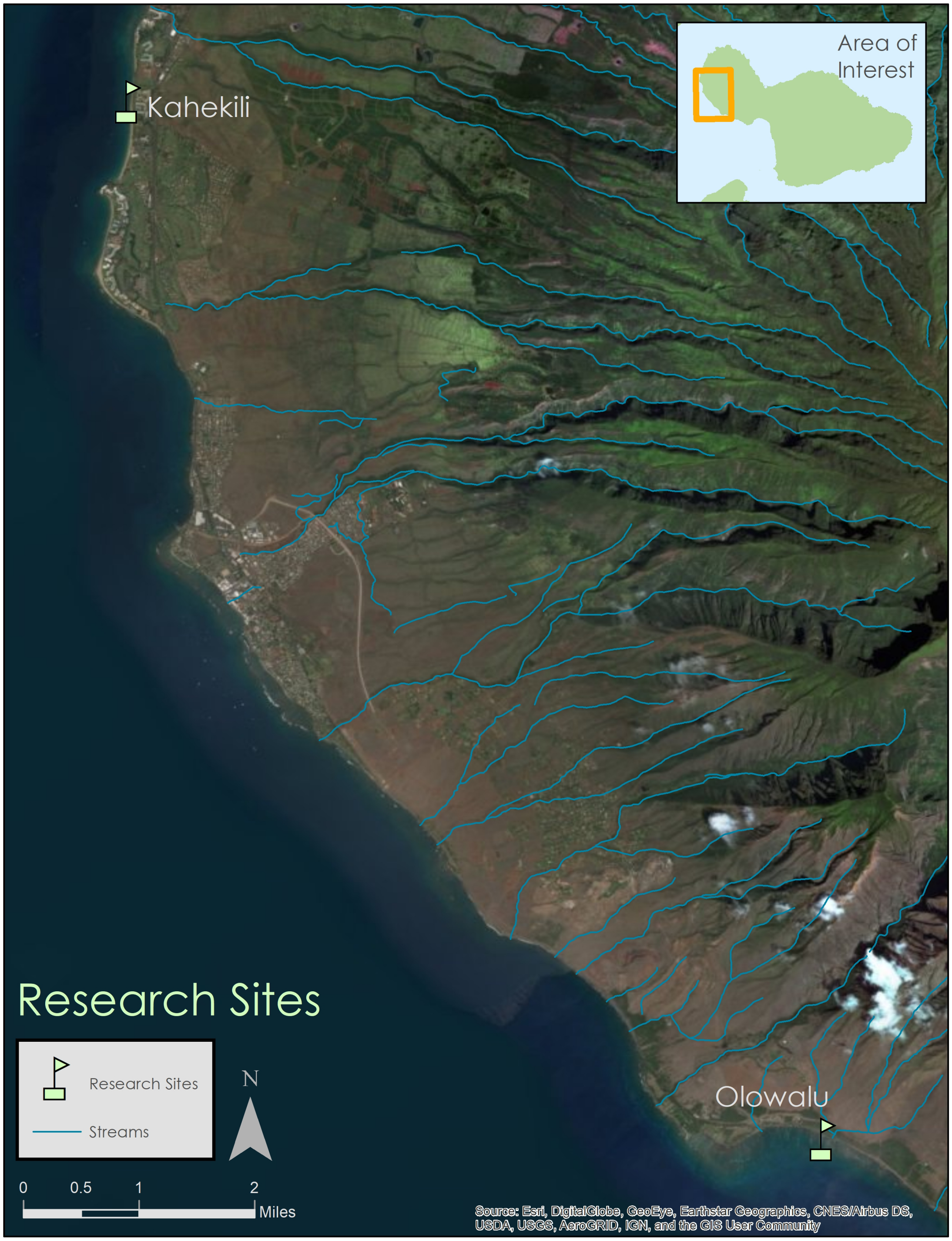

Figure 2.1. West Maui from Kahekili to Olowalu.

Figure 2.2. Kahekili study site and proximity to the Lahaina Wastewater Reclamation Facility (LWRF). Streams in the immediate vicinity have been diverted.

Figure 2.3. Olowalu study site. Streams in the area are a source of sediment to the reef during rainy periods. Note the lack of vegetation in the uplands (māuka).

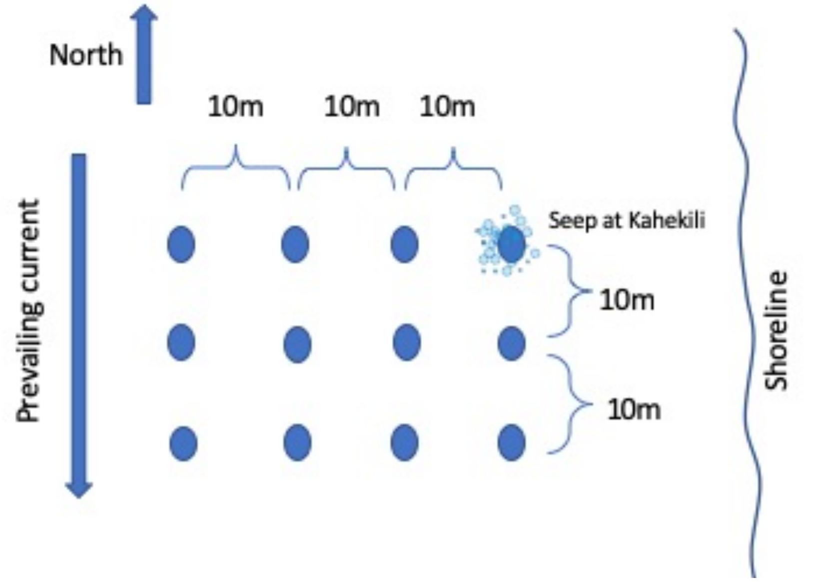

Figure 2.4. Layout of study sites. A grid was laid out with each point 10 meters apart. At Kahekili, the start point was at a visible seep. A dead *Porites* spp.coral head nearest each ten meter mark was sampled. At each sample location, five 1.33 cm^2 area plugs of turf with sediment were taken. The layout was set up to fit the reef at Kahekili and then duplicated at Olowalu.

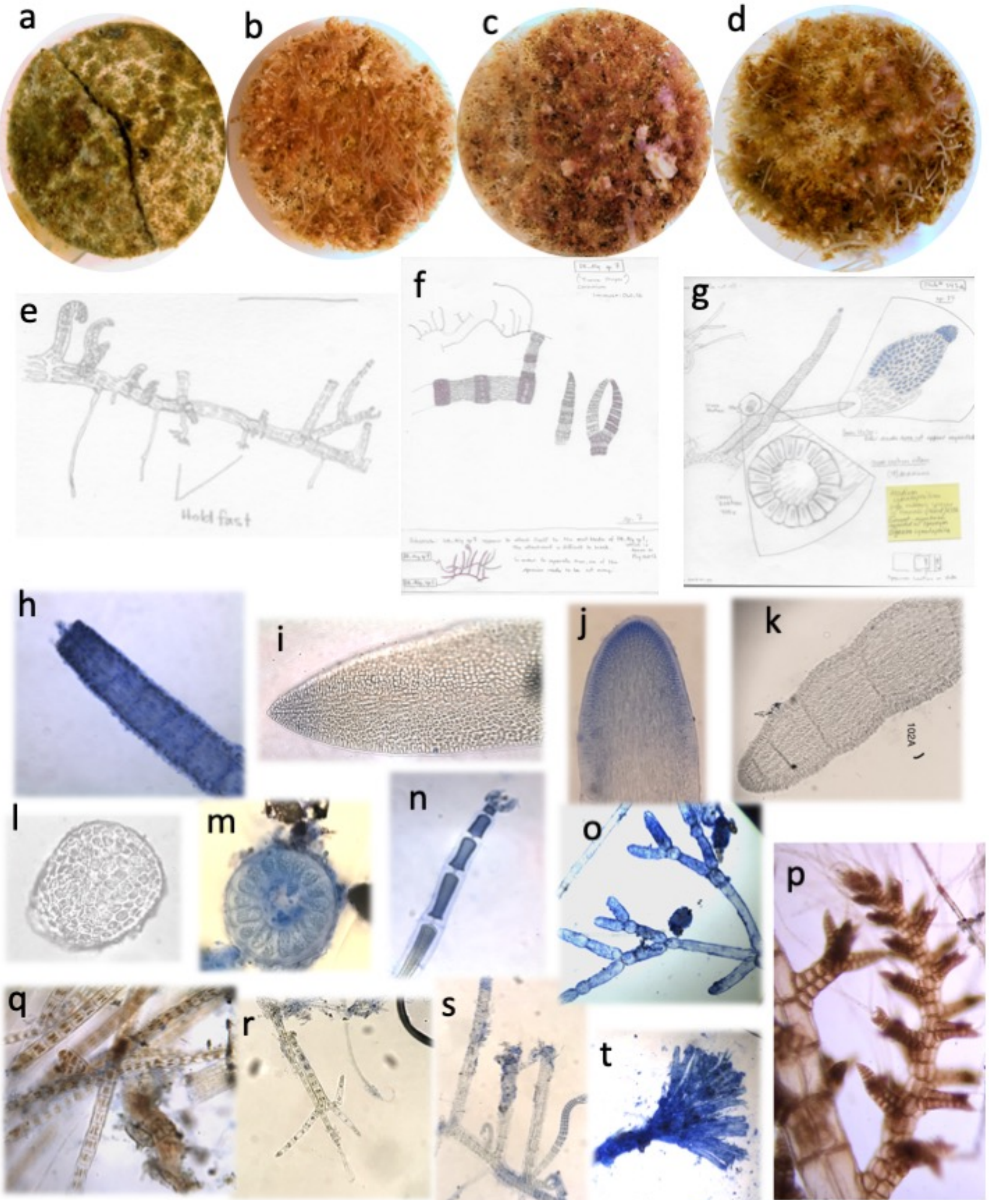

Figure 2.5 a-d. Examples of pictures of turf plugs used for percent cover analysis. Each plug is 1.33 cm^2. e-g. Examples of microscope drawings, (Iris Altamira). Examples of turf species seen in microscope examination: h. grazed tip, i. *Gelidiella sp.,* j. *Gelidiopsis sp,* k.*Champia sp*, l. *Gelidiopsis sp*. cross section, m. *Centroceras sp*. cross section, n. *Anotrichium sp.*, o. *Chlorodesmis caespitosa,* p. *Tolypiocladia glomerulata,* q. *Sphacelaria novae-hollandiae,* r. *S. rigidula* propagule, s. *Herposiphonia sp.,* t. *Rhipidosiphon javensis*, (Abbott 1999, Abbott and Huisman 2004, Huisman et al. 2007).

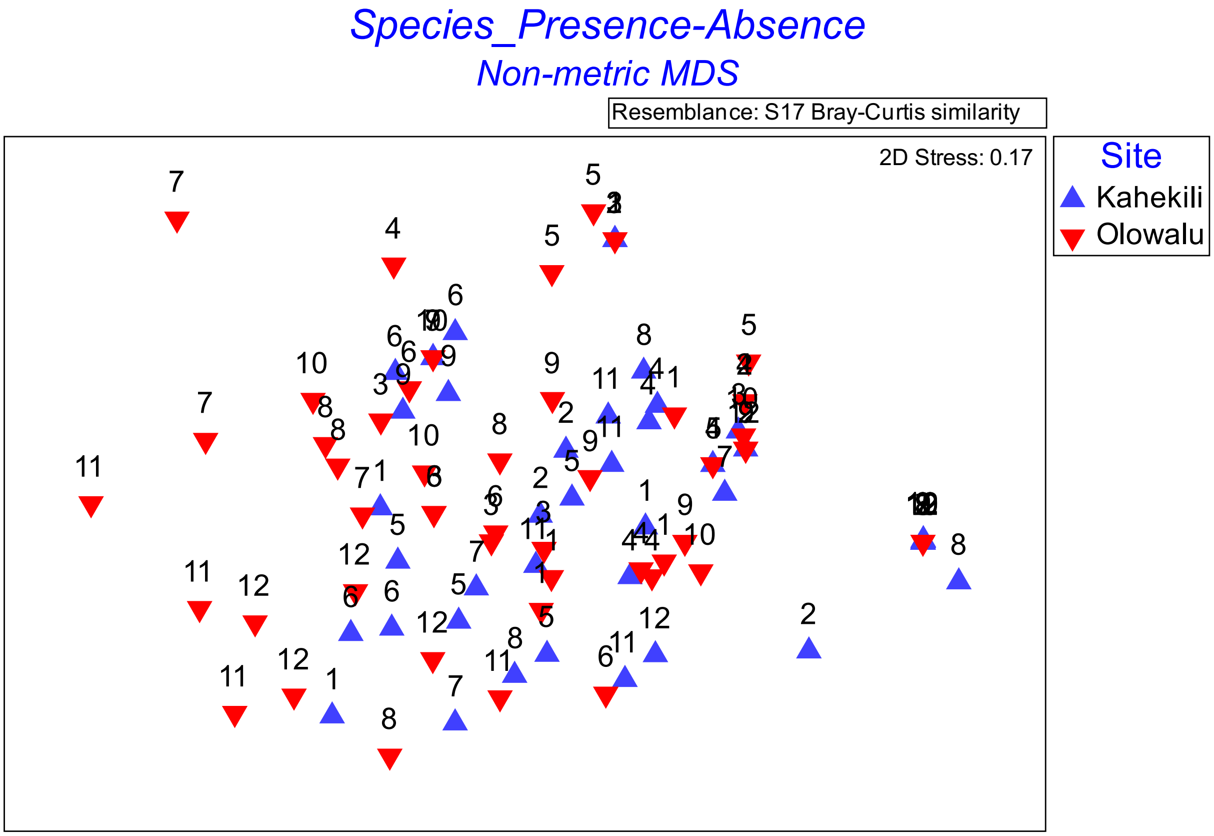

Figure 2.6: Nonmetric multi-dimensional scaling plot of the presence/absence of turf algae taxa on dead *Porites* spp. colonies by site. Colony number within a site is indicated above each symbol.

Outliers at Olowalu (7, 11, 12) have high species richness and only 1 plug with cyanobacteria.

The outliers at Kahekili (2, 8) all have primarily cyanobacteria with very few other taxa.

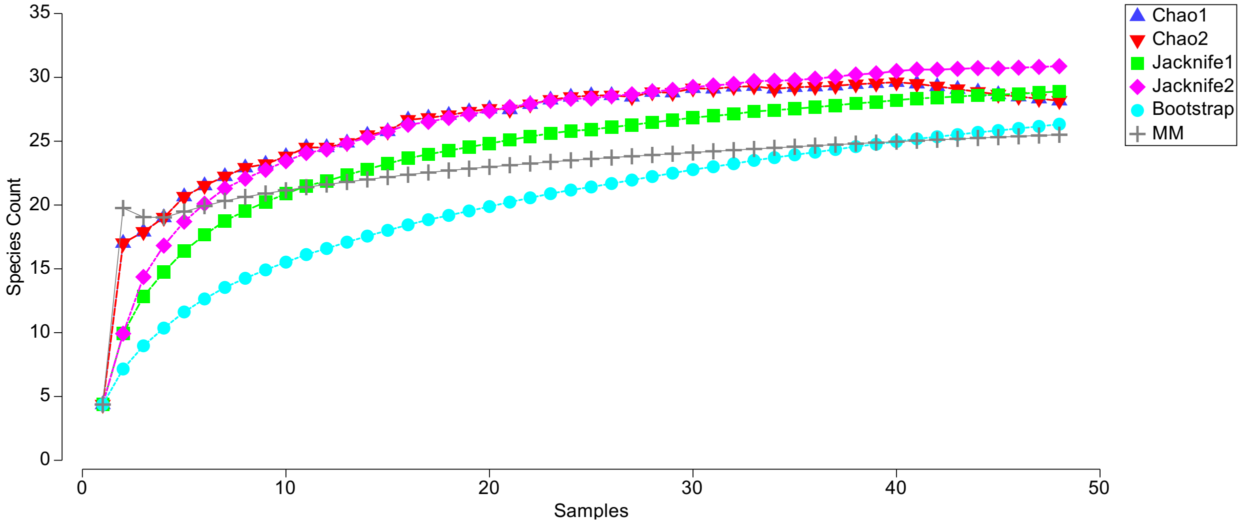

Figure 2.7a. Species accumulation plots at Kahekili for six *S* estimators predicting the total number of species observed depending on the number of samples collected. The Michaelis-Menton estimator (MM) predicted an asymptote of 25.5 total species.

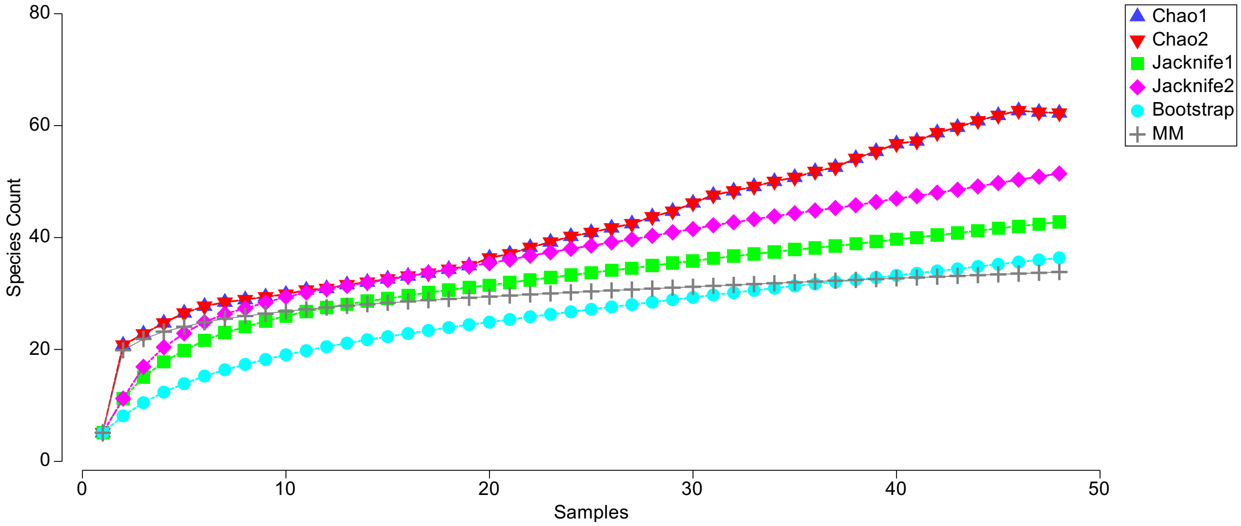

Figure 2.7b. Species accumulation plots at Olowalu for six *S* estimators predicting the total number of species observed depending on the number of samples collected. The Michaelis-Menton estimator (MM) predicted an asymptote of 33.8 total species.

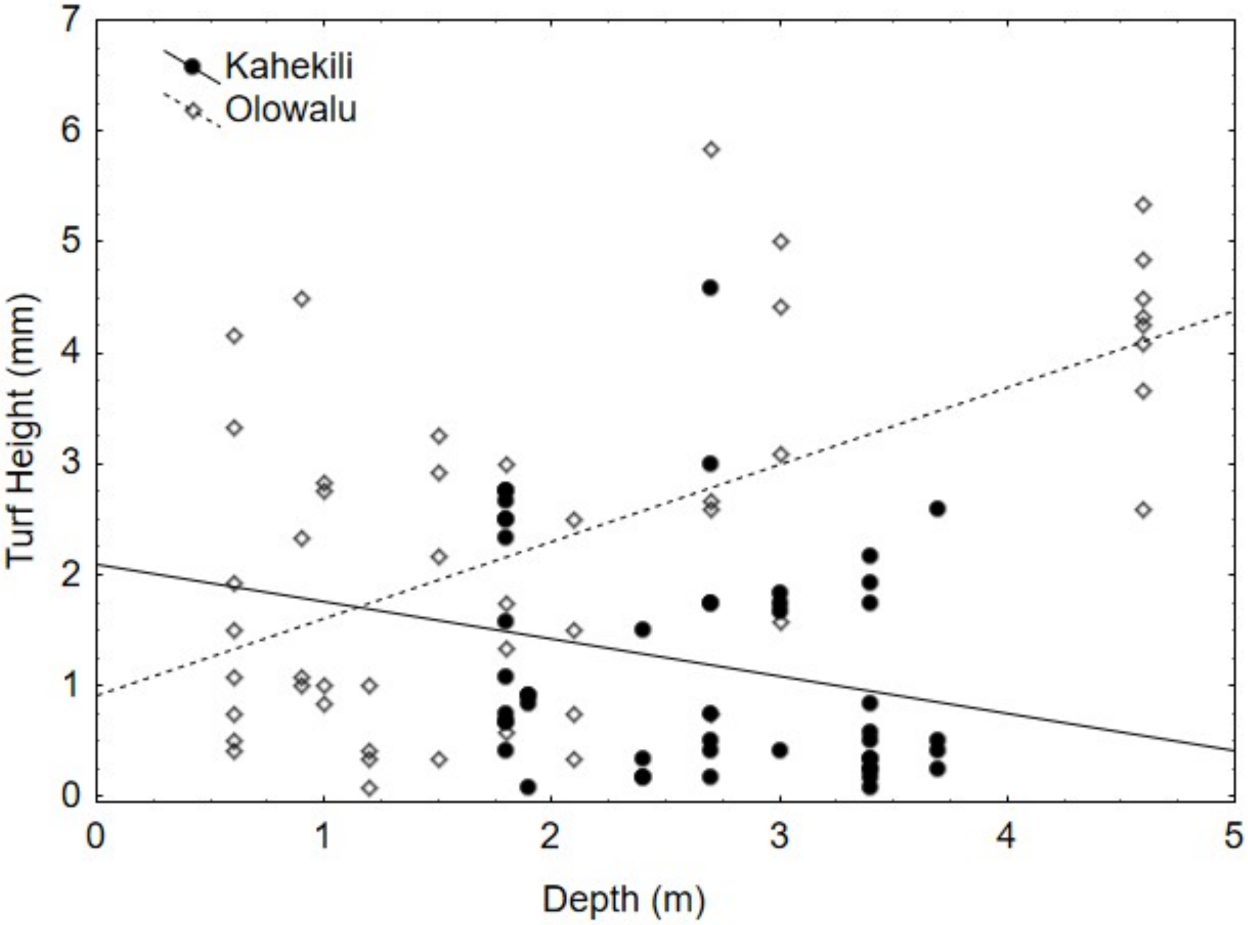

Figure 2.8: Height of turf algae (mm) versus depth (m) showing linear regression fit for each site. Turf canopy height tends to inverse relationship between sites (t = 1.94, p = 0.057).

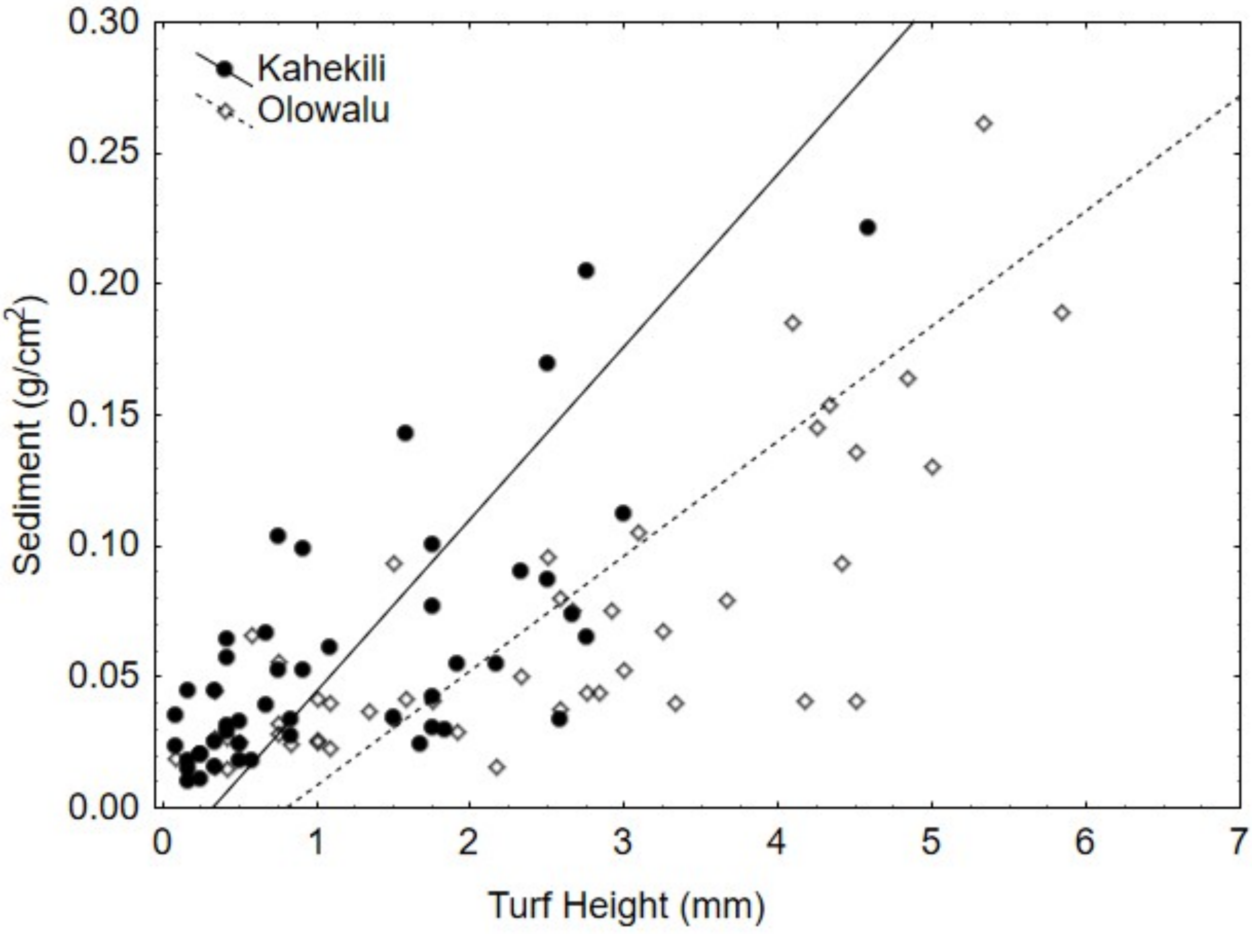

Figure 2.9: Linear regression of sediment load and height of turf at Kahekili and Olowalu. Sediment load and height of turf are linearly related for both sites. There was more sediment overall at sites sampled in the reef at Olowalu (t = 2.78, p = 0.007).

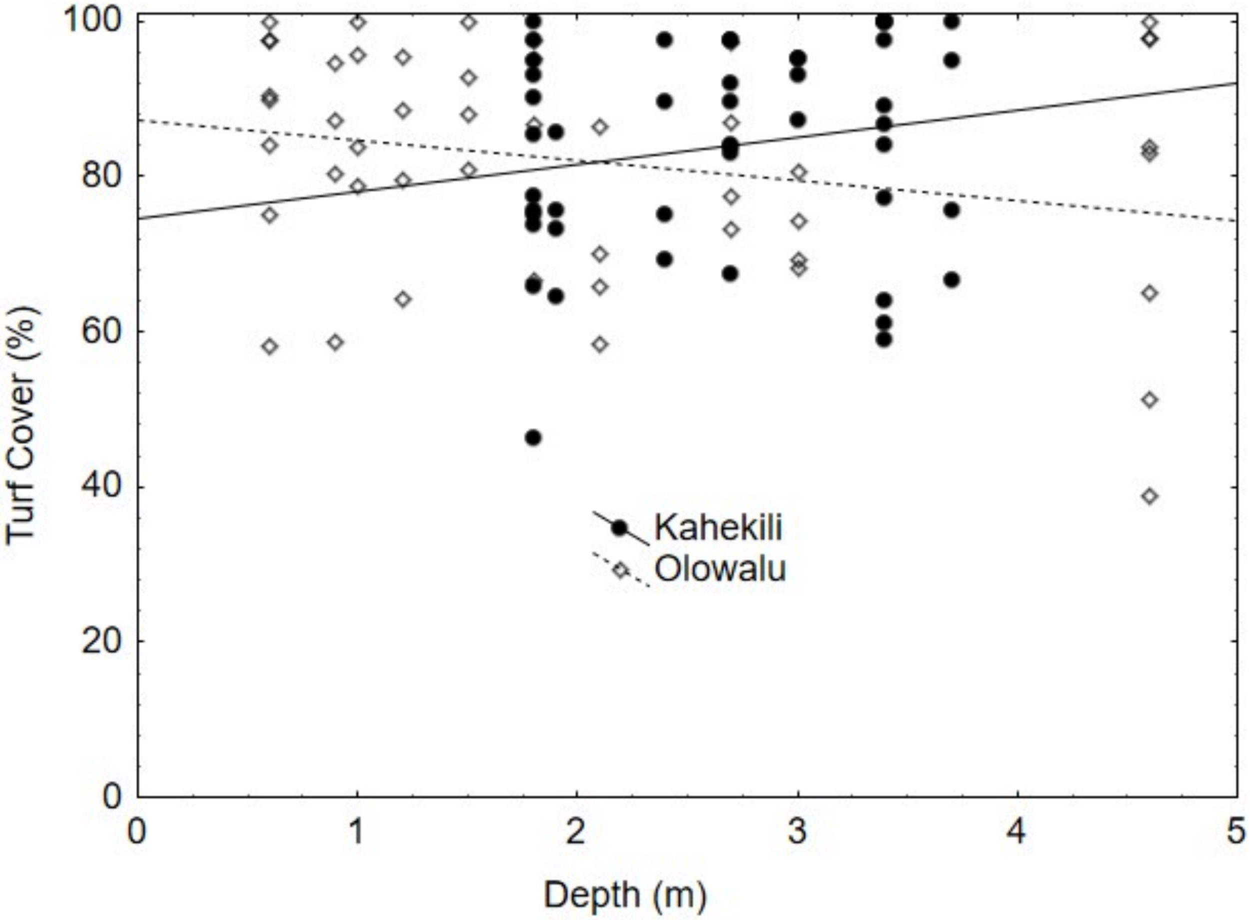

Figure 2.10: Relationship between depth of sample and % cover for turf at Kahekili and Olowalu. There is not a statistically significant difference of turf cover between sites. It is important to note that these are percentages of the samples taken on dead *Porites lobata* heads with turf, not a representation of the whole reef. ($t = -2.76$, $p < 0.01$)

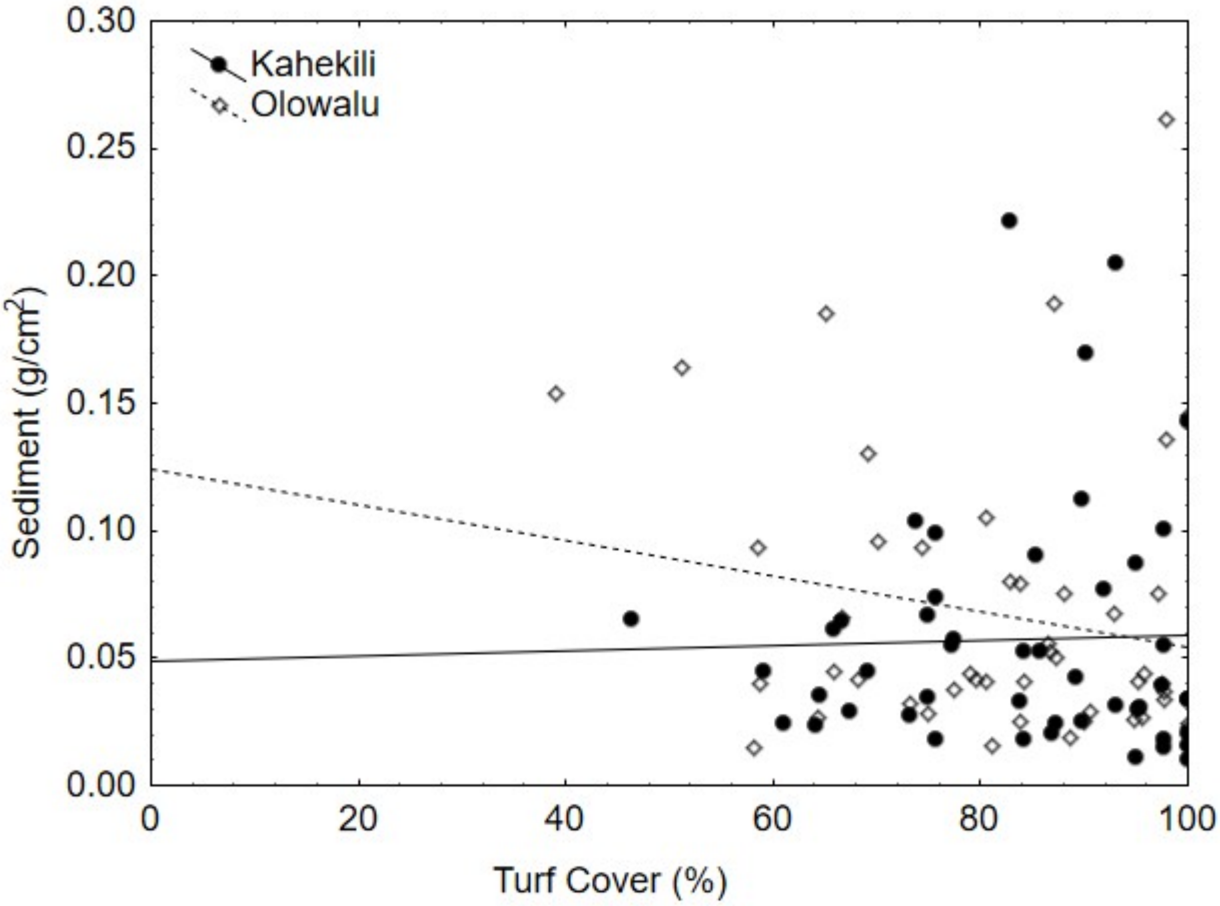

Figure 2.11. Linear regression of sediment load versus % cover of turf at Kahekili and Olowalu.

(t = -2.05, p 0.053)

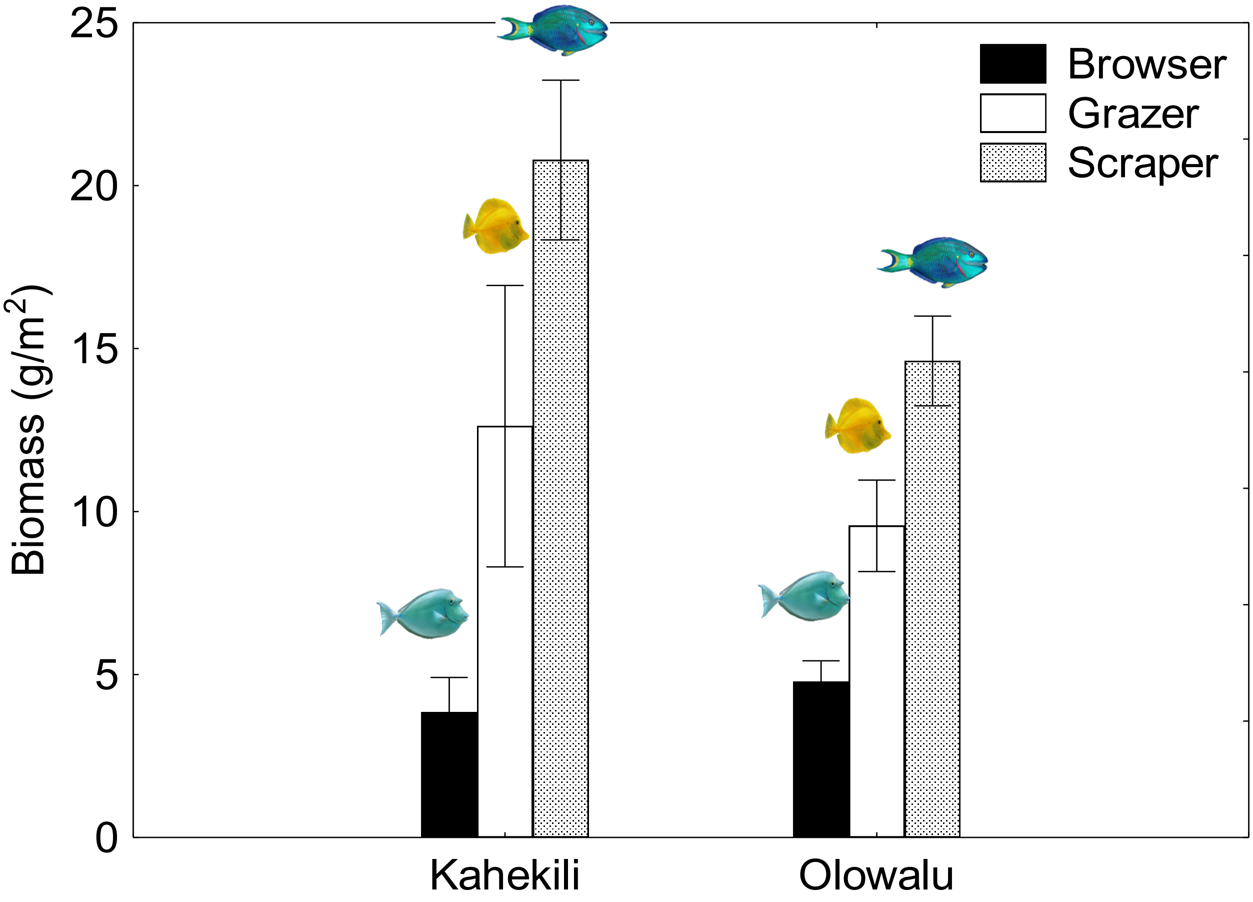

Figure 2.12. Mean fish biomass by herbivore functional groups. Overall mean herbivore biomass at Kahekili (12.4 g/m^2 ± 1.7 SE) trended higher than Olowalu (9.6 g/m^2 ± 0.7 SE) but not statistically significant (estimate = 1.4, W = 3.7, p = 0.055). However, scraper biomass was higher at Kahekili (20.8 g/m^2 ± 2.4 SE) than at Olowalu (14.6 g/m^2 ± 1.4 SE) (estimate = -1.8, W = 5.8, p = 0.16).

Table 1. List of taxa and number of samples with each taxon per site.

Phyla	**Genera**	**Kahekili**	**Olowalu**
Chlorophyta	*Cladophora* sp.	4	7
Chlorophyta	*Chlorodesmis caespitosa*	0	9
Chlorophyta	*Rhipidosiphon javensis*	1	0
Chlorophyta	*Ulothrix subflaccida*	1	0
Chlorophyta	*Valoniopsis*	1	0
Chlorophyta	Unknown 2	0	7
Chlorophyta	Unknown 3	0	3
Chlorophyta	Unknown 6	0	1
Chlorophyta	Unknown 9	0	2
Cyanophyta	Cyanobacteria	34	24
Ochrophyta	*Sphacelaria*	32	40
Ochrophyta	Unknown 5	0	1
Rhodophyta	*Amphiroa*	0	3
Rhodophyta	*Anotrichium*	8	4
Rhodophyta	*Centroceras with no spines*	8	10
Rhodophyta	*Centroceras clavulatum (spines)*	2	1
Rhodophyta	*Ceramium*	11	7
Rhodophyta	*Champia*	2	8
Rhodophyta	*Chondria*	5	8
Rhodophyta	*Digenea*	5	3
Rhodophyta	*Erythrotrichia carnea*	1	1
Rhodophyta	*Gelidiella*	14	24
Rhodophyta	*Gelidiopsis*	21	26
Rhodophyta	*Gelidium*	3	5
Rhodophyta	*Griffithsia*	3	1
Rhodophyta	*Herposiphonia*	17	7
Rhodophyta	*Herpo/Polysiphonia fragments (unknown)*	10	16
Rhodophyta	*Jania*	5	7
Rhodophyta	*Polysiphonia*	15	16
Rhodophyta	*Stylonema alsidii*	1	1
Rhodophyta	*Tolypiocladia glomerulata*	0	1
Rhodophyta	Unknown 1	2	0
Rhodophyta	Unknown 4	0	1
Rhodophyta	Unknown 8	0	1
Unknown	Unknown 7 (tiny 3-fingered fan)	0	1

Table 2. Similarity percentage (SIMPER) analysis of the presence/absence data of turf algae taxa on dead *Porities* spp. Colonies by site.

Group Kahekili
Average similarity: 37.52

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Cyanobacteria	0.71	17.59	0.70	46.89	46.89
sp 18 Sphacelaria	0.67	9.23	0.75	24.60	71.48

Group Olowalu
Average similarity: 36.89

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
sp 18 Sphacelaria	0.83	15.26	1.21	41.36	41.36
Cyanobacteria	0.50	5.50	0.51	14.92	56.27
sp 22 Gelidiopsis	0.54	5.01	0.60	13.58	69.85
sp 28 Gelidiella (with apical cell)	0.50	4.04	0.54	10.95	80.80

Groups Kahekili & Olowalu
Average dissimilarity = 66.06

Species	Group Kahekili Av.Abund	Group Olowalu Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Cyanobacteria	0.71	0.50	6.63	0.79	10.04	10.04
sp 22 *Gelidiopsis*	0.44	0.54	6.23	0.87	9.42	19.47
sp 18 *Sphacelaria*	0.67	0.83	6.14	0.67	9.29	28.75
sp 28 *Gelidiella* (with apical cell)	0.29	0.50	5.65	0.89	8.55	
sp 14 *Polysiphonia*	0.31	0.33	4.81	0.78	7.28	44.59
sp 13 *Herpo/Poly*	0.21	0.33	4.66	0.69	7.05	51.64
sp 15 *Herposiphonia*	0.35	0.15	4.00	0.74	6.05	57.69
sp 25 *Centroceras* with no spines	0.17	0.21	2.99	0.61	4.53	
sp 7 *Ceramium*	0.23	0.15	2.82	0.61	4.27	66.49
sp 16 *Anotrichium*	0.17	0.08	2.24	0.50	3.39	69.88
sp. 35 *Cladophora* type green	0.08	0.15	2.04	0.45	3.09	72.97

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