

EVALUATING THE POTENTIAL OF AN ENDEMIC HAWAIIAN SOFT CORAL,
SARCOTHELIA EDMONDSONI,
AS A BIOINDICATOR OF ANTHROPOGENIC INFLUENCE



A THESIS SUBMITTED TO THE GRADUATE DIVISION OF THE
UNIVERSITY OF HAWAI'I AT MĀNOA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE
IN
NATURAL RESOURCES AND ENVIRONMENTAL MANAGEMENT

AUGUST 2021

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ACKNOWLEDGEMENTS

I would like to acknowledge and thank the Hawai'i Division of Aquatic Resources for sharing their data used in this research, and for their collaboration and help with the data collected at Pila'a, Kaua'i. The following have also provided invaluable assistance in completing my benthic surveys: Andrew Graham, Ilikea McElroy, Cameron Ogden-Fung, Paige Mino, Jonathan Rosen, and Matthew Stefanak. I also would not have been able to complete this study without the help of Dr. Jake Ferguson, who helped tremendously in the statistical analyses. This research was funded by the Coral Reef Assessment and Monitoring Program, and scholarships received that aided in this project include the Paul L. Jokiel Memorial Endowed Scholarship Fund, Colonel Willys E. Lord, DVM & Sandina L. Lord Endowed Scholarship, and the Ruth D. Gates Memorial Fund.

ABSTRACT

Bioindicators, organisms which reflect an ecosystem's health or condition, are frequently used in natural resource management and monitoring as an early warning sign for ecosystem degradation, allowing managers to recognize and address the issue at hand. Octocorals, soft corals belonging in the subclass Octocorallia, are used globally in coral reef monitoring protocols as an indicator of poor coastal water quality and nutrient contamination from human sources. *Sarcothelia edmondsoni*, an endemic Hawaiian octocoral, has had unusual high abundances in heavily polluted or developed areas around the main Hawaiian Islands, however, inadequate empirical evidence of how octocorals respond to environmental stressors hinders their use as an ecological indicator for coral reefs here in Hawai'i. This study comprises a thorough evaluation of *S. edmondsoni* as a bioindicator following the U. S. Environmental Protection Agency's Evaluation Guidelines for Ecological Indicators, and included assessments of the octocoral abundance on spatial and temporal scales. To examine the temporal variation of *S. edmondsoni*, I conducted repeated benthic surveys on O'ahu and Kaua'i to quantify and track changes in populations. Environmental variables such as rainfall, temperature, stream discharge, and distances from shore were also collected to examine possible effects on octocoral abundance. To explore the spatial variability of *S. edmondsoni*, quantitative data was extracted from existing natural and anthropogenic land use spatial datasets to investigate correlations with species abundance on O'ahu, Kaua'i, and West Hawai'i. Natural and human land use factors included precipitation, human population, density of underground injection wells, and percent coverage of agricultural land, development, and impervious surfaces. Significant positive correlations were found with human population, impervious surfaces, development levels, and distance from shore, which represents the extent of human impacts nearshore. In addition, *S. edmondsoni* meets indicator criteria as it is relevant to management concerns, is easy to incorporate into existing monitoring methodologies, displays a response gradient relative to level of stress, and provides a direct linkage to management decisions. This supports the use of *S. edmondsoni* as a bioindicator of anthropogenic influences, which will be an important management tool for the conservation and protection of Hawai'i's coral reef ecosystems.

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1.0 INTRODUCTION

Bioindicators, organisms which reflect an ecosystem's health or quality, are frequently used in natural resource management and monitoring as early warning signs for ecosystem degradation (Siddig et al. 2016; Jackson et al. 2000; McGeoch 1998). The presence or abundance of bioindicators can convey biological, physical, or chemical changes taking place in the environment, allowing observers to quickly detect harmful pressures. Managers primarily use ecological indicators to characterize the integrity of an ecosystem and identify major stressors such as pollution to mitigate and control damage (Niemi et al. 2004; Niemi & McDonald 2004). Local bioindicators as a monitoring tool pose notable advantages compared to direct measures of environmental parameters. For example, sampling and subsequent laboratory analyses for water quality can be costly and time consuming (Cooper et al. 2009), as opposed to simply noting the presence or abundance of a known water quality indicator. Thus, many natural resource management agencies employ ecological indicators as a rapid, easy, and inexpensive method of detecting environmental deterioration on a large scale.

The use of local bioindicators will play an increasingly critical role in coral reef conservation and management efforts (Dale & Beyeler 2001; Niemi et al. 2004). Roughly 75% of the Earth's coral reefs are threatened by anthropogenic impacts (Burke et al. 2011), and approximately half of all coral reefs worldwide have disappeared in the last 30 years (National Academies of Sciences, Engineering, and Medicine 2019) due to intermittent and persistent exposure to local and global stressors (Hoegh-Guldberg 1999; Burke et al. 2001). Local anthropogenic disturbances include eutrophication from agriculture, storm drains, or industrial sources (Rani et al. 2018; Duprey et al. 2016; Dubinsky & Stambler 1996), runoff and sedimentation from urban development and storms (Erftemeijer et al. 2012; Jones et al. 2016), fishing pressures which can cause ecosystem phase shifts (Loh et al. 2015; Jessen et al. 2014), dredging (Uchino 2004; Miller et al. 2016), direct damage from ship groundings (Victoria-Salazar et al. 2017; Negri et al. 2002), and tourism (Rodgers & Cox 2003; Lachs & Oñate-Casado 2020 ; Severino & Rodgers 2019). Primary global pressures include the increasing detrimental effects of climate change: rising sea water temperatures, the increasing frequency and intensity of storms, sea level rise, and ocean acidification (Shaw et al. 2012; Speers et al. 2016; Baker et al. 2008; Bellwood et al. 2006; Easterling 2000; Karl et al. 2009; Mora et al.

2013). These extreme ecological alterations are projected to continue and the use of bioindicators that detect these changes will be important for the preservation of our reefs.

Growing worldwide concern about environmental degradation has led to the increased exploration and use of bioindicators in monitoring assessments (Siddig et al. 2016; de Mata et al. 2008; Hodgkinson & Jackson 2005; Füreder & Reynolds 2003); as such, several frameworks and criteria have been developed to aid in the selection of an appropriate indicator, which can be used to estimate ecological conditions or assess the efficacy of management actions (Siddig et al. 2016; Kurtz et al. 2001; Jackson et al. 2000; Jameson et al. 1998). The main criteria most widely accepted for dependable bioindicator organisms include displaying response gradients relative to level of stress (Podani 1992), sessile organisms that are chronically exposed to local environmental conditions (Alcolado et al. 1994), and being easily quantifiable (Jameson et al. 1998). Due to the rise in popularity of national, state, and community-based environmental programs using indicator species, the United States Environmental Protection Agency (U. S. EPA) also created their own evaluation guidelines for ecological indicators as an iterative process during indicator development and review (Jackson et al. 2000). Ultimately, proposed indicators should satisfactorily meet all criteria and fulfill expectations before its recommendation for use, and the acceptability of an ecological indicator depends on specific needs and objectives.

Although numerous bioindicators of stress exist for freshwater systems (Su et al. 2018; Lorenz 2003; Adams et al. 1989), few have been established for coral reefs due to complex interactions and high variability in coastal reef ecosystems (Crosby et al. 1996; Jameson et al. 1998; Jameson et al. 2001; Bradley et al. 2009). Common indicators used in coral reef ecosystem monitoring and assessments include sea cucumbers, foraminiferans, and macroalgae (Culha et al. 2016; Hallock et al. 2003; Smith et al. 1981; Cooper et al. 2009). Sea cucumbers have been used in determining trace metal contamination (Culha et al. 2016), foraminiferans in detecting water quality (Hallock et al. 2003), and changes in macroalgal cover are associated with nutrient input (Smith et al. 1981; Cooper et al. 2009).

Octocorals—soft, non-reef building corals in the subclass Octocorallia—are also a reef ecosystem indicator used in many countries to detect poor coastal water quality caused by anthropogenic influence (Fabricius & McCorry 2006; Hernandez-Munoz et al. 2008; Baker et al. 2010; Baum et al. 2016). High abundances of octocorals in Hong Kong harbors and Jakarta Bay,

Indonesia were linked with elevated turbidity levels and increased concentrations of nutrients and contaminants from land source pollutants (Fabricius & McCorry 2006; Baum et al. 2016). In Cuba, octocoral abundance was positively correlated with submarine discharge of urban wastewater (Hernandez-Munoz et al. 2008). Octocorals in the Caribbean have also been used to obtain stable isotope values over the past century to detect rising anthropogenic input of carbon and nitrogen caused by fossil fuel combustion and use of agricultural fertilizers (Baker et al. 2010).

While octocoral species have been studied extensively and are utilized as bioindicators of coastal water quality issues and environmental degradation caused by human activities elsewhere, relatively little is known about octocorals in Hawai'i. In particular, a lack of empirical evidence of how octocorals respond to environmental stressors hinders their use as an ecological indicator for Hawaiian coral reefs.

2.0 BACKGROUND

2.1 Octocorals

Octocorals are soft corals belonging in the order Alcyonacea (which include sea fans and sea whips), and differ from the hard, reef building corals (Order Scleractinia) in that they lack a hard, calcium carbonate skeleton. Instead, octocorals house calcium carbonate spicules within their tissue for structural support, and are named because each polyp within an octocoral colony contains eight tentacles. With the exception of one species (Bayer & Muzik 1976), all octocorals are colonial, and can be zooxanthellate or azooxanthellate. Zooxanthellae are algal symbionts that live within the coral's tissue, providing food for the coral host through photosynthesis. Most octocorals are heterotrophic feeders however, able to capture fine particulate matter and zooplankton using their polyp tentacles and rows of pinnules lining each tentacle (Lewis 1982). While Alcyonacean corals are widespread throughout the tropical Indo-Pacific region and are considered an important component of benthic reef communities on many of these reefs (Lasker et al. 2020b; Pérez et al. 2016; Etnoyer et al. 2010), increased abundance and dominance of soft corals within the last few decades have raised concern (Lasker et al. 2020a; Lasker et al. 2020b; Wood & Dipper 2008). Specific families of octocorals in the Indo-Pacific region have been documented as opportunistic colonizers of disturbed reef habitats, capable of monopolizing and overgrowing other hard, reef-building corals (Fabricius 1998; Fox et al. 2003; Tilot et al. 2008; Wood & Dipper 2008). Several Caribbean and Indonesian reef communities have been overtaken and are now dominated by these “octocoral forests” due to human-mediated disturbances (Lasker et al. 2020a; Lasker et al. 2020b; Baum et al. 2016).

Octocorals are generally known to be more resilient against environmental changes due to the display of unique traits which contribute to their success in habitat competition on coral reefs (Lasker et al. 2020b; Abdel-Lateff 2019). Many octocoral species have weaker or few nematocysts (specialized stinging cells used for capturing prey and protection) as compared to hard corals (Mariscal & Bigger 1977; Sammarco & Coll 1992), and to account for their lack of nematocysts and skeletal structure, octocorals utilize chemical defenses to protect themselves. A wide variety of bioactive compounds have been identified in octocorals (Abdel-Lateff 2019), which can be released in defense when they are near a competitor. These compounds are often poisonous and toxic to many other marine organisms. Many studies have documented retardation

of growth, a decline in recruitment, and complete mortality of scleractinian corals both in laboratory and field experiments due to the chemical interactions from octocorals, even in situations with no direct contact (Coll & Sammarco 1983; Sammarco et al. 1983; Aceret et al. 1995; Maida et al. 2001). Octocoral tissue has also been suggested to play a protective role against decreasing pH levels (Gabay et al. 2014), giving them a greater advantage in acidified conditions than hard corals. Octocorals' chemical defenses and resiliency against lowered pH levels hint at their adaptability in degraded conditions, allowing them to be a strong competitor for space in benthic marine habitats.

2.2 Octocorals in Hawai'i

There are currently 11 known species of octocorals in Hawai'i, with the endemic *Sarcothelia edmondsoni* (previously *Anthelia edmondsoni*) as one of the most commonly found. While other invasive octocorals such as *Carijoa riisei* have been extensively studied in Hawai'i (Grigg 2003; Kahng & Grigg 2005; Kahng 2006; Wagner et al. 2009), few papers have been published on *S. edmondsoni* (Mercer & Singh 1975; Davis 1977; Pugh 2019). Its common name, the blue or snowflake octocoral, reflects one of the two dominant color morphologies: the bluish purple morph and the brown morph (Fig. 1). The blue octocoral is a zooxanthellate species capable of heterotrophic feeding, and experiments have shown its capacity to survive up to 28 days in the dark in filtered seawater, indicating the adaptability of this species to persist without food for at least a month (Davis 1977). Gametogenesis appears to be continuous throughout the year with spawning triggered by lunar phases, similar to other Hawaiian corals in which lunar cycles, seasonal, and temperature changes can also induce spawning (Davis 1977; Jokiel 1985; Hunter 1988; Padilla-Gamiño & Gates 2012).



Figure 1. Photograph from Pila‘a, Kaua‘i representing the brown (top) and blue/purple (bottom) morphologies of *Sarcothelia edmondsoni*.

S. edmondsoni blooms, or rapid increases in populations that may last from months to years, have been detected and may be positively associated with water quality conditions that are detrimental to most corals and other benthic organisms in Hawai‘i. There is evidence of *S. edmondsoni* blooms near areas where human activities and natural events have impacted water quality. Abnormally high concentrations of *S. edmondsoni* in Honokōhau Harbor on the island of Hawai‘i and adjacent developed areas may be associated with poor water quality and coastal development, as Honokōhau Harbor is polluted and impacted by a strong presence of submarine groundwater discharge (Walsh et al. 2010; Hunt 2014). A brief, episodic bloom of *S. edmondsoni* at Pila‘a, Kaua‘i was recorded after a heavy rainfall and flood event (Rodgers et al. 2019a; Rodgers et al. 2021), and high populations of the octocoral have also been detected on O‘ahu near stream mouths, suggesting they may be indicative of terrigenous inputs of freshwater or pollution. A variety of factors or variables may be responsible for driving these blooms, yet a lack of research on these drivers limit our understanding of this species and its use as an indicator in Hawai‘i.

2.3 Potential Drivers of *S. edmondsoni* Populations

Drivers that influence marine benthic habitats, and therefore most likely *S. edmondsoni*, include rainfall, temperature, water quality, distance from shore, and stream discharge. Increased precipitation and stream discharge from heavy rain and flood events lead to polluted runoff from impermeable surfaces and disturbed landscapes. This inflates discharge of nutrients and sediments from watersheds into adjacent coastal ecosystems, causing habitat degradation and poor coastal water quality (Rodgers et al. 2021; Erftemeijer et al. 2012; Jones et al. 2016). Extreme storm events can also lead to an influx of freshwater, lowering salinity levels in nearshore, shallow reef habitats. Freshwater “reef kills” have been well documented, which result in high mortality of corals and other associated benthic reef organisms in shallow waters (Rodgers et al. 2021; Banner 1968; Jokiel et al. 1993; Jones & Berkelmans 2014; Bahr et al. 2015). Lower salinity due to heavy rainfall and consequently increased discharge can cause full coral mortality, initiate ecological phase shifts, and impacted coral reef communities may take up to 15 years or longer for full recovery (Jokiel et al. 1993; Jones & Berkelmans 2014). Exposure to freshwater for only 30 minutes can be fatal to most Hawaiian coral species, and lowered salinity levels reduce the ability of corals to survive in elevated temperatures (Edmonson 1928; Coles & Jokiel 1978). Average salinity tolerance limits for coral reefs are approximately 28.7-40.4 ppt (Guan et al. 2015). However, because high abundances of *S. edmondsoni* have been detected after large storm events and are found in areas subjected to a high presence of submarine groundwater discharge (Rodgers et al. 2019a; Rodgers et al. 2021; Walsh et al. 2010; Hunt 2014), the octocoral species may be more resilient to lowered salinity levels as compared to scleractinian corals.

Distance from shore may also be a driver of octocoral abundance, as the extent of human influences are more concentrated in nearshore areas where higher populations of *S. edmondsoni* have been found (Rodgers et al. 2020). The distance gradient from nearshore to offshore represents a gradient of environmental conditions that are influenced by both anthropogenic and natural environmental factors. Inner-shelf reefs are more exposed to freshwater input from river/stream mouths and anthropogenic and land-based influences such as runoff that carry sediments, nutrients, and pollutants (Basterretxea 2018; Heery et al. 2018; Fabricius 2005; Ryan et al. 2018; Tebbet et al. 2018; Kroon et al. 2016). Outer-shelf reefs are mainly subjected to environmental variables such as wave action and ocean currents (Bellwood & Wainwright 2001;

Emslie et al. 2010; Cleary et al. 2005; Ryan et al. 2018). Furthermore, depth plays a stronger role in community structure at outer reefs, as water column depth tends to generally increase offshore (Hoeksema et al. 2019; Pearson & Stevens 2015; Fricke et al. 2014; Ziegler et al. 2014), aiding in the dispersion and diffusion of pollutants. Indeed, due to these varying characteristics and complex interactions along a cross-shelf gradient perpendicular to shore, distinct belts of spatially diverse communities have been found in bands parallel to the coastline (Hoeksema et al. 2019; Basterretxea et al. 2018).

Temperature, water quality, and hard coral cover may also be correlated with *S. edmondsoni* abundance. Water quality and dissolved inorganic nutrients play a substantial role in coral reef health and status. Nutrient input onto reefs has persistently increased over the last 150 years (Richmond 1993; McCulloch et al. 2003), an increase that is projected to continue, concurrent with the growing human population and development. Eutrophication is associated with coral reef decline and negatively impacts coral growth and fitness (Guan et al. 2015; D'Angelo & Wiedenmann 2014). In addition, excess nutrients in coral reef ecosystems can lead to algal blooms, which may cause toxic water quality conditions, habitat competition, and ecosystem imbalance (McCormick et al. 2017; Al-Yamani et al. 2020; Berdalet 2017). Nutrient thresholds for most corals are 4.51 $\mu\text{mol/L}$ for nitrate, and 0.63 $\mu\text{mol/L}$ for phosphate (Guan et al. 2015). Increased sea water temperatures can lead to coral bleaching and may also affect *S. edmondsoni*, as thermal tolerances for corals worldwide have similar thresholds of 1-2 $^{\circ}\text{C}$ above summer ambient temperatures (Jokiel & Coles 1990; Coles et al. 1976). Correlations with scleractinian coral cover may also exist, as increases in octocoral cover elsewhere have been attributed to declines in hard coral cover (Lasker et al. 2020a; Lasker et al. 2020b; Baum et al. 2016). This may be due to the availability of substrate resulting from mortality of coral colonies, or other possible competitive interactions such as chemical defenses which would allow *S. edmondsoni* to displace hard corals in the competition for space.

A number of knowledge gaps need to be addressed to establish *S. edmondsoni*'s potential as a reliable indicator of poor water quality and human impacts deleterious to coral reefs in Hawai'i, including the factors driving these blooms. In addition, a recent experimental study revealed decreased growth rates and polyp production of *S. edmondsoni* colonies under enhanced nitrate conditions above ambient *in situ* concentrations, implying that *S. edmondsoni* may not be a suitable indicator of nutrient pollution (Pugh 2019). However, these laboratory-based

experimental studies did not factor in synergistic environmental factors on a broader scale that may affect octocoral populations, such as salinity declines from freshwater input or competition (or lack of) from other hard corals.

3.0 OBJECTIVES, RESEARCH QUESTIONS, AND HYPOTHESES

The drivers of *S. edmondsoni* blooms in Hawai‘i are poorly understood, hindering the use of this species as a bioindicator of coastal water quality problems. This research aims to improve our understanding of *S. edmondsoni* by investigating the presence and abundance of the octocoral in relation to environmental conditions and assess its utility as a bioindicator. The specific research objectives of this thesis include:

- Examine temporal variability and identify the major environmental and anthropogenic drivers of changes in *S. edmondsoni* abundance (i.e. rainfall, stream discharge, water quality, etc.)
- Assess spatial variability and correlation of *S. edmondsoni* to land-based or anthropogenic influences along the coastline (i.e. population, development, agriculture, etc.)
- Evaluate whether this octocoral species can serve as a bioindicator of anthropogenic influence in Hawai‘i by applying the U.S. EPA evaluation guidelines for ecological indicators

The two main questions I aim to answer are: 1) Does *S. edmondsoni* abundance and distribution across a range of sites correlate to stream discharge, rainfall, or anthropogenic influences such as urban development? and 2) Can *S. edmondsoni* be used as a bioindicator of changing environmental conditions from freshwater input and human impacts (e.g. development, agriculture, population, etc.)?

I hypothesize that *S. edmondsoni* will predominantly be found in coastlines near developed, polluted land areas or near stream mouths. I predict that *S. edmondsoni* abundance will positively correlate with urban development and human population, and negatively correlate with distance from shore. I further hypothesize that *S. edmondsoni* can tolerate higher freshwater and nutrient inputs than other scleractinian, reef building corals. I predict higher relative abundance of *S. edmondsoni* at sites after heavy rainfall and storm events due to freshwater and associated nutrient inputs.

4.0 MATERIALS & METHODS

To answer my research questions related to factors that may affect spatial and temporal patterns of *S. edmondsoni* abundance, I combined a number of approaches. All parameters investigated in an attempt to describe the temporal and spatial variability of *S. edmondsoni* are provided in Figure 2, shown with the methods approach I used to assess the influence of each variable on octocoral abundance and distribution.

To examine temporal variability, I established and conducted benthic transect surveys at Kailua and Kualoa on the windward (east) side of O‘ahu, Hawai‘i where octocoral is present, deliberately placing stations nearshore and offshore to assess distance gradients that may reveal impacts of freshwater and nutrient input. I combined these datasets with transect data from previous surveys at Pila‘a, Kaua‘i, collected by myself and the Coral Reef Ecology Laboratory (Hawai‘i Institute of Marine Biology), in collaboration with the Hawai‘i Division of Aquatic Resources (DAR). Survey methodologies were identical to ensure comparability. The effects of environmental drivers on octocoral abundance were then examined, which included temperature, hard coral cover, water quality, stream discharge, and rainfall.

To explore *S. edmondsoni* populations on a larger spatial scale, I combined existing abundance data from the Island of Hawai‘i with data from my benthic transects on O‘ahu and Kaua‘i to conduct a spatial analysis comparing abundance and physical/anthropogenic variables using Geographic Information System (GIS) layers. Physical and anthropogenic variables that were examined for correlation with *S. edmondsoni* abundance included rainfall, distance from shore, human population, development, agriculture, impervious surfaces, and density of underground injection wells.

A qualitative assessment was conducted to evaluate the appropriateness of using *S. edmondsoni* as a bioindicator of anthropogenic influence. The U. S. EPA guidelines for ecological indicators were used to assess the strength of the octocoral species, and how well *S. edmondsoni* met indicator criteria.

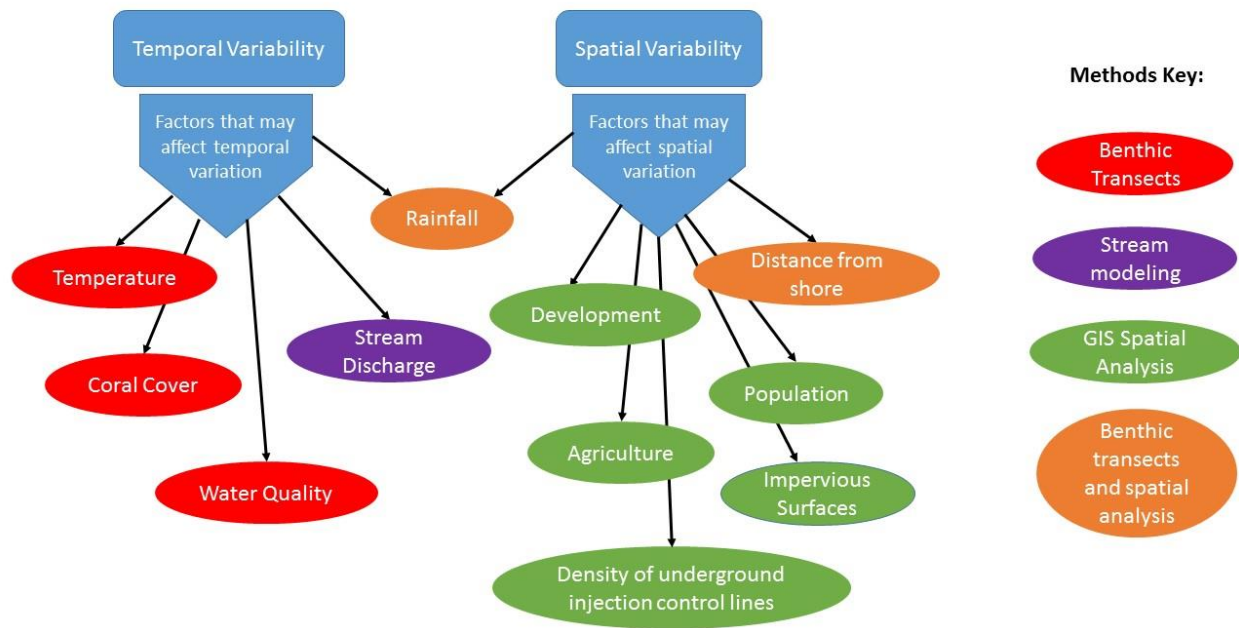


Figure 2. Physical and anthropogenic variables examined to assess the temporal and spatial variability of *S. edmondsoni*, color coded and shown with the methods approach utilized for each factor.

4.1 Site Descriptions

Repeated benthic surveys were conducted at three different study sites to examine temporal variability and associated influential abiotic and biotic factors of *S. edmondsoni* abundance. Three study sites were chosen for the known presence of the octocoral, and are distinctive in varying levels of development, population, and land use/land cover. This allows a unique opportunity to assess patterns of *S. edmondsoni* abundance in different environments over time, and fortifies the attempt to differentiate responses due to natural environmental changes or anthropogenic influence.

4.1.1 Kualoa/Hakipu‘u

The Kualoa study site is adjacent to the Hakipu‘u watershed, located on the windward side of O‘ahu (Fig. 3). It is approximately 3.1 km² reaching a maximum elevation of 673 m due to the Ko‘olau mountain range (Hawai‘i Watershed Atlas). Hakipu‘u stream is a perennial stream located within the watershed (Fig. 4), with a length of 3.9 km. The majority of the land area is

classified as conservation land (59.8%), and is mainly protected but unmanaged. Shrubs and evergreen forests cover most of the land, with a population of only about 400 residents. The well-known 4,000 acre Kualoa Ranch Private Nature Reserve extends through this area, which is a working cattle ranch and a popular tourist and movie site for many films. The ranch was established in 1850 with a vision and goal to protect and enhance the natural resources of the land, while creating sustainable recreational, agricultural and aquacultural operations. Moli'i Fishpond (part of Kualoa Ranch) directly fronts my study stations, and is one of the largest, original remaining fishponds in Hawai'i encompassing 125 acres. Hakipu'u stream restoration efforts from 2012-2016 helped remove invasive species upstream, replanted native plant species to help reduce sediment discharge into the ocean, and installed enclosure fencing to prevent domestic cattle and wild pigs from damaging native vegetation.

The reef system in front of Hakipu'u watershed consists of fringing reefs, patch reefs, and a shallow protective outer reef within a lagoon environment accommodating a deep channel. The maximum depth is 9-12 meters (m), with deep areas consisting mainly of mud bottom. Higher coral cover is found at shallow depths, and the deeper zones are marked by sand, mud, and low coral cover. This study site is located in the northern section of Kāne'ohe Bay, which is more exposed to ocean swells as compared to the central and southern sections of the bay. As a result, water exchange is adequate, however, north Kāne'ohe Bay is known to receive large amounts of freshwater input from the larger Waiāhole and Waikāne streams.

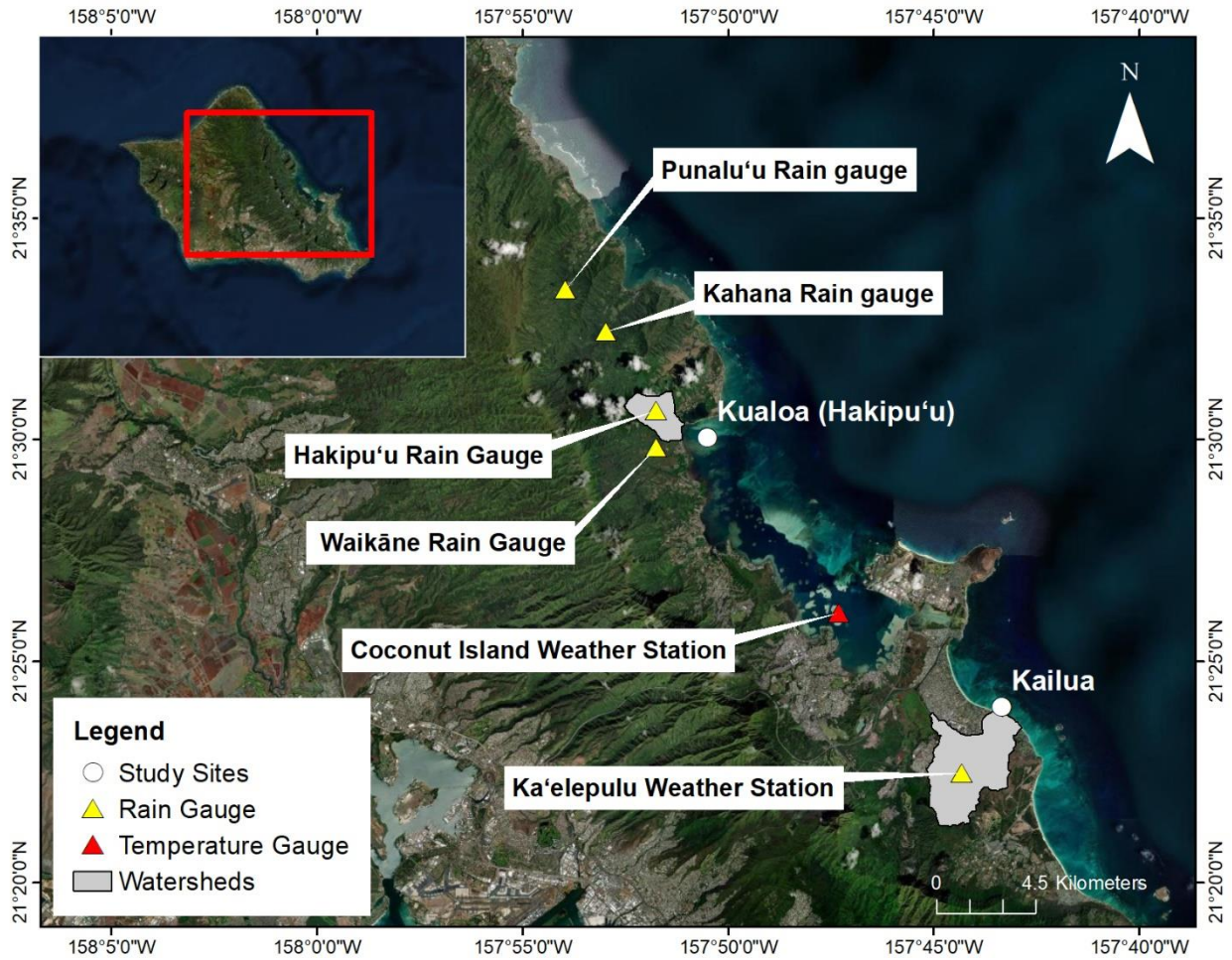


Figure 3. Map depicting Kualoa and Kailua study sites along with their adjacent watersheds, and rain and temperature gauges tested or utilized for temporal analysis. Inset map shows extent of mapped area delineated in red.

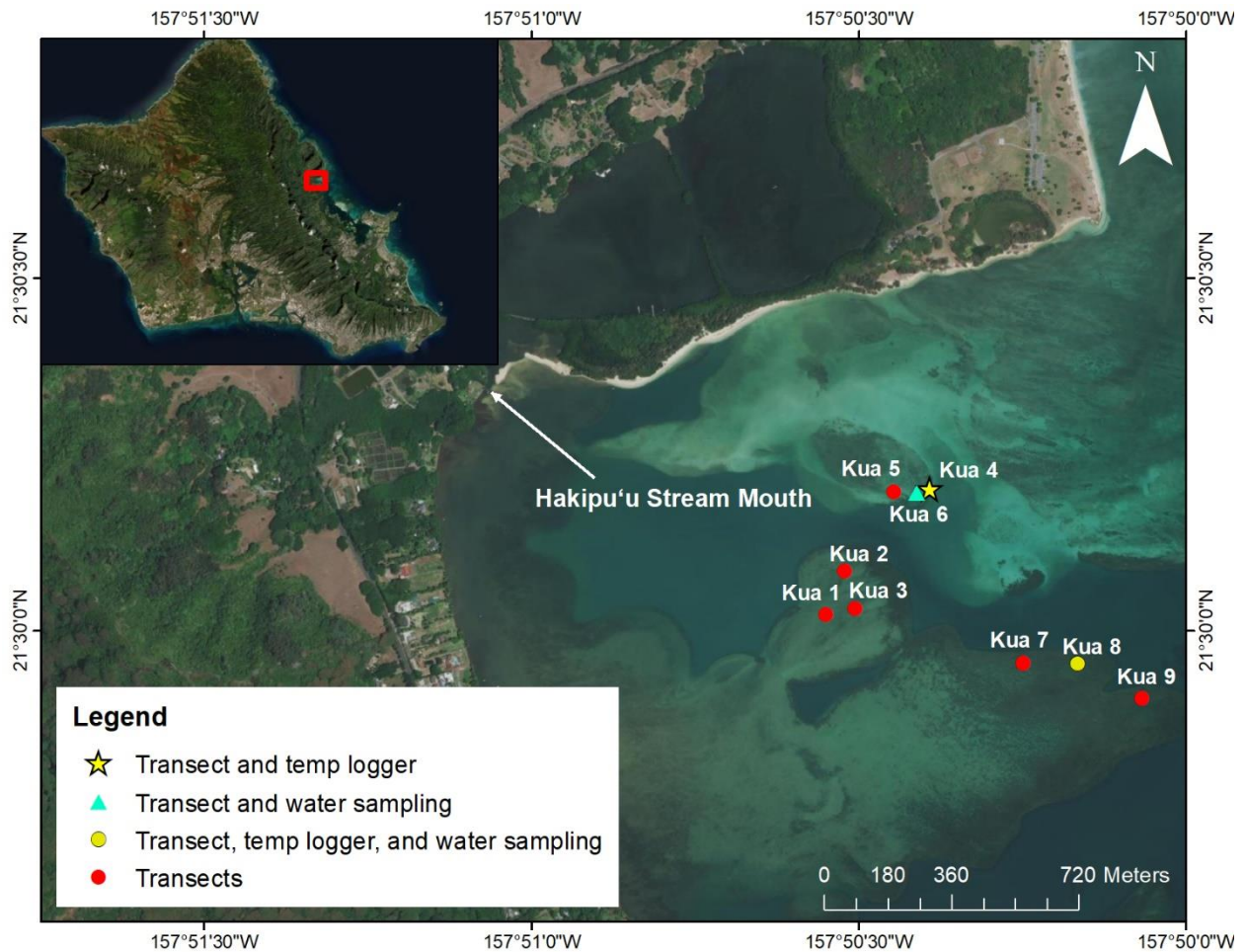


Figure 4. Map showing Kualoa transects, location of temperature loggers, and water sampling sites. Inset map shows extent of mapped area delineated in red.

4.1.2 Kailua/Ka‘elepulu

The Kailua site is within the Ka‘elepulu watershed, also on the windward side of O‘ahu, and is roughly 11.8 km² (Fig. 3). The Ka‘elepulu watershed encompasses the residential areas of Keolu (Enchanted Lake), Lanikai, and Kailua, which are densely populated towns with a combined estimate of 38,000 residents according to the 2019 U.S. Census. Development accounts for 40% of the land use within the watershed, with 66% classified as urban districts. The Ka‘elepulu stream is a perennial stream, with a length of 10.2 km. It is the only natural outlet for the entire watershed, and in response to the growth of Kailua Town in the 1950s, heavy development began from the 1950s to late 60s to accommodate the booming population.

The original Ka‘elepulu watershed was mostly marsh and wetlands until the 1950s, when the building of a new canal and the dredging of Ka‘elepulu Pond to create the urban community of Keolu began. With Ka‘elepulu stream being the only natural outlet, heavy rainfall events would frequently cause flooding to the area from Kawainui Marsh, which prompted the construction of the Oneawa canal (completed in 1952) to drain the water from the northeast extent of the marsh to the north end of Kailua Beach. While this new outlet minimized the severity of flooding events, it was still not entirely efficient, and by 1966 the Kawainui levee was completed to further prevent overflow. In the late 1960s, Ka‘elepulu Pond, which was surrounded by 90 acres of marsh land, was dredged and filled to create the present community of Keolu. Subsequent housing development and non-point source pollution from the neighborhoods contributed major amounts of sediment to the pond (connected to the Ka‘elepulu stream), which eventually drained directly into the ocean at the south end of Kailua Beach. Biological diversity in the pond was reduced, turbidity increased, waterfowl became endangered, and the development of a sewage/storm drain system that discharged into the pond led to the degradation of coastal water quality along Kailua Beach. Furthermore, in the mid-1960s, new pumping stations began to pump sewage discharge from Keolu to the newly constructed Kailua Wastewater Treatment Plant, but sewage leaks from faulty pipes occurred often until the early 2000s, contaminating the pond and further reducing coastal water quality in Kailua Bay. During large storm events, runoff from storm drains and canals upland contribute to sediment and nutrient loads entering the pond, including drainage from city streets.

As a consequence of the intense construction of canals, levees, and drainage systems, by the 1990s, Ka‘elepulu pond and the stream were isolated from all natural stream flows, and now receives the majority of runoff from streets and storm drains. Drainages from city streets and canals contribute about 200 cubic yards of road gravel and tar to the pond each year, which is equivalent to 20 large dumpsters. In addition, following significant rainfall and storm events, large quantities of trash are introduced into the pond with a portion collecting and floating on the surface, requiring monthly removals by clean-up crews. The pond is clearly deteriorated, and Ka‘elepulu stream is now managed as a storm drain and retention basin with about 480 storm drain inlets emptying directly into the lake/pond system. The lack of natural stream flow to Ka‘elepulu resulted in a 575,000 m² area of stagnant water, and precipitated a build-up of sand at

the stream mouth, blocking oceanic exchange with Kailua Bay. The sand berm prevents water from draining into the ocean, which hinders the critical functionality for estuaries. The City now has to periodically open the sand berm using heavy machinery (about 6-10 times per year) to promote water circulation and minimize flood threats. The Ka'elepulu watershed and Kailua Beach coastal ecosystems have been historically impacted and heavily altered as early as the 1950s, and poor infrastructure, planning, and development elucidates the current condition of the watershed.

The major marine benthic substrate categories found in Kailua are areas of carbonate sand, hard bottom, and reef habitats of coral and algae. At the center of Kailua Bay is a large sand channel that cuts across the reef, connecting seaward and nearshore sand fields. While steep bathymetric slopes occur along the sand channel, corals are mainly found on spur and groove surfaces south of the sand channel closer to shore. The reefs in Kailua are patchy, with some occurrences of large mounding coral colonies. Coral cover is relatively low, with higher live coral cover in deeper depths, as most of the reef is degraded and large areas of sand are dispersed between hard bottom habitat. Depths range from 1.5 m nearshore to 3 m near Popoi'a Island (Fig. 5), with coral reef habitats found in up to 22 m depths further offshore.

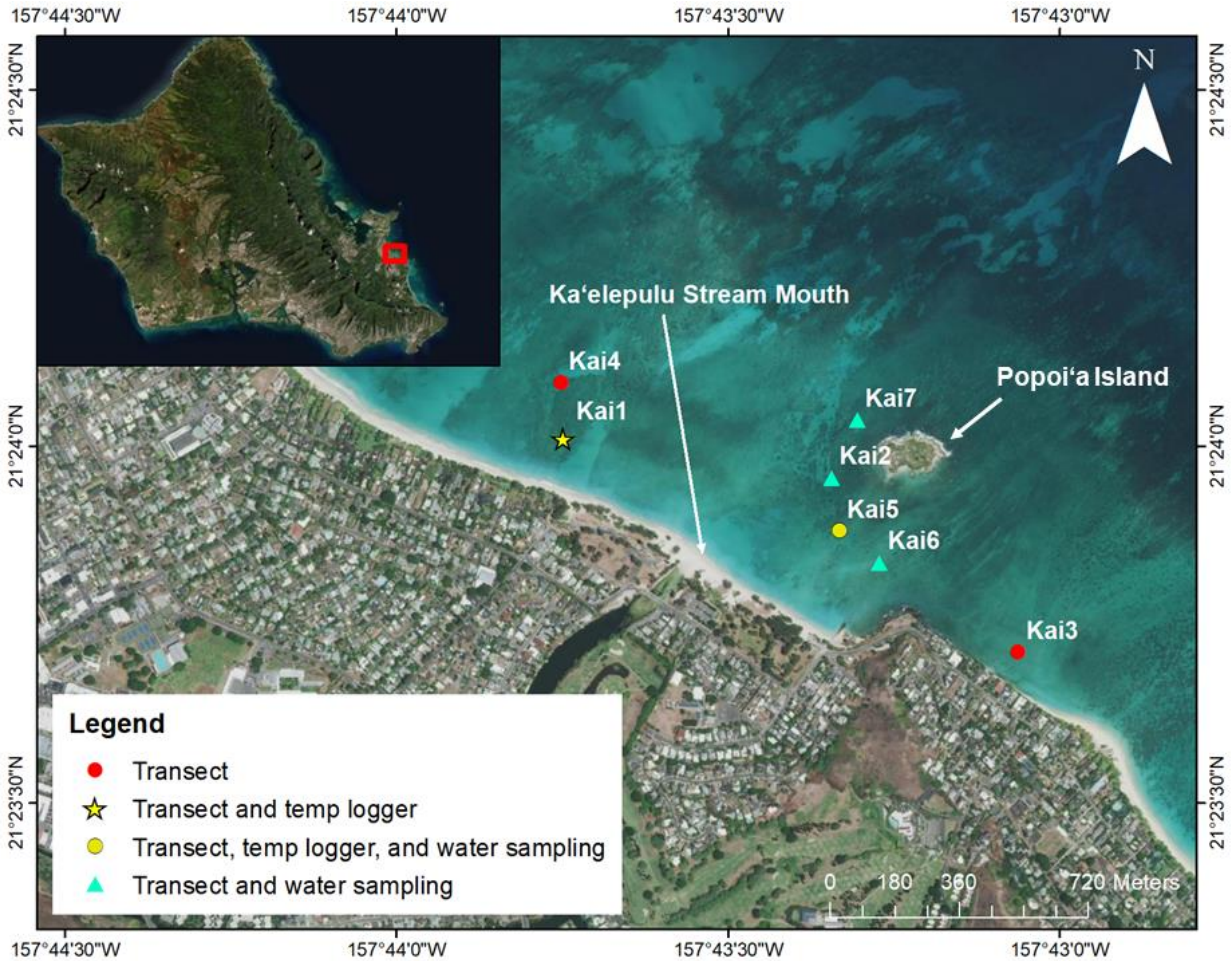


Figure 5. Map of Kailua transects, location of temperature loggers, and water sampling sites. Inset map shows extent of mapped area delineated in red.

4.1.3 Pila'a

The Pila'a site is located on the northeastern side of the island of Kaua'i (Fig. 6). The Pila'a watershed is directly upland of the reef study stations, covering 5.8 km² with a maximum elevation of 288 m (Hawai'i Watershed Atlas). Agriculture comprises over half of the land use, with a population of roughly 200 and 99.9% of the land belonging to private ownership. It is unprotected, and covered mainly by grassland (42%) and evergreen forests (27%). The perennial Pila'a stream is 4.9 km long, which empties out and forms a channel that bisects the adjacent shallow reef flat (Fig. 7). Two intermittent streams are found on the east side of Pila'a beach (Fig. 7), contributing to additional freshwater input in the eastern sector.

A shallow fringing reef is found at Pila‘a, with a deep channel dividing the reef flat into distinct east and west sectors that vary in current directions, water motion, and sedimentation impacts. The channel reaches a depth of 9-15 m at the outer edge of the reef, where waves constantly break over the reef crest. The reef flat ranges in depth from 0.5 to 2 meters, and during low tides shallow portions are exposed. A more topographically complex forereef extends into deeper water after the reef crest, and is subject to higher and persistent wave action. The eastern sector of the reef flat is more prone to freshwater input due to water circulation patterns, proximity to three streams, and depth characteristics (Jokiel et al. 2002; Rodgers et al. 2021). Transects in the eastern sector were therefore exclusively selected to assess freshwater impacts to *S. edmondsoni* populations. It is further important to note that in the western sector, the octocoral species studied was virtually absent from 2016-2019 (0% detected), most likely due to the lack of freshwater input.

Pila‘a has had an interesting history of land use and development, with many historical conflicts regarding land ownership (Watson 2019). In the late 1990s, the landowner at the time began to develop Pila‘a and substantial grading, filling, and other construction work were conducted without legal authorized permits. The extensive work included large-scale grading on a plateau above Pila‘a beach, the creation of a cliff 40-60 ft in height by vertical cutting, construction of roads, and an installation of a 30-inch pipe that drained water, mud, and other wastes directly to the ocean and onto the Pila‘a reef flat. The un-permitted work caused severe damage not only to the land, but during a heavy rainstorm in November of 2001, heavy mudslides resulting from the illegal grading operations devastated the eastern portion of Pila‘a reef. The western end of the reef flat was outside the influence of sediments, and surveys conducted the following year to assess damages found statistically significant differences in coral populations and conditions between the east impacted area vs. the western unimpacted area. Results revealed higher numbers of stressed, bleached, and dead corals, larger amounts of terrigenous mud and sediments, abnormal anoxic conditions, and high turbidity in the eastern impacted sector (Jokiel et al. 2002). Fields of large dead coral colonies were also recorded, which were determined to be caused by previous chronic sedimentation events (also as a result of development) in addition to the 2001 event. The eastern Pila‘a reef is still presently in a degraded state not fully recovered, thus serving as a unique study site to examine chronic anthropogenic

impacts not from population or high development, but from land development and consequent sedimentation input.

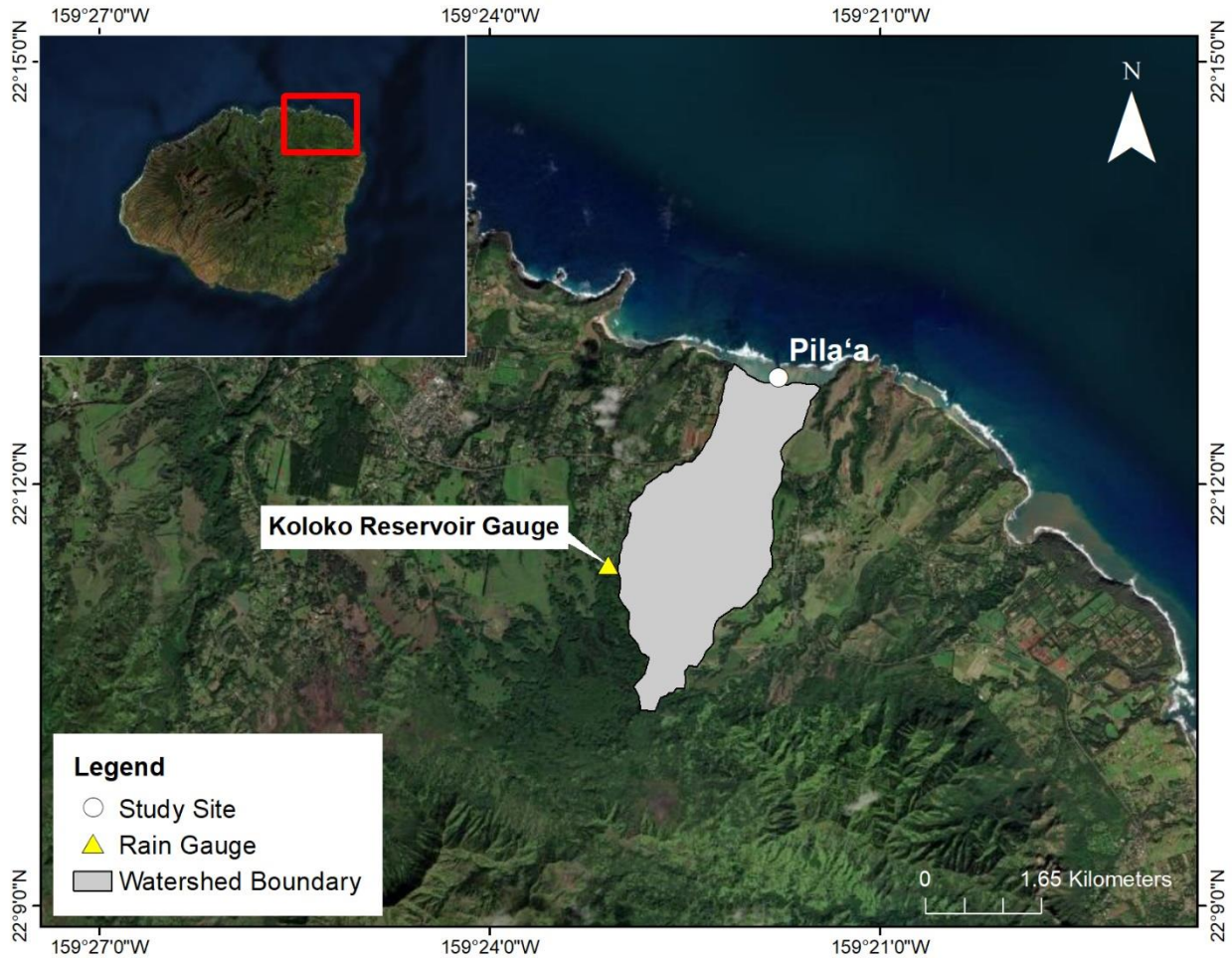


Figure 6. Map of the Pila'a study site shown with adjacent watershed and location of rain gauge used for temporal analysis. Inset map shows extent of mapped area delineated in red.

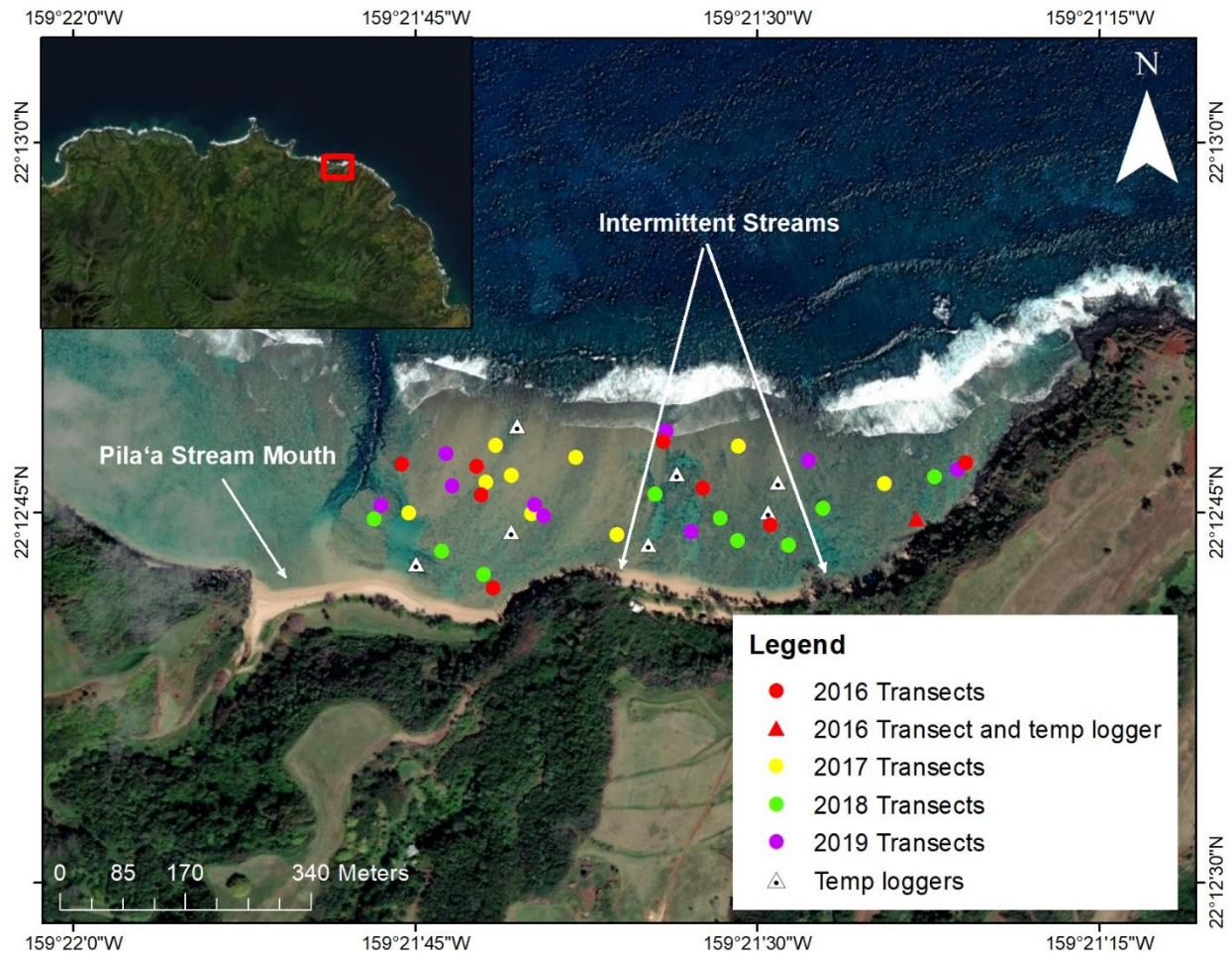


Figure 7. Map depicting Pila'a transects and location of temperature loggers from 2016-2019. Inset map shows extent of mapped area delineated in red.

4.2 Temporal Analysis

4.2.1 Benthic Transects

Benthic transects were conducted to quantify hard coral cover (excludes *S. edmondsoni*) and *S. edmondsoni* abundance at three sites on two islands: Kualoa and Kailua on the island of O'ahu, and Pila'a, Kaua'i. Transect locations were selected based on high to low presence of the octocoral and varied with distance from shore (25 to 1,300 meters offshore). Nine transects were established at the Kualoa study site and seven in Kailua (Figs. 4 & 5). Start and end points of

transects were recorded using a Garmin GPSmap 78s unit, along with bearings and photos taken at the start and end to aid in navigation and accurate relocation. Nine spatially comparable transects were selected from Pila‘a for each year (out of a sample size of approximately 50 transects/year) from 2016-2019 (Fig. 7). Dates surveys were conducted at Kualoa, Kailua, and Pila‘a are shown in Table 1. While data collection for Kualoa and Kailua transects were largely dependent on weather and the availability of resources, approximately 4-month intervals between surveys were targeted.

Table 1. Dates transect benthic surveys were conducted at the Kualoa, Kailua, and Pila‘a study sites along with sample sizes of each survey period.

Site	n	Survey Period 1	Survey Period 2	Survey Period 3	Survey Period 4
Kualoa	9	July 17, 2020	December 2, 2020	March 4, 2021	N/A
Kailua	7	August 16, 2020	December 6, 2020	March 23, 2021	N/A
Pila‘a	9	August 29, 2016	June 19-21, 2017	July 13-15, 2018	June 24-25, 2019

Transect survey methodology is based on the Fisheries Ecology Research Laboratory’s Fish Habitat Utilization Surveys (FHUS). This method is also utilized by Maui DAR and is consistent with most statewide surveys throughout the main Hawaiian Islands (Rodgers et al. 2019). Benthic photos were taken along a 25 m transect at every meter along the line starting at the 0 m mark (26 photographs per transect), using a Canon Powershot G16 camera and underwater housing mounted on a monopod kept perpendicular to the bottom to avoid parallax. The camera monopod is set to photograph an area of 50 x 69 cm, and photos were downloaded into the coral reef image analysis program CoralNet for processing (Beijbom 2015, Williams et al. 2019). Generation of 25 random points within each photograph allowed for identification of species under each point. Data was then exported and percent cover was calculated in Microsoft Excel to examine benthic composition, including coral and octocoral cover. The methodology selected and employed in this study was to ensure comparability and compatibility with other data, but also incorporates previous research in determining precision and statistical power of various methods to detect changes (Brown et al. 2004).

4.2.2 Environmental Data

Environmental data including distance from shore, precipitation, temperature, and water quality at each site were collected to determine the major drivers of *S. edmondsoni* abundance. Transect distances from shore were calculated in ArcGIS ArcMap version 10.3.1. Daily precipitation records for Kailua were obtained from the Ka‘elepulu Wetland weather station maintained by Hugo De Vries, located approximately 2.9 km upstream of the Kailua study site (Fig. 3; <https://kaelepuluwetland.com/weather>). Rainfall records for Kualoa were obtained from the United States Geological Survey (USGS) Kualoa Ranch/Hakipu‘u rain gauge (USC00514828), roughly 2.2 km from the Kualoa study site (Fig.3). Precipitation for Pila‘a was retrieved from the National Oceanic and Atmospheric Administration’s (NOAA) National Centers for Environmental Information (NCEI) Climate Data Online database. No rain gauges are installed at Pila‘a, therefore the Koloko Reservoir gauge (USC00514758) was selected as the best representative based on elevation and proximity to the watershed and study site. The Koloko rain gauge is located approximately 3.1 km from the Pila‘a study site (Fig. 6).

To examine the possible effects of temperature, I installed two temperature loggers at each of my established study sites (Kualoa and Kailua, Figs. 4 & 5) and eight temperature loggers previously deployed at Pila‘a throughout 2016-2019 were used in data analyses (Fig. 7). Onset HOBO® Water Temp Pro v2 loggers were employed and set to record data at 30-min intervals. The HOBOWare Pro software program was used to download and export data. At the Kualoa and Kailua sites, loggers were inserted into artificial rocks made of Quikrete® concrete mix to minimize detection and prevent human tampering (Fig. 8). Due to limited access at Pila‘a, loggers were attached to stainless steel pins using metal cable ties and directly inserted into the reef flat, as there was less concern for human interference. Temperature loggers were calibrated before deployment, and offsets along with deployment and retrieval dates are shown in Table 2. Daily average values were extracted and calculated using midday temperatures between 11:00-14:00.



Figure 8. Artificial rock used to deploy temperature loggers at the Kualoa and Kailua study sites (left), and an example photograph of a temperature logger inside the rock on the reef flat (right).

Table 2. Temperature logger offsets/deviation from calibration, and deployment and retrieval dates.

Transect/logger name	Deviation	Deployment Date	Retrieval Date
Kai 1	± 1.3	8/16/2020	3/23/2021
Kai 5	± 1.5	8/16/2020	3/23/2021
Kua 4	± 1.5	7/17/2020	3/4/2021
Kua 8	± 2.1	7/17/2020	3/4/2021
Pila‘a 2016	± 0.7	8/29/2016	6/19/2017
Pila‘a 2017	ND	6/19/2017	7/12/2018
Pila‘a 2018-2019	± 0.1	7/12/2018	6/25/2019

Water quality samples were obtained by collecting replicate sea water samples from Kualoa and Kailua at two locations during each survey period (Figs. 4 & 5). Thermo Scientific™ Nalgene™ Amber HDPE wide mouth bottles were used to collect one liter of water from approximately 1 m below the sea water surface. The bottles were pre-washed with 10% hydrochloric acid and rinsed three times with seawater at corresponding stations before sampling. Samples (50 mL) were filtered onto Whatman™ glass 24mm microfiber filters grade GF/C (1.2 μm) using a 60 mL syringe and placed in 50 mL falcon tubes. Samples were analyzed

by the School of Ocean & Earth Science & Technology Laboratory for Analytical Biogeochemistry for nutrient analyses. Total phosphate, nitrate and nitrite were acquired using a Seal Analytical AA3 HR Nutrient Autoanalyzer. A detailed description of the instrument and outlined procedures can be found at http://www.soest.hawaii.edu/S-LAB/equipment/slab_autoanalyzer.htm.

4.3 Hydrological Modeling

To explicate the possible effects of stream discharge on octocoral temporal variation at the Kualoa site, a hydrological model was used and parameters were extrapolated from historical discharge records at Hakipu‘u stream (USGS #16295300; Fig. 4) that were available between the period of October 1, 2002 to October 14, 2008 (no gauges are currently operating there). Both the Pila‘a and Kailua sites have streams within their corresponding watersheds as well, however, no historical stream gauge records at Pila‘a are available (and therefore cannot be modeled). The Ka‘elepulu stream at Kailua is blocked by a sand berm predominantly year round, preventing the influx of freshwater into the ocean the majority of the time. Therefore the influence of stream discharge at Kailua and Pila‘a were not investigated.

4.3.1 Environmental Parameters for Model Input

Environmental variables obtained for stream model inputs included daily precipitation, historical stream discharge, and air temperature for evapotranspiration values. While no historical precipitation data was available within the Hakipu‘u watershed during the discharge time period records, three USGS gauges are in close proximity: the Waikāne (#213000157515401), the Kahana (#2132371575730701), and Punalu‘u rain gauges (#213335157540601) (Fig. 3). All three rain gauges were used separately and tested in the model to evaluate efficiency, best fit, and correlation with discharge and alternative rain gauges.

Air temperature data was obtained from the Hawai‘i Institute of Marine Biology’s (HIMB) weather station on Moku o Lo‘e Island (<http://www.pacioos.hawaii.edu/weather/obs-mokuoloe/>; Fig. 3). The HIMB weather station was the nearest station to the Kualoa study site providing air temperature data (located approximately 9.7 km away), and is therefore the most representative of temperatures within the Hakipu‘u watershed.

4.3.2 Analyses and Stream Modeling

Precipitation and stream modeling analyses were performed in R Studio with R version 4.0.3. The R-packages used to model, interpret and analyze hydrological data and characteristics included *airGR*, *airGRteaching*, *devtool*, *dataRetrieval*, *xts*, *hydroTSM*, and *dplyr*. To model the rainfall-runoff process, the GR5J model, a five parameter daily lumped hydrological model (Le Moine 2008), was used. The five parameters utilized in this model include the maximum capacity of soil moisture accounting storage, the groundwater exchange coefficient, the capacity of routing store, the time base of UH, and the threshold for change in water exchange function sign. The input data frame needed to run the model requires daily values of precipitation (mm), potential evapotranspiration (PET, mm/day), and stream discharge (mm/day). PET was calculated using the Hargreaves formula (Hargreaves & Allen 2003) with minimum and maximum temperature data, and was computed in R Studio using a written function. Gaps in temperature data which resulted in missing PET values were replaced with the mean PET during the corresponding time period. To evaluate model efficiency, the performance metric or objective function chosen was the Kling-Gupta Efficiency criterion (KGE). The KGE criterion is a weighted combination that includes simulated mean flow, flow variability, and daily correlation which has been documented to improve flow variability estimates (Gupta et al. 2009). A negative value of KGE is considered poor or unsatisfactory, and a value of 1 is optimal.

4.4 Spatial Analysis

To examine spatial correlations of *S. edmondsoni* abundance with human influences (population, development, impervious surfaces, agriculture, and underground injection wells) and other environmental/physical factors (rainfall and distance from shore) from adjacent watersheds, octocoral percent cover data provided by DAR for the west coast of the Island of Hawai‘i (West Hawai‘i) was combined with my benthic transect datasets from O‘ahu and Kaua‘i. and mapped against state GIS layers of land-based information data. Table 3 shows the factors (predictor variables) examined and the source of data utilized for the spatial analysis.

Table 3. Land-based and environmental factors examined for the *S. edmondsoni* spatial analysis shown with data sources.

Factor	Unit	Source
Rainfall	mm/yr	Hawaii Rainfall Atlas ¹
Population	total # in catchment	SEDAC ² (2015)
Impervious Surfaces	%	CCAP ³ (2011)
Open Development	%	CCAP ³ (2011)
Agriculture	%	CCAP ³ (2011)
Underground Injection Wells	#/km ²	Hawaii DOH ⁴ (2010)
Distance from shore	m	calculated in ArcGIS

- 1) Hawai‘i Rainfall Atlas (Giambelluca et al. 2013), University of Hawai‘i. <http://rainfall.geography.hawaii.edu/>.
- 2) SEDAC Gridded Population of the World, v4.11. <https://sedac.ciesin.columbia.edu/data/set/gpw-v4-population-count-adjusted-to-2015-unwpp-country-totals-rev11/data-download#close>
- 3) Coastal Change Analysis Program 2011, NOAA, <https://coast.noaa.gov/digitalcoast/tools/lca.html>.
- 4) State of Hawai‘i Department of Health, <http://health.hawaii.gov/>.

Watershed boundaries obtained from the Hawai‘i Statewide GIS Program were plotted to examine catchments adjacent to each survey site, after which specific land-based and environmental factors corresponding to the specific watershed were compiled to examine influence on octocoral populations. The selection of corresponding watersheds to each DAR survey site was determined by assessing distance to the nearest stream mouth, presence of a stream mouth and data availability, and ocean surface current patterns which contribute to the distribution of human land use effects on coastal habitats. Population counts were extracted from the Socioeconomic Data and Applications Center (SEDAC) 2015 adjusted population count dataset. Global raster layers were downloaded and clipped by watershed boundaries, and total population numbers for each catchment were subsequently calculated using the Zonal Statistics geoprocessing tool in ArcMap 10.3.1. Population maps were created using downloaded population density raster datasets from SEDAC (<https://sedac.ciesin.columbia.edu/data/set/gpw-v4-population-density-adjusted-to-2015-unwpp-country-totals-rev11>), and land cover maps were created from the National Oceanic and Atmospheric Administration’s Coastal Change Analysis Program (NOAA C-CAP). All GIS maps were created using ArcGIS ArcMap version 10.3.1.

For statistical analyses, previously compiled quantitative values for each land-based and anthropogenic factor attributed to each watershed (Wang et al. 2001, Tingley et al. 2019; Crawford et al. 2015) and aggregated to upstream scales (Tsang et al. 2014, Tingley et al. 2019) were used. Factors examined included mean annual rainfall (mm/yr), population, distance from

shore (m), coverage of impervious surfaces (%), open development (%), agriculture (%), and underground injection control wells (#/km²). Impervious surfaces are water-resistant surfaces such as asphalt, concrete, or brick, and are mainly artificial structures like pavement roads, parking lots, and major industrial areas. These artificial surfaces limit absorption of nutrients and water into soil, which increase the amount of runoff carrying pollutants and other contaminants into our waterways (Slonecker et al. 2001; Guan et al. 2016; Ren et al. 2014; Chormanski et al. 2008). Open development zones contain areas with a mixture of constructed materials (concrete, asphalt, etc.) with varying amounts of vegetation or other cover. This class commonly includes family housing areas, suburban neighborhoods, and managed grasses or low-lying vegetation planted in developed areas for recreation or aesthetic purposes, where constructed surfaces account for less than 20% of total land cover (<https://coast.noaa.gov/digitalcoast/training/ccap-land-cover-classifications.html>). Land cover data from C-CAP combines low, medium, and high intensity developed categories into one impervious surfaces class, as the percentage breakdown of impervious surfaces for Hawai‘i within each development category was not adequate for high resolution mapping. Underground injection wells are wells used for injecting water and other fluids such as sewage, geothermal effluents, and other wastewater mainly from industrial sources.

West Hawai‘i DAR provided octocoral abundance data (% of total benthic cover) for the years 2003-2017 (Fig. 9). Surveys conducted more recently (2016 and 2017) detected a sudden decline and virtual absence of the octocoral, due most likely to increased temperatures and the 2014/2015 bleaching events that occurred across Hawai‘i (Rodgers et al. 2017a; Couch et al. 2017; Bahr et al. 2015). Therefore, the 2014 dataset was used and combined with my O‘ahu and Kaua‘i datasets to conduct a spatial analysis for correlation of predictor variables influencing octocoral abundance. Methodologies are similar and comparable for both datasets; a full description of the methods for the West Hawai‘i transect surveys can be found in the 2010 Long-Term Monitoring of Coral Reefs of the Main Hawaiian Islands Final Report (Walsh et al. 2010). Ten of 23 sites were selected for analysis (Fig. 10), as over half the original sites contained zeros for octocoral proportions, and/or there were no quantitative data available for the corresponding watershed due to the absence of stream networks within the catchment. Five of the 15 transects that reported zero abundance of *S. edmondsoni* were kept to evaluate the potential drivers that may cause the absence of the octocoral species.

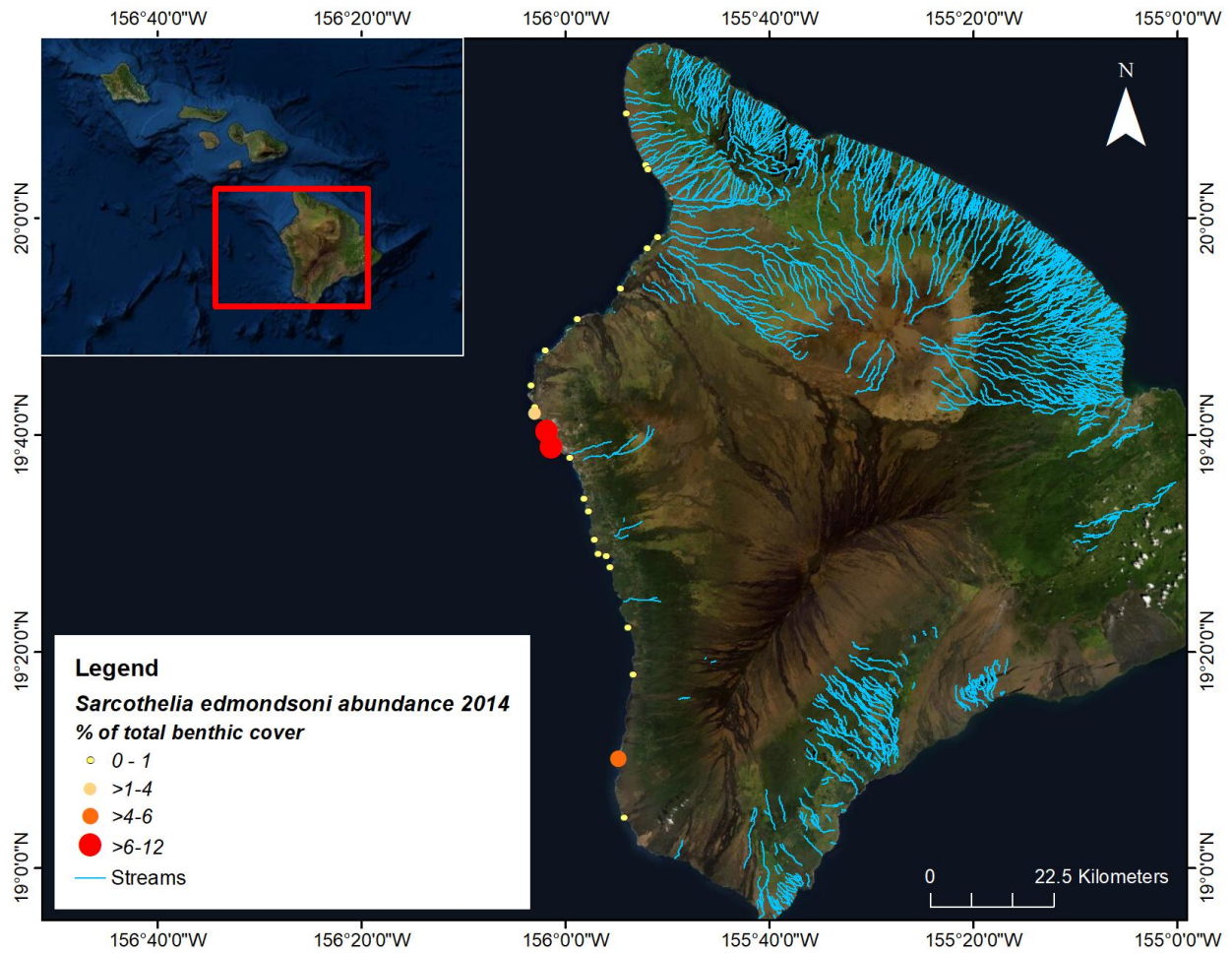


Figure 9. West Hawai'i *Sarcothelia edmondsoni* abundance (% of benthic cover) shown as graduated symbols based on abundance (n=23) and stream networks. Inset map shows extent of mapped area delineated in red.

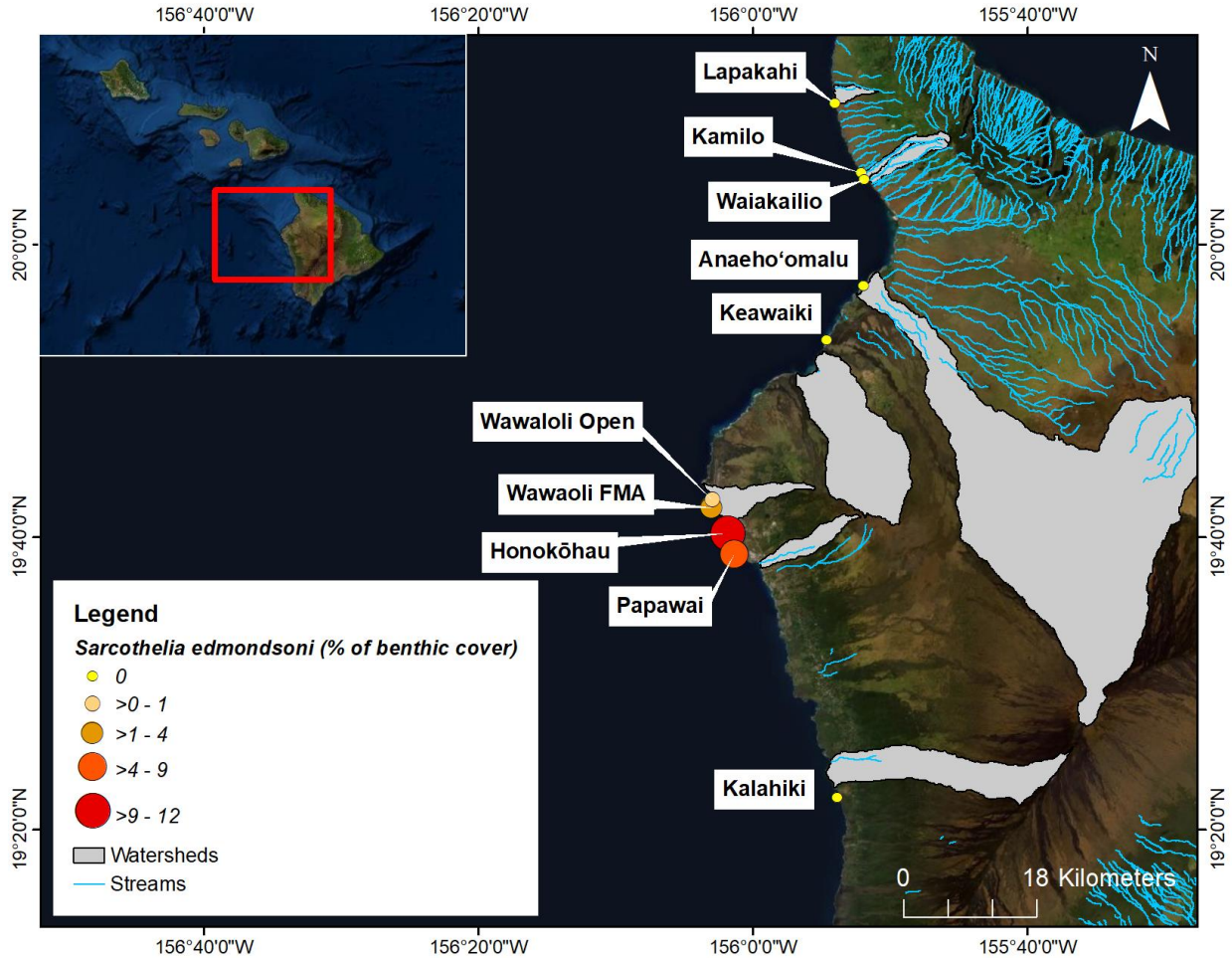


Figure 10. West Hawai'i *Sarcothelia edmondsoni* abundance (% of benthic cover) shown as graduated symbols based on abundance (n=10), along with stream networks and adjacent watersheds used in spatial analysis. Inset map shows extent of mapped area delineated in red.

4.5 Statistical Methods

All statistical analyses were performed in R (Version 4.0.3) and the integrated development environment, R-Studio Desktop (Version 1.4.1103, RStudio Team 2021). Significance level was set at $\alpha = 0.05$ for all analyses. All figures were generated using the R package *ggplot2* (Wickham 2016).

4.5.1 Hard Coral Cover and Octocoral Abundance

Friedman tests, the non-parametric alternative to the repeated measures or paired data ANOVA test (Cleophas & Zwinderman 2016), were performed to assess any significant changes

in *S. edmondsoni* abundance and hard coral cover between each survey period for the Kailua and Kualoa sites since identical transects were repeated each period. A non-parametric Kruskal-Wallis test was conducted to assess any significant changes in octocoral and hard coral cover at the Pila‘a site between survey periods, as new transects (unreplicated) were surveyed each year. Pairwise Wilcoxon signed rank tests, with Bonferroni corrections to control for Type I errors (false positives), were then applied for post hoc comparisons at all sites.

4.5.2 Environmental Variables

Environmental data for precipitation and temperature were collected to examine correlations with changes in *S. edmondsoni* abundance. Octocoral response times to rainfall were examined to determine the appropriate gap or lag time that may allow for responses. Simple linear regressions were conducted and R^2 values were assessed for a one, two, or three-month response time. The same method was applied to examine the best window (1, 2, or 3-months) of precipitation data to use in statistical analysis. The response time and window showing the strongest relationship with changes in *S. edmondsoni* abundance were then used to extract precipitation values for use in analysis examining correlations of octocoral abundance with different environmental predictor variables.

To obtain temperature values and test for correlation with *S. edmondsoni* changes, two-sample t-tests were performed to check for significant differences in temperatures between the two loggers installed at each of the Kailua and Kualoa sites. This was conducted to ensure rationality of combining the mean from both temperature loggers within each site as a predictor variable.

4.5.3 Octocoral Correlations with Environmental Variables

To examine the strength of predictor variables affecting the octocoral species abundance on temporal scales, generalized linear models (GLMs) were applied to analyze the non-normal *S. edmondsoni* abundance (proportion of coral cover) data from benthic surveys. Transects with no *S. edmondsoni* consistently throughout all survey periods (0% cover) were removed from GLMs to clearly distinguish correlation of predictor variables to *changes* in octocoral abundance through time (Kua 7, 8 and 9; Fig. 4). Predictor variables tested in GLMs for established study

sites (Kualoa, Kailua, and Pila‘a) included rainfall, distance from shore, temperature, and coral cover, with the addition of stream discharge for the Kualoa site. Proportion data were transformed following the formula below (where n = sample size) to account for the presence of zero’s and one’s in the original dataset (Smithson & Verkuilen 2006), prior to logit transformations so as to prevent invalid values (e.g. the log of 0 is undefined).

$$\frac{\textit{Proportion} * (n - 1) + 1/2}{n}$$

Data were subsequently logit transformed to aid in interpretability and increase power (Warton & Hui 2011). The logit transformation pulls out the ends of a distribution, expanding the scale so that smaller differences in proportion will have a larger difference that can easily be detected. The logit scale also prevents nonsensical model predictions, such as having negative or greater than 100% in proportion values.

The R-packages *plyr* and *MuMIn* were used for summarizing data and performing model selection. Best fit models were selected by examining residual plots, Akaike information criterion corrected for small sample sizes (AICc), delta, and weights. Residual plots are graphs that show residuals (difference between the observed value of the dependent variable and the predicted value) on the y-axis and the independent variable on the x-axis. Residual plots that show points randomly scattered around the horizontal axis indicate a linear regression model is appropriate for the data and heteroscedasticity, or unequal variability, is not present. AICc values measure how well a model fits the data, and are used to compare two or more models with the model having the lowest score ranked as best. Delta values and weights are also commonly used to compare and evaluate models. Delta measures relative differences between candidate models and the best ranked model, where models that have a delta of greater than 10 show the model is highly unlikely and should be rejected (Burnham & Anderson 2002). Weights are the proportion of the total amount of predictive power relative to the whole set of candidate models, where a weight of 0.96 means that the model contains 96% of the total explanation from the full set of models evaluated. Overall model fits were also assessed using pseudo R^2 values, which represent how well the model predicts the outcome and explains total variability. Larger pseudo R^2 values are stronger, with 0.2-0.4 representing an excellent model fit (McFadden 1979).

4.5.4 Spatial Analyses

To assess the strength of natural and anthropogenic factors on spatial patterns of *S. edmondsoni*, simple GLMs were conducted to examine the influence of each individual predictor variable on octocoral abundance. Variables were scaled prior to running GLMs to allow comparability of effect sizes. Model estimates, which indicate the sign of the relationship (positive or negative) and effect size of the predictor variable on the response, pseudo R², and *p* values were examined for correlations with octocoral abundance. Predictor variables included population, development, impervious surfaces, agriculture, number of underground injection wells, rainfall, and distance from shore. *S. edmondsoni* abundance data was transformed following the same methods applied in the temporal analysis (4.5.1).

4.6 Bioindicator Evaluation

In addition to the quantitative analysis of *S. edmondsoni* abundance and response patterns, I conducted a qualitative assessment to evaluate the strength and utility of the species as a bioindicator. Numerous researchers have compiled major criteria for ecological indicators (Jameson et al. 1998; Erdmann & Caldwell 1997; Crosby & Reese 1996; Jones & Kaly 1996; Alcolado et al. 1994; Podani 1992; Cranston 1990; Lang et al. 1989; Brown 1988), and the U. S. EPA additionally established their own evaluation guidelines. The U. S. EPA guidelines expanded on existing frameworks for effective ecological indicator performance, and is broken down into four phases of evaluation (Jackson et al. 2000): (1) Conceptual Foundation, (2) Feasibility of Implementation, (3) Response Variability, and (4) Interpretation and Utility. Incorporated within these four phases are an additional 15 guidelines listed in Table 4, which can be customized to address the needs of a specific management problem.

Table 4. U. S. Environmental Protection Agency phases and evaluation guidelines for ecological indicators (Jackson et al. 2000).

Phases	Guidelines
Conceptual Foundation	1) Relevance to the assessment 2) Relevance to ecological function
Feasibility of Implementation	3) Data collection methods 4) Logistics 5) Information management 6) Quality assurance 7) Monetary costs
Response Variability	8) Estimation of measurement error 9) Temporal variability (within the field season) 10) Temporal variability (across years) 11) Spatial variability 12) Discriminatory ability
Interpretation and Utility	13) Data quality objectives 14) Assessment thresholds 15) Linkage to management action

A methodical assessment following the above framework is employed to review, discuss, and evaluate the strength of *S. edmondsoni* as a bioindicator. I combined EPA guidelines (Table 4) with additional criteria from various researchers, specifying questions for each of the four phases of evaluation (conceptual foundation, feasibility of implementation, response variability, and interpretation/utility). The four fundamental phases and corresponding questions addressed are:

1) Conceptual Foundation

- Is the indicator relevant to the assessment question or management concern?
- Does the indicator have an ecological function or is it linked to the critical resource?

2) Feasibility of Implementation

- Are the methods for sampling and measuring the environmental variables technically feasible, appropriate, and cost-efficient for use in a monitoring program?

- Is the indicator species relatively abundant and easily quantified?
- Can the species be identified by non-specialists?
- Does the indicator species have a stable taxonomy?
- Is it a sessile organism that is chronically exposed to local environmental conditions?

3) Response Variability

- Is the temporal variability within field season and across years understood?
- Is spatial variability understood and does it show gradations in response relative to level of stress?
- Does it respond to same stressors as other organisms within same habitat, but in a more sensitive manner?
- Does it respond specifically to a small number of stressors, or contrarily, show a generalized response to a wide range of stressors?
- Is it a long-lived organism that can provide signals of historical stress in the environment, or a species with short generation times that can respond quickly to changes?

4) Interpretation and Utility

- Will the indicator convey information on ecological condition that is meaningful to environmental decision-making?
- Does it have a direct linkage to management action?
- Will it provide information to support a management decision or quantify the success of past decisions?

5.0 RESULTS

5.1 Environmental Data

5.1.1 Precipitation

Total monthly rainfall (mm) from January 2020 to February 2021 for Kualoa and Kailua are shown in Figure 11. Kualoa is generally wetter year-round compared to Kailua, receiving a monthly precipitation average of 130.1 ± 22.0 mm (SE) as compared to 60.4 ± 16.5 mm in Kailua. The wettest month for both sites occurred in March 2020, receiving a total rainfall of 352.2 and 238.3 mm, respectively. Kualoa received the highest amount of rainfall on March 3, 2020 (141.7 mm, Fig. 12), and Kailua received the highest amount of rainfall on March 15, 2020 (70.4 mm, Fig. 13).

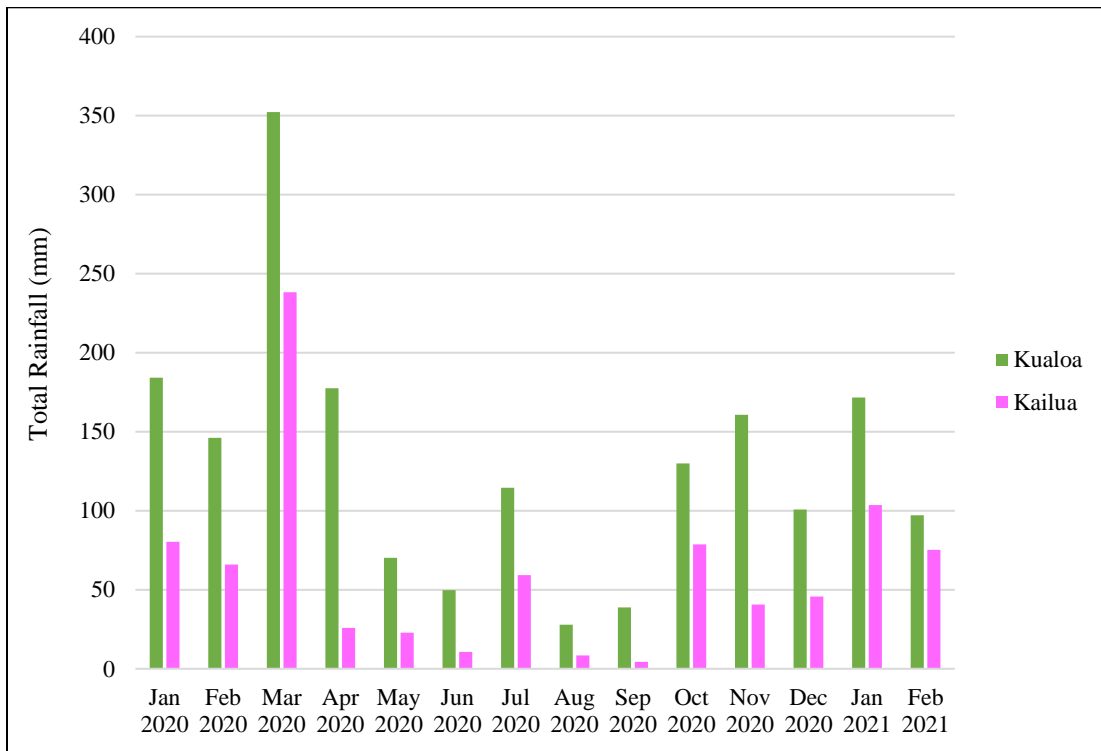


Figure 11. Monthly total rainfall (mm) at Kualoa and Kailua from January 2020 to February 2021.

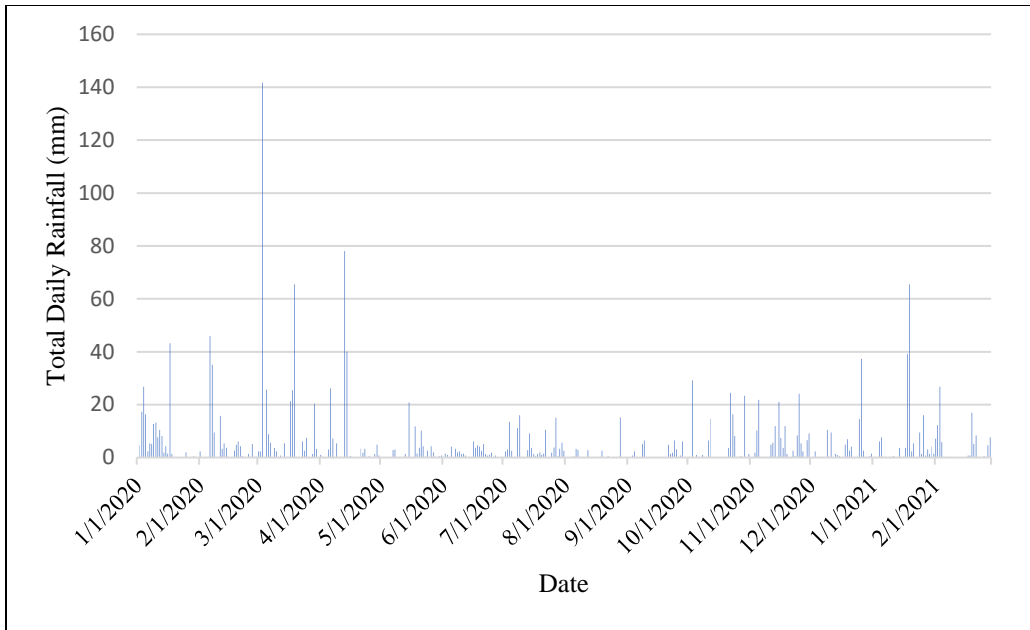


Figure 12. Total daily precipitation (mm) for the Kualoa site from January 2020 to February 2021 (Kualoa Ranch/Hakipu‘u gauge USC00514828).

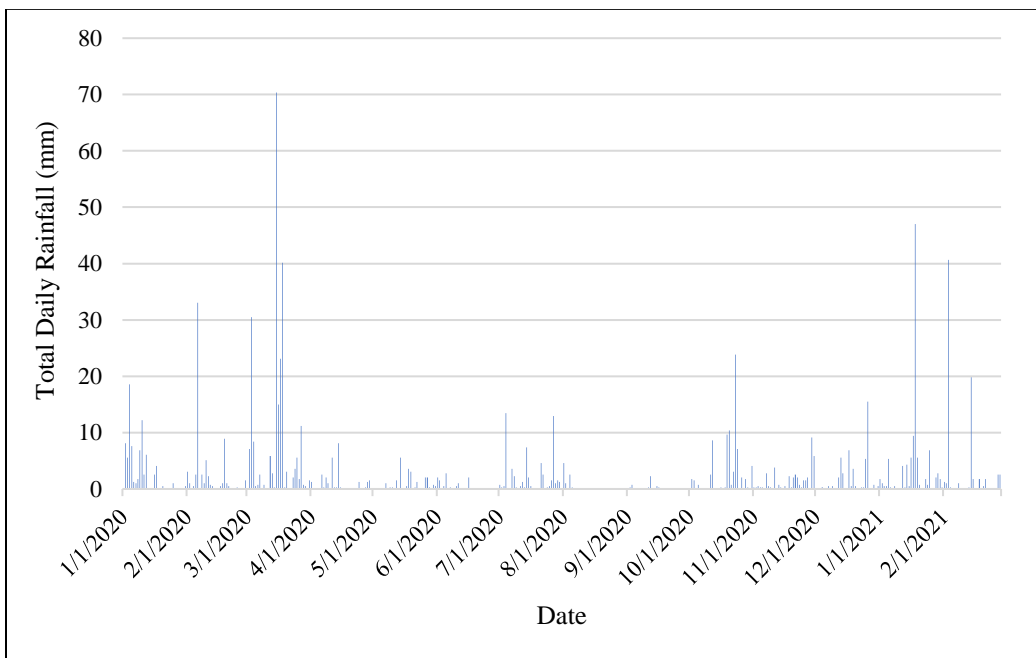


Figure 13. Total daily precipitation (mm) for the Kailua site from January 2020 to February 2021 (Ka‘elepulu Wetland weather station).

Total annual rainfall for Pila‘a from 2016-2019 is shown in Table 5, with the year 2018 receiving the highest level of rainfall (3,082.3 mm). April 2018 was the wettest month during all

four years, receiving a total of 483.9 mm of rain (Fig. 14). This is congruous to State of Hawai‘i records, where during 13–15 April, 2018, heavy rain and thunderstorms causing massive flooding occurred on the northern coast of Kaua‘i. The Waipā rain gauge, located approximately 15.3 km west from Pila‘a, recorded a total of 1,262 mm of rainfall from 14-15 April, 2018, setting the record for the highest amount of rainfall received in a 24-hour period in the United States (<https://www.weather.gov/hfo/RecordKauaiandOahuRainfallAndFlooding-April2018>; Rodgers et al. 2019b).

Table 5. Total annual precipitation (mm) for Pila‘a, Kaua‘i from 2016-2019 (USC00514758).

Year	Total Rainfall (mm)
2016	1551.6
2017	1907.3
2018	3082.3
2019	2264.5

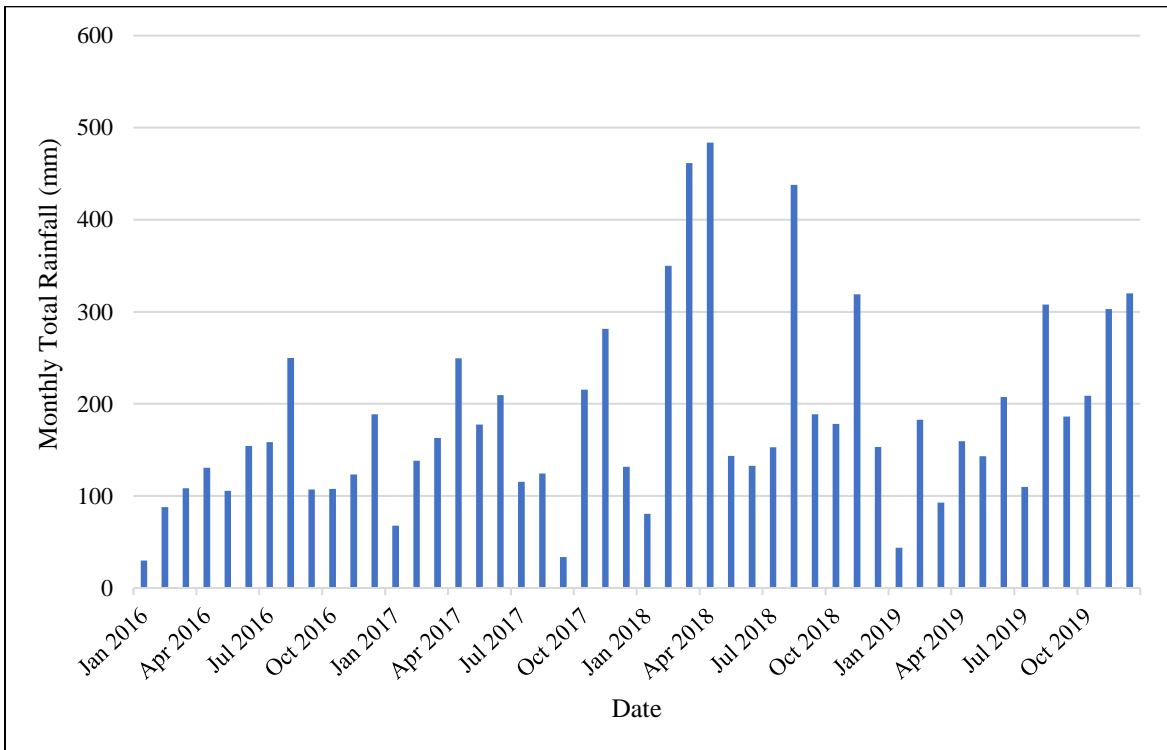


Figure 14. Monthly total rainfall (mm) for Pila‘a, Kaua‘i from January 2016 to December 2019 (USC00514758).

Octocoral response times to rainfall were tested to evaluate the appropriate gap or lag time that should be allowed (1, 2, or 3-month lag times), along with the best window or timespan of data (1, 2, or 3-months). Simple linear regressions using a three-month response or lag period and a one-month window for precipitation yielded the highest, albeit low, R^2 values (0.14 and 0.16, respectively; Table 6). Specifically, rainfall values used in GLMs were obtained from the total rainfall occurring for the month, three months prior to survey dates.

Table 6. Rainfall response and window tests using simple linear regressions, shown with corresponding R^2 values.

Rainfall Response Times	R^2	Rainfall Windows	R^2
1-month	0.107	1-month	0.164
2-month	0.102	2-month	0.086
3-month	0.138	3-month	0.138

5.1.2 Temperature

Kualoa minimum, maximum, and average midday temperatures ($^{\circ}\text{C}$) from July 2020 to February 2021 for the two loggers installed (Kua 4 & Kua 8, Fig. 4) are shown in Table 7. Temperature variability between stations was low and not significantly different. The maximum temperature recorded occurred in August of 2020 at the Kua 8 station (30.3°C), and midday average temperatures were lower in the fall/winter months as expected.

Table 7. Kualoa minimum, maximum, and average midday temperatures (°C) shown with standard deviations at the Kua 4 and Kua 8 stations from July 2020 to February 2021.

Kua 4 Temperatures			
Month	Min	Max	Midday Average
July	26.3	29.8	28.1 ± 0.9
August	26.1	29.8	28.3 ± 0.7
September	26.6	29.7	28.3 ± 0.5
October	26.9	29.7	28.4 ± 0.5
November	23.6	28.5	26.4 ± 1.0
December	23.6	27.0	25.7 ± 0.5
January	22.6	26.6	24.8 ± 0.7
February	21.7	26.3	24.4 ± 0.8
Kua 8 Temperatures			
Month	Min	Max	Midday Average
July	26.3	29.8	28.0 ± 1.0
August	25.9	30.3	28.4 ± 0.8
September	26.9	29.4	28.4 ± 0.3
October	26.6	29.8	28.5 ± 0.5
November	24.7	28.8	26.6 ± 0.9
December	23.9	27.0	25.8 ± 0.5
January	23.2	26.8	24.8 ± 0.7
February	22.2	26.3	24.4 ± 0.8

Minimum, maximum, and midday average temperatures for Kailua stations Kai 1 and Kai 5 (Fig. 5) from August 2020 to March 2021 are shown in Table 8. Temperature variability between stations was low and not significantly different. The maximum temperature recorded was 30.2 °C, occurring in October 2020 at both stations, and midday average temperatures were lower in the fall/winter months, analogous to the Kualoa site.

Table 8. Kailua minimum, maximum, and average midday temperatures (°C) shown with standard deviations at the Kai 1 and Kai 5 stations from August 2020 to March 2021.

Kai 1 Temperatures			
Month	Min	Max	Midday Average
August	26.7	28.9	28.0 ± 0.3
September	26.6	29.1	27.8 ± 0.4
October	26.7	30.2	28.2 ± 0.5
November	24.3	28.6	26.3 ± 0.9
December	24.5	26.8	25.6 ± 0.4
January	23.1	26.5	24.8 ± 0.7
February	22.2	26.5	24.3 ± 0.8
March	22.7	25.5	24.2 ± 0.5
Kai 5 Temperatures			
Month	Min	Max	Midday Average
August	26.8	29.1	28.0 ± 0.3
September	26.6	29.3	27.8 ± 0.4
October	26.6	30.2	28.2 ± 0.6
November	24.5	28.6	26.5 ± 0.8
December	24.5	26.8	25.7 ± 0.4
January	23.5	26.5	24.9 ± 0.6
February	22.3	26.5	24.4 ± 0.8
March	22.9	25.5	24.3 ± 0.4

Pila‘a minimum, maximum, and midday average temperatures (°C) during the corresponding time periods when surveys were conducted from 2016-2019 are shown in Table 9. Primary surveys at Pila‘a were initiated on 29 August, 2016, and as no prior temperature loggers were installed at that location, September 2016 temperatures were utilized to represent that survey period in GLMs. Midday average temperatures were similar during survey months throughout all years, with a maximum temperature of 32.0 °C recorded in May of 2019.

Table 9. Pila‘a minimum, maximum, and average midday temperatures (°C) shown with standard deviations from 2016-2019 during corresponding survey dates.

Month/Year	Min	Max	Midday Average
September 2016	25.9	28.8	27.6 ± 0.2
May 2017	24.2	29.3	26.7 ± 0.7
June 2017	25.0	29.2	27.2 ± 0.6
July 2018	25.0	28.5	27.2 ± 0.4
August 2018	25.0	29.5	27 ± 0.7
May 2019	23.6	32.0	26.7 ± 1.2
June 2019	24.8	30.9	27.7 ± 0.8

5.1.3 Water Quality

Replicate water samples were collected at selected Kailua and Kualoa transects during each survey period for nutrient analysis to detect any major differences between sites. Water samples were not collected at Pila‘a. Averages for total nitrite and nitrate (N+N) and phosphate were calculated from the replicate samples for each station and survey period, and are shown in Table 10.

Table 10. Mean total nitrite and nitrate (N+N) and phosphate concentrations at Kailua and Kualoa stations during each survey period from July 2020 to March 2021.

Site: Kailua			
Station	Sample Date	Mean N+N (µmol/L)	Mean Phosphate (µmol/L)
Kai 2	10/18/2020	0.25	0.08
Kai 5		0.32	0.06
Kai 6		0.22	0.05
Kai 5	12/6/2020	0.98	0.07
Kai 7		0.76	0.08
Kai 5	3/23/2021	1.00	0.21
Kai 7		0.98	0.21
Site: Kualoa			
Station	Sample Date	Mean N+N (µmol/L)	Mean Phosphate (µmol/L)
Kua 6	7/17/2020	0.07	0.22
Kua 8		0.07	0.09
Kua 6	12/2/2020	0.21	0.08
Kua 8		1.60	0.14
Kua 6	3/4/2021	0.98	0.06
Kua 8		0.98	0.23

Nutrient concentrations were fairly similar between sites. Average N+N concentrations combined from all stations and survey periods at Kailua and Kualoa were 0.64 and 0.65 $\mu\text{mol/L}$, respectively. Mean phosphate concentration at Kailua was 0.11 $\mu\text{mol/L}$, and 0.14 $\mu\text{mol/L}$ at Kualoa. N+N levels at Kualoa during the July survey period were lower compared to the subsequent time periods and Kailua stations.

5.2 Benthic Transects

5.2.1 Hard Coral Cover

Hard coral cover at all three sites were low, ranging from a mean of 1.1 to 5.2% of total benthic cover (Fig. 15). Kualoa had the highest mean scleractinian coral cover of 3.8% throughout all survey periods, followed by Kailua (3.2%) and Pila'a (1.8%). No significant differences were found in hard coral cover throughout survey periods for all sites.

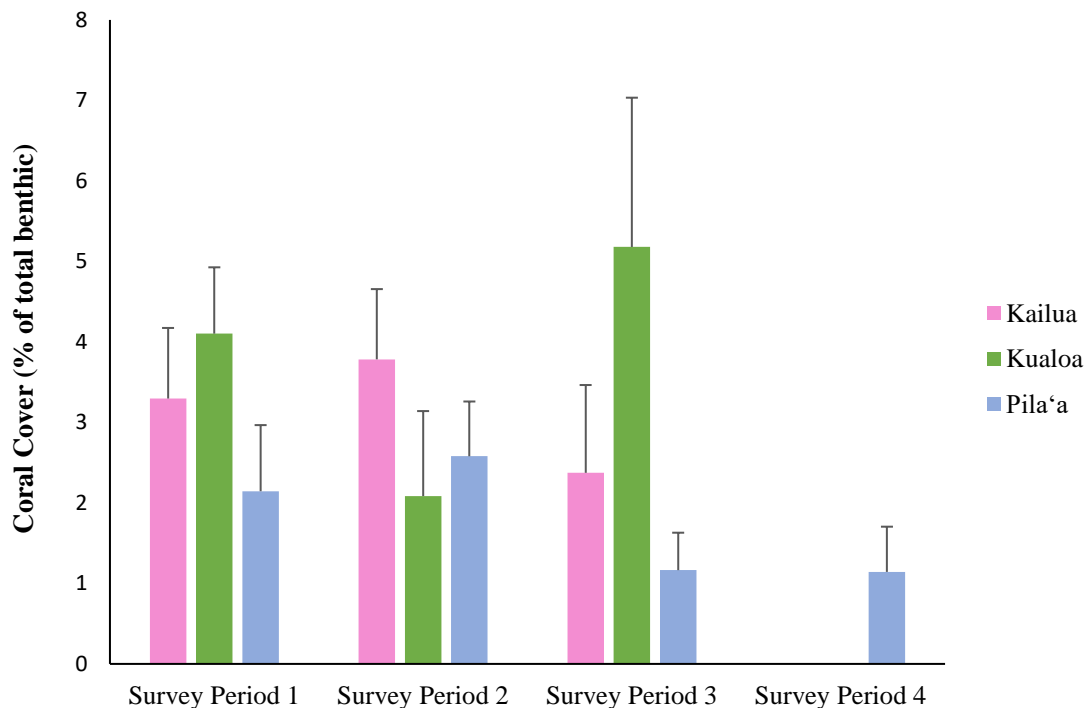


Figure 15. Mean hard coral cover (% of total benthic cover) shown with standard errors for Kailua, Kualoa, and Pila'a throughout all survey periods.

5.2.2 Octocoral Cover

Octocoral cover is reported as a proportion of total coral cover after no significant changes in hard coral cover were found between survey periods at all sites. This permits easier comprehension of proportions as reporting octocoral cover as a percent of total benthic can typically result in extremely small values (ex. 0.15% of total benthic cover vs. 4.3% of total coral cover). Reporting octocoral cover as a percent of total coral cover also allows for better comparability of *S. edmondsoni* cover between sites, and accounts for differences in availability of substrate. For instance, a site that is primarily comprised of sand bottom would generally lead to lower abundances of coral cover due to unsuitable substrate, which may skew results if one is comparing and attempting to differentiate coral cover between sites. Therefore, *S. edmondsoni* abundance data is reported here as a proportion of total coral cover to improve comprehension and comparability of octocoral populations between sites.

S. edmondsoni abundance at Kualoa were significantly different among survey periods (Friedman's test; $p=0.006$, $W=0.86$), and pairwise Wilcoxon signed rank tests revealed a significant increase in the octocoral between the July to December 2020 survey periods ($p=0.013$; Fig. 16). No significant differences in octocoral abundance were found at Kailua throughout survey periods (Fig. 17). At Pila'a, octocoral abundance was significantly greater in 2018 compared to all other years (Kruskal-Wallis & Wilcoxon test; $\chi^2=27.664$; 2016: $p=0.011$, 2017: $p=0.001$, 2019: $p=0.001$, Fig. 18).

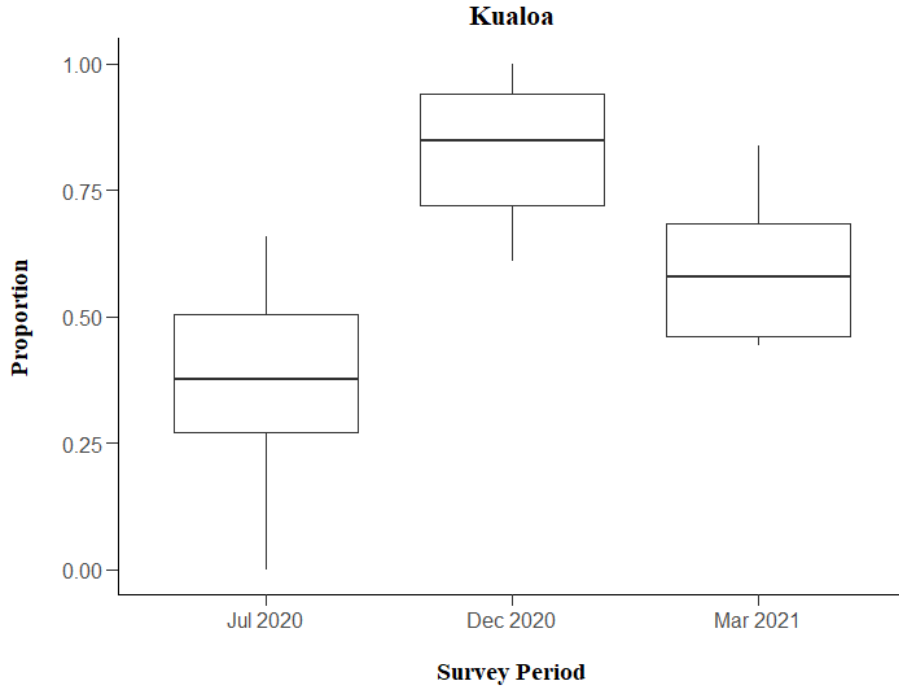


Figure 16. *Sarcothelia edmondsoni* abundance boxplots (% of total coral cover) throughout survey periods from July 2020 to March 2021 at Kualoa. Lines (whiskers) extending from boxes indicate the variability outside the upper and lower quartiles.

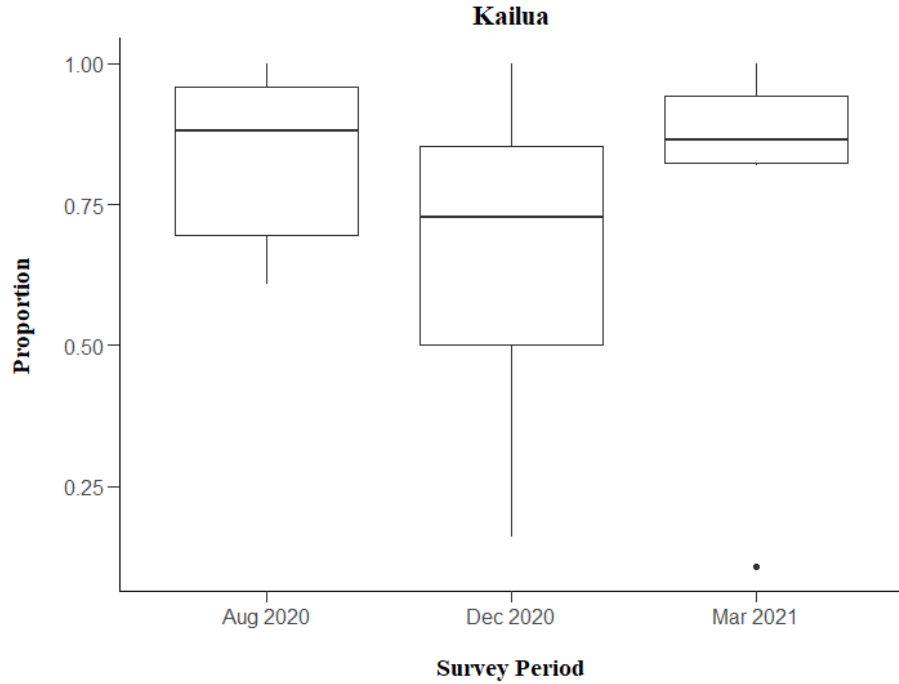


Figure 17. *Sarcothelia edmondsoni* abundance boxplots (% of total coral cover) throughout survey periods from August 2020 to March 2021 at Kailua. Lines (whiskers) extending from boxes indicate the variability outside the upper and lower quartiles. Outliers are plotted as individual points.

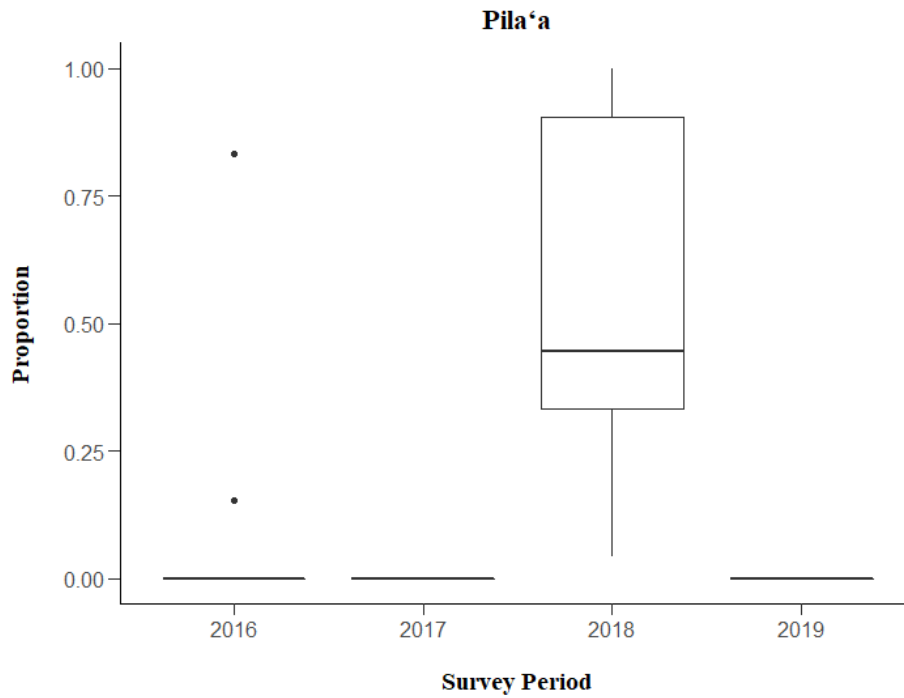


Figure 18. *Sarcothelia edmondsoni* abundance boxplots (% of total coral cover) throughout survey periods from 2016 to 2019 at Pila'a. Lines (whiskers) extending from boxes indicate the variability outside the upper and lower quartiles. Outliers are plotted as individual points.

5.3 GLM Temporal Analysis

A total of 17 different GLMs were tested using different combinations of simple and additive predictor variables, and interactive effects of site (Appendix A). The GLM selected as the best model included distance from shore and coral cover as significant predictors, and rainfall with an interactive effect of site (delta of second ranked model= 15.36, pseudo R^2 = 0.80; Appendix A). GLM outputs are shown in Table 11. Distance (Fig. 19) and coral cover (Fig. 20) had significant negative correlations with *S. edmondsoni* abundance (GLM; $p < 0.001$ and $p < 0.001$, respectively). While not significant, rainfall at the Kailua and Pila'a sites were positively correlated with *S. edmondsoni* abundance, and negatively at the Kualoa site (Table 11, Fig. 21).

Table 11. Generalized linear model output with parameter estimates along with standard errors (SE), t statistic, *p* values, and confidence intervals. Significant *p* values are indicated in bold.

	Estimate	SE	t statistic	<i>p</i> value	2.50%	97.50%
(Intercept)	4.149	0.883	4.699	<0.001	2.396	6.613
Rainfall	0.022	0.018	1.237	0.221	-0.013	0.067
Site Kualoa	3.806	0.960	3.965	<0.001	1.882	6.874
Site Pilaa	-6.689	1.105	-6.053	<0.001	NA	-4.840
Distance from Shore	-0.008	0.002	-4.465	<0.001	-0.013	-0.004
Coral Cover	-0.328	0.079	-4.160	<0.001	-0.542	-0.157
Rainfall:Site Kualoa	-0.028	0.018	-1.554	0.125	-0.075	0.007
Rainfall:Site Pilaa	-0.014	0.018	-0.778	0.439	-0.060	0.021

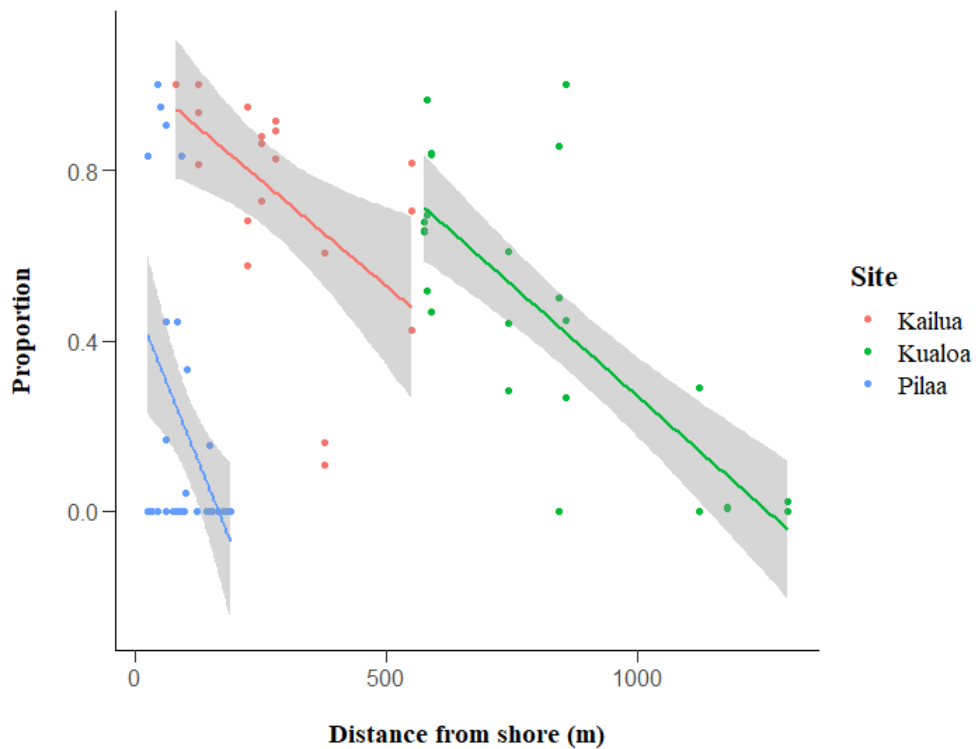


Figure 19. *Sarcothelia edmondsoni* proportion vs. distance from shore (m) colored by site, shown with best fit linear regression lines and 95% confidence intervals.

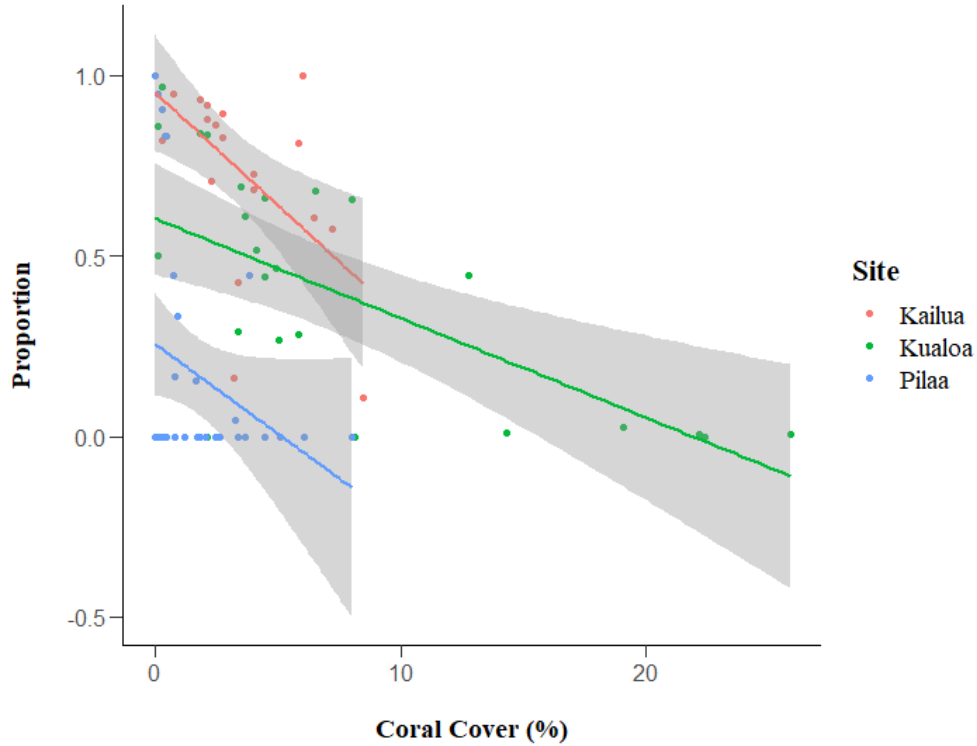


Figure 20. *Sarcothelia edmondsoni* proportion vs. coral cover (%) colored by site, shown with best fit linear regression lines and 95% confidence intervals.

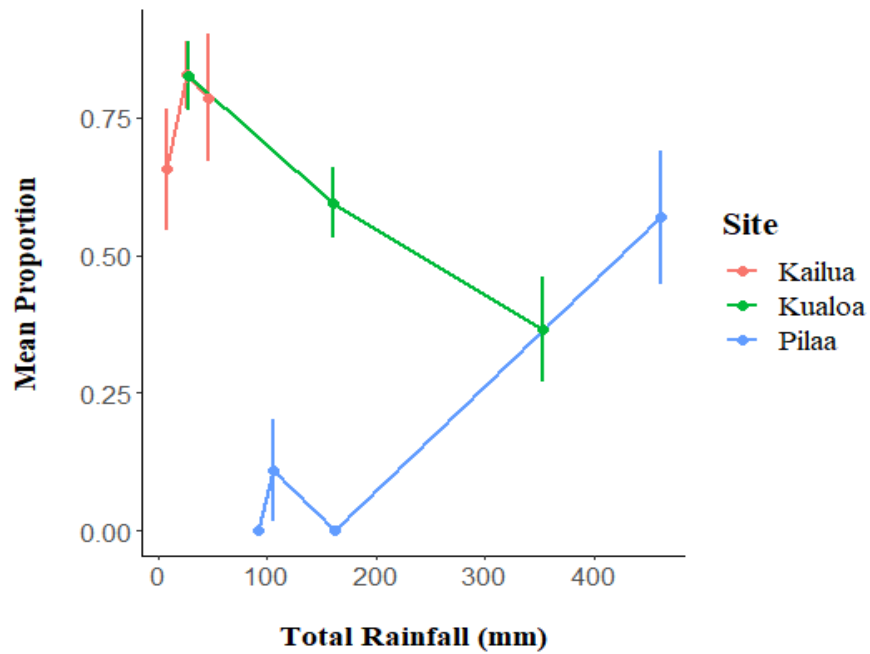


Figure 21. *Sarcothelia edmondsoni* mean proportions from each survey period vs. total rainfall in one month three months prior to survey dates (mm), colored by site and shown with standard error bars.

5.4 Hydrological Modeling

In addition to the previous predictor variables tested that may influence *S. edmondsoni* populations (rainfall, distance from shore, temperature, and hard coral cover), stream discharge was also investigated for effects on octocoral abundance at the Kualoa site. Stream discharge was not examined at the Pila‘a and Kailua sites due to either absence of stream input (Kailua) or a lack of both historical and current records (Pila‘a).

5.4.1 Stream modeling

The Kahana rain gauge was determined to adequately represent Hakipu‘u stream characteristics based on correlation plots with stream discharge (Figs. 22, 23, & 24) and model evaluation scores (Table 12). The Kahana rain gauge had the highest correlation with peak stream flows (Fig. 24). While models one and two utilizing the Waikāne and Punalu‘u rain gauge resulted in higher calibration scores as compared to model three (Table 12), model three yielded the highest calibration score (0.83) and therefore was chosen for the final hydrological model. The date gap between the warm-up period and calibration period was due to missing rainfall data, hence the calibration period used excluded the data gap to improve model performance.

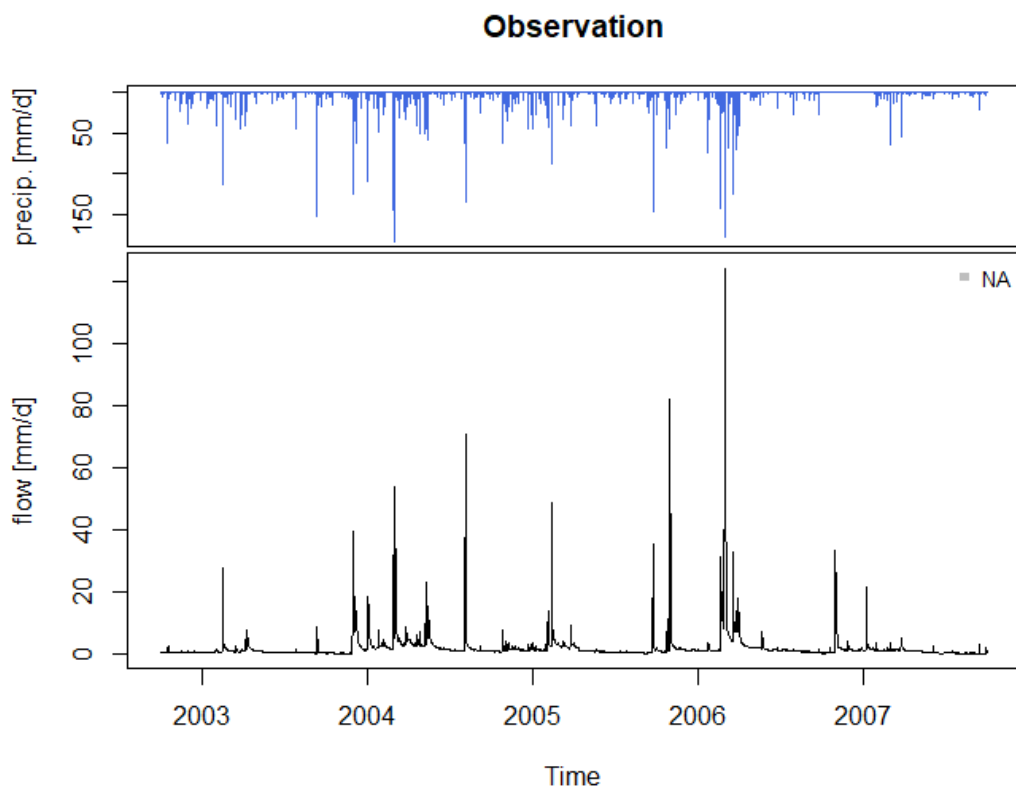


Figure 22. Observed total daily precipitation (mm/day) from the Waikāne rain gauge (USGS #213000157515401) shown above observed Hakipu‘u stream discharge (mm/day, USGS #16295300) from 2002 to 2008.

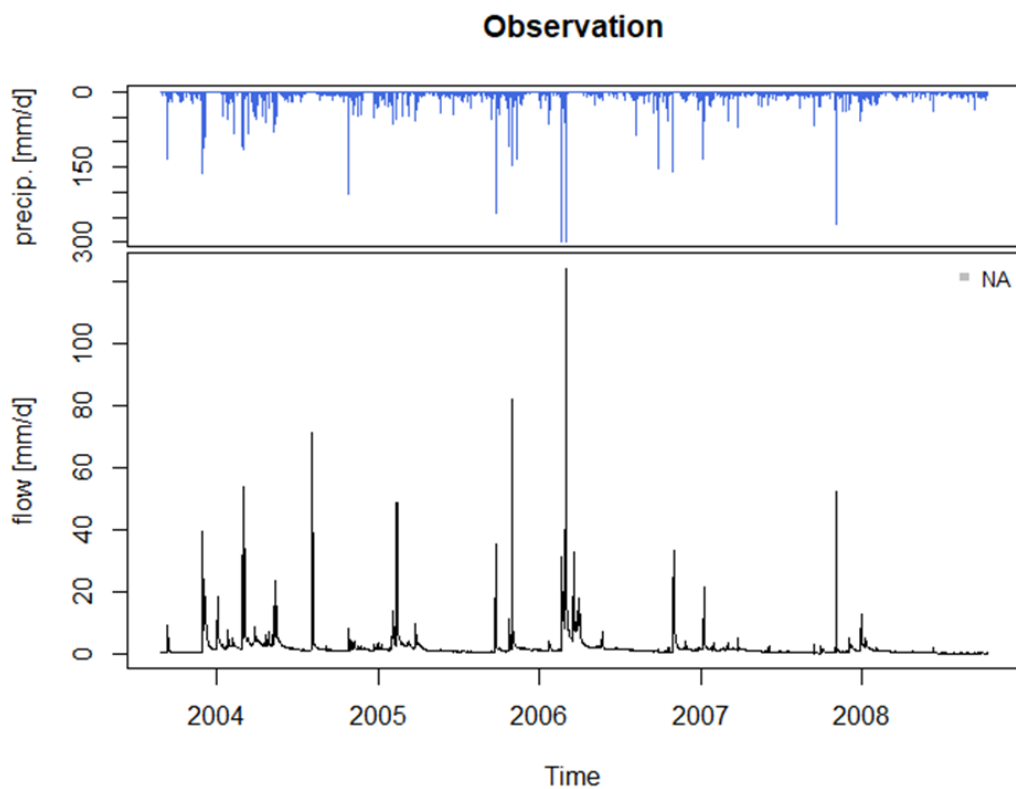


Figure 23. Observed total daily precipitation (mm/day) from the Punalu‘u rain gauge (USGS #213335157540601) shown above the Hakipu‘u stream discharge (mm/day, USGS #16295300) from 2003 to 2008.

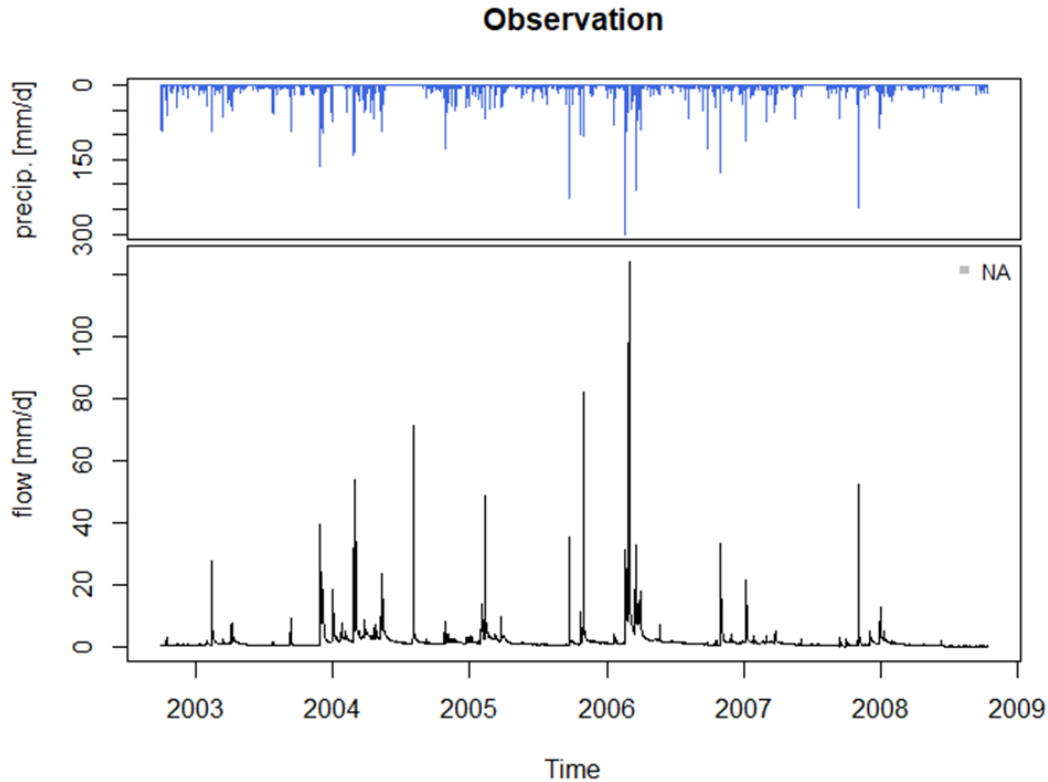


Figure 24. Observed total daily precipitation (mm/day) from the Kahana rain gauge (USGS #2132371575730701) shown above the Hakipu‘u stream discharge (mm/day, USGS #16295300) from 2002 to 2008.

Table 12. Date ranges used for the warm-up, calibration, and simulation periods for the Hakipu‘u stream model, along with KGE scores from calibration and simulation tests utilizing the Waikāne (USGS #213000157515401), Punalu‘u (USGS #213335157540601), and Kahana (USGS #2132371575730701) rain gauges.

Model	Rain gauge used	Warm-up Period	Calibration Period	Simulation Test Period	KGE from Calibration	KGE from Simulation
1	Waikāne	10/1/2002-10/1/2003	10/2/2003-10/4/2007	10/3/2006-10/4/2007	0.83	-0.24
2	Punalu‘u	8/27/2003-8/27/2004	8/28/2004-8/28/2007	8/29/2007-10/13/2008	0.85	0.41
3	Kahana	10/1/2002-10/1/2003	9/1/2004 - 10/2/2008	10/2/2007-10/13/2008	0.50	0.83

When examining calibration performance plots (Fig. 25), the final model captured most peak flows, with the exception of three high flows that occurred sometime around February/March of 2005, November 2005, and March 2006. However, the model was generally

sufficient in capturing high flows, and instead tended to underestimate low discharge flows (Fig. 25d and 25e).

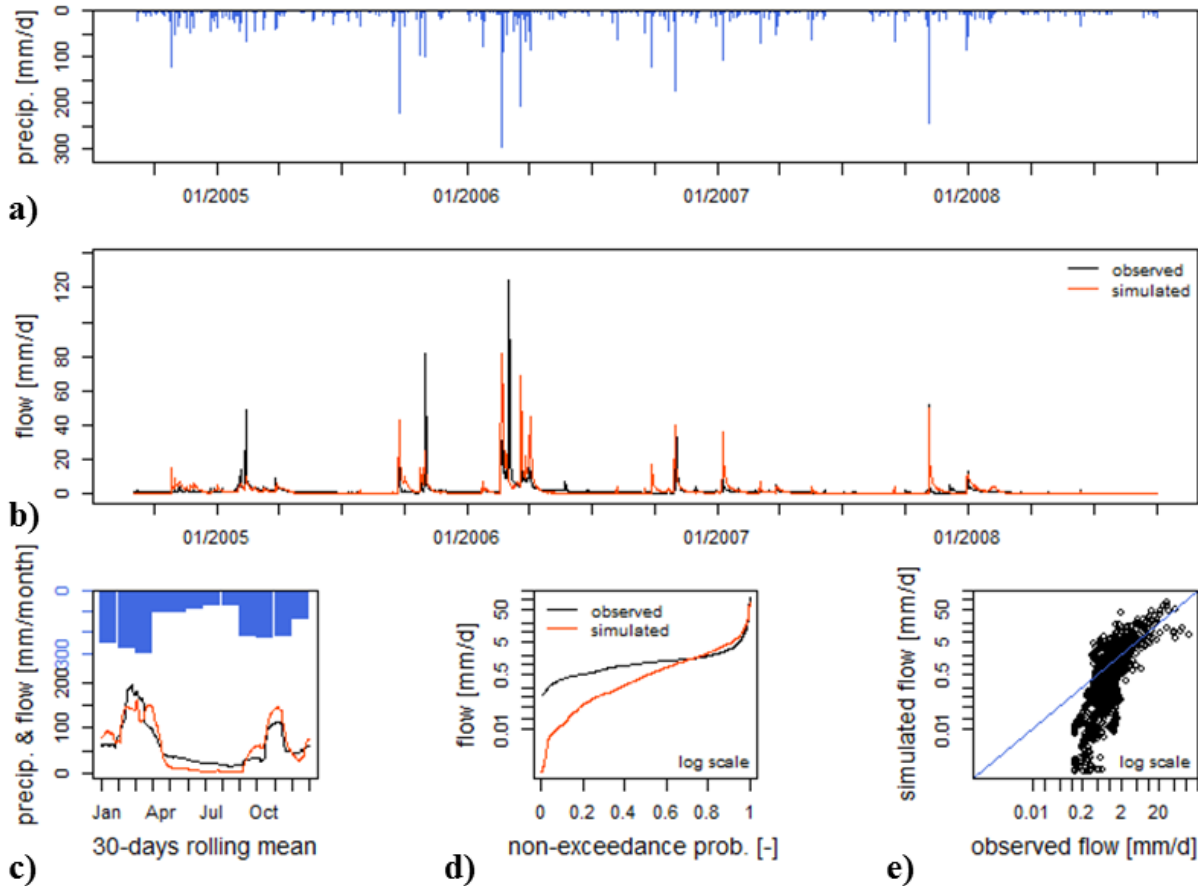


Figure 25. Model calibration performance plots showing **a)** Daily precipitation (mm/day) from the Kahana rain gauge (USGS #2132371575730701) in relation to **b)** the observed and simulated flow from model calibration (mm/day), **c)** Monthly mean precipitation and observed vs. simulated flow from model calibration (mm/month), **d)** Non-exceedance probability of observed vs. simulated flow from model calibration (mm/day), and **e)** Observed vs. simulated flow (mm/day) from model calibration results.

The simulated test captured the peak flows from October 2007-2008 relatively well, although 2008 seemed to be a dry year as evidenced by the low precipitation and discharge records (Fig. 26). High flow and rainfall events occur often when examining simulated discharge and precipitation records from 2008 to 2020 (Fig. 27), usually taking place in the early spring or fall/winter months which is consistent with stream and hydrology patterns on the windward side of O‘ahu.

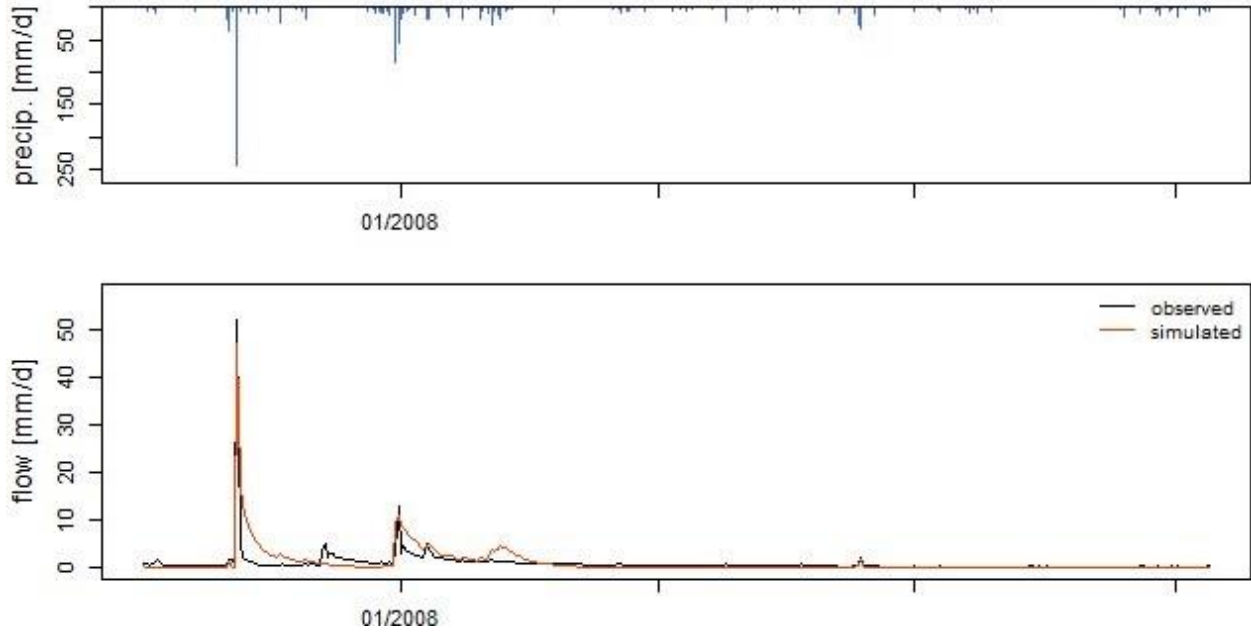


Figure 26. Simulation plot of daily discharge (mm/day) vs. observed values from the Hakipu'u stream gauge (USGS #16295300) shown with daily precipitation (mm/day) from the Kahana rain gauge (USGS #2132371575730701).

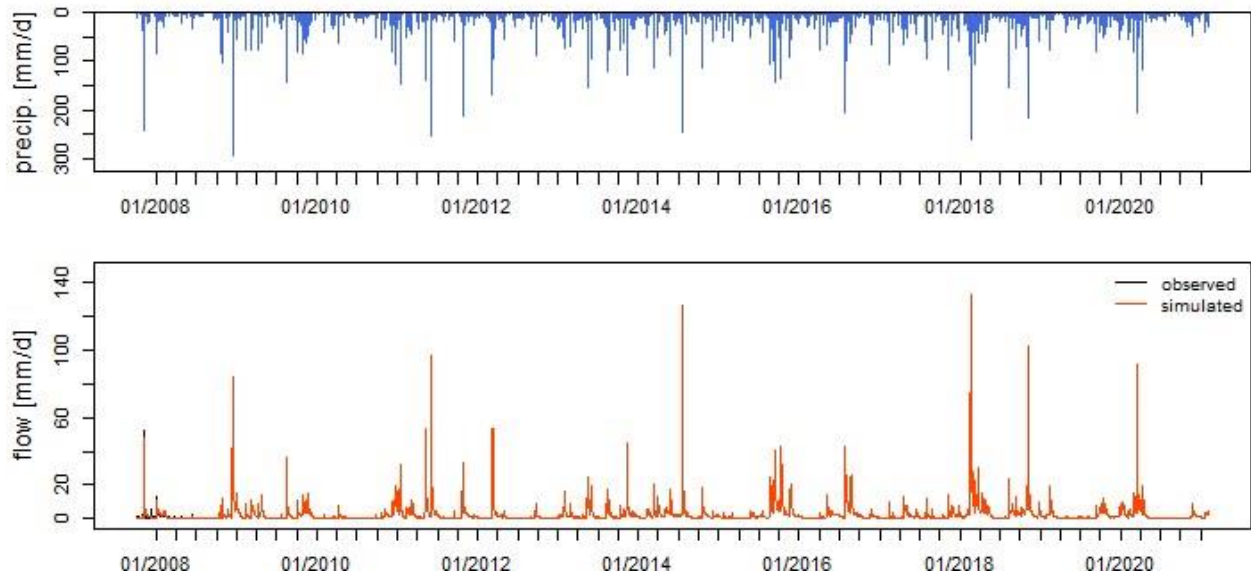


Figure 27. Model simulation of Hakipu'u stream daily discharge (mm/day) (bottom) shown with daily observed precipitation (mm/day) (top) from the Kahana rain gauge (USGS #2132371575730701) from 2008 to 2020.

In congruence with rainfall data in the year 2020, stream discharge was highest in March of 2020, with the hydrological model estimating a total discharge of 450.4 mm (Fig. 28).

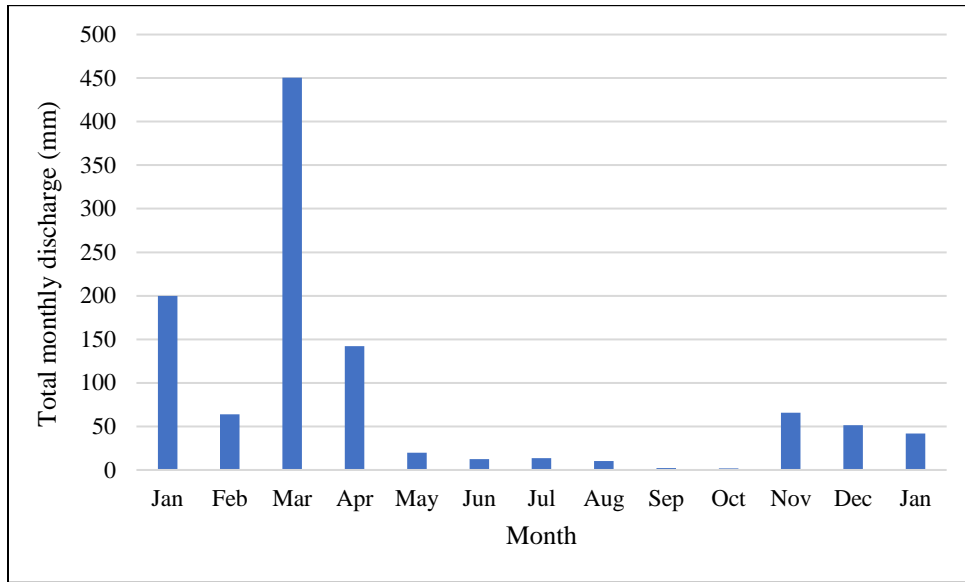


Figure 28. Model estimated total monthly discharge (mm) from January 2020 to January 2021 at Hakipu‘u stream.

5.4.2 Kualoa GLM with estimated discharge

When exclusively testing Kualoa site data with extrapolated stream discharge values along with previous predictor variables (rainfall, temperature, distance from shore, and hard coral cover), both distance from shore and modeled discharge as fixed effects resulted in the strongest GLM model (delta= 0.18, pseudo R²= 0.71). The window of data used and lag times to allow for response of *S. edmondsoni* to discharge were identical to the precipitation approach (3-month response time, 1-month window). Model outputs are shown in Table 13, with distance and discharge both having significant negative correlations with *S. edmondsoni* abundance (GLM; $p= 0.016$ and $p < 0.001$, respectively).

Table 13. Generalized linear model output testing added influence of stream discharge at Kualoa with parameter estimates, shown with SE, t statistic, p values, and confidence intervals. Significant p values are shown in bold.

	Estimate	SE	t statistic	p value	2.50%	97.50%
(Intercept)	4.273	1.141	3.745	0.002	2.190	7.047
Distance	-0.004	0.001	-2.704	0.016	-0.007	-0.001
Discharge	-0.015	0.003	-4.563	< 0.001	-0.023	-0.009

5.5 Spatial Analysis

In addition to the temporal analysis from my own transect surveys and compiled environmental parameters, a spatial analysis was undertaken to explore *S. edmondsoni* patterns in relation to natural and anthropogenic factors on a larger scale. Quantitative values relating to a number of natural and human variables were compiled for each site (n= 13; Appendix B) for statistical analyses. West Hawai‘i percent cover data (% of total benthic cover) was combined with my data from O‘ahu (Kualoa and Kailua) and Kaua‘i (Pila‘a). O‘ahu and Kaua‘i octocoral proportions as a percent of total coral cover were converted to percent of benthic cover to ensure comparability with West Hawai‘i data. Simple GLM results assessing the correlation of distance from shore, rainfall, population, percent coverage of impervious surfaces, development, agriculture, and underground injection wells to octocoral abundance are presented in Table 14. Population (GLM; $p < 0.01$, pseudo $R^2 = 0.49$; Figs. 29 & 30), open development ($p = 0.01$, pseudo $R^2 = 0.36$; Figs. 31 & 32), and impervious surfaces ($p = 0.01$, pseudo $R^2 = 0.37$; Figs. 31 & 32) had significant positive correlations with octocoral abundance.

Table 14. Simple generalized linear model outputs with individual scaled parameter estimates, SE, pseudo R^2 , and p values. Significant p values are indicated in bold.

Variable	Estimate	SE	pseudo R^2	p value
Population (total # within watershed)	0.342	0.091	0.493	0.003
Open Development (%)	0.304	0.103	0.357	0.013
Impervious Surfaces (%)	0.292	0.094	0.373	0.010
Underground Injection Wells (#/km ²)	0.262	0.172	0.177	0.156
Rainfall (mm/yr)	0.082	0.194	0.016	0.683
Distance from stream (m)	-0.122	0.211	0.035	0.575
Agriculture (%)	-0.393	0.295	0.212	0.210

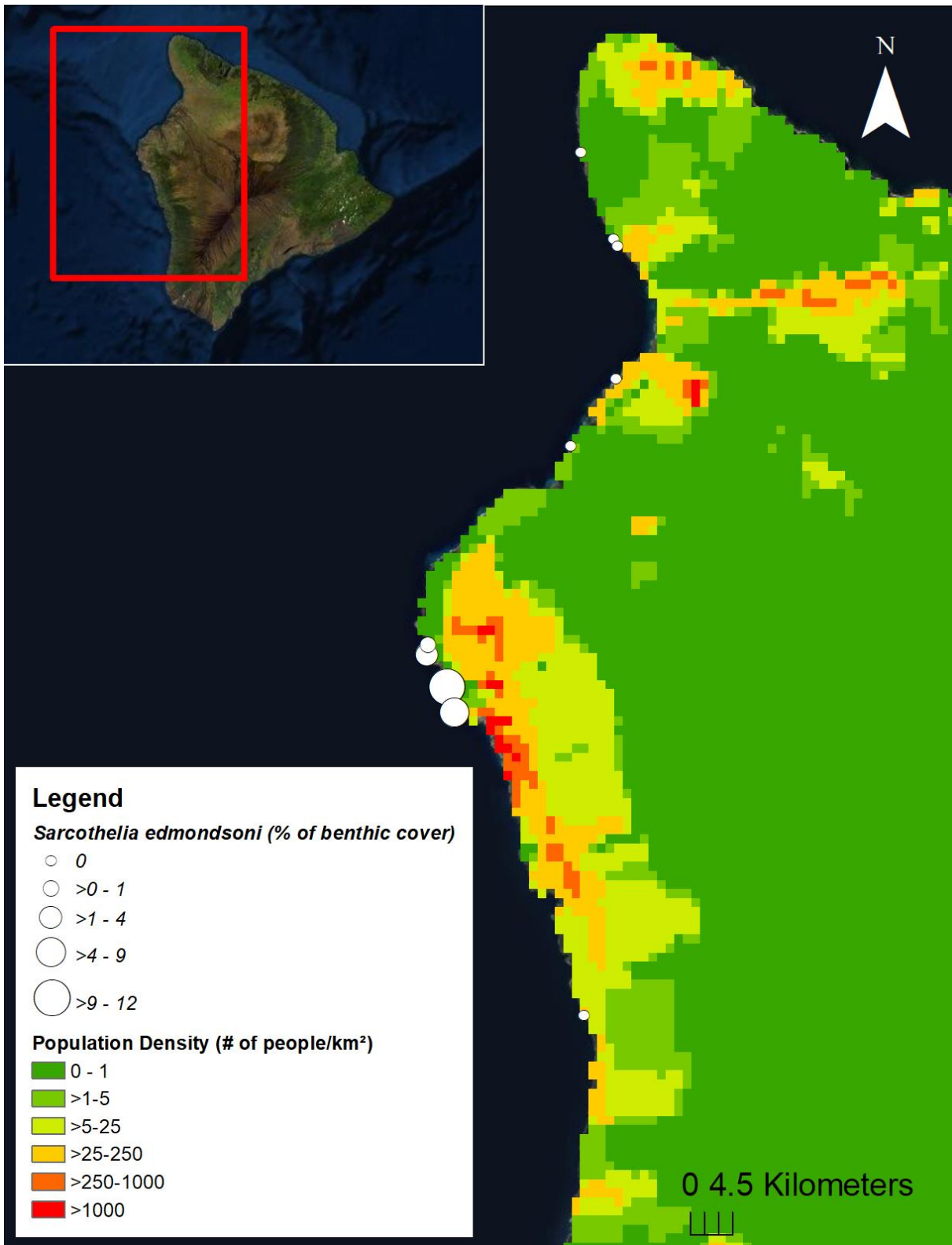
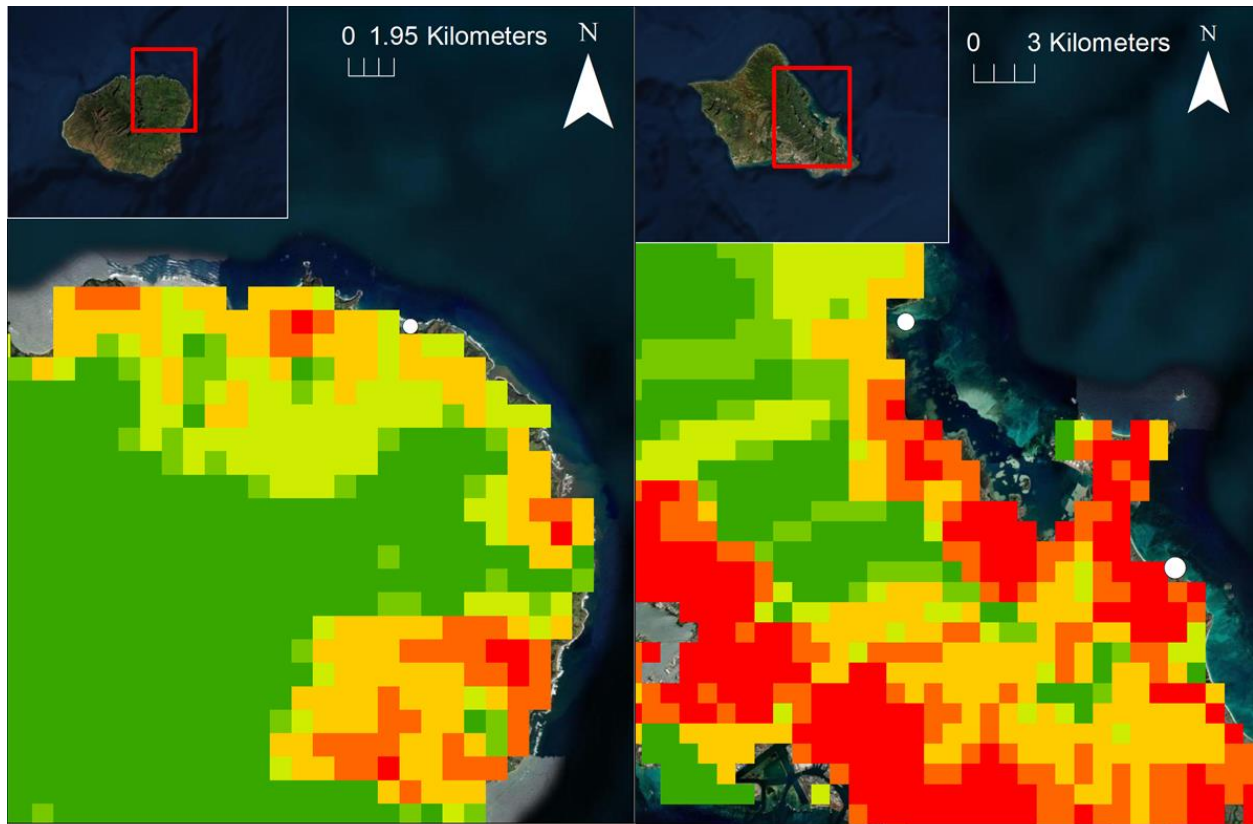


Figure 29. Map of *S. edmondsoni* abundance on West Hawai'i with population density (# of people/km²) provided by NASA's Socioeconomic Data and Applications Center (SEDAC 2015). Inset map shows extent of mapped area delineated in red.



Legend

***Sarcothelia edmondsoni* (% of benthic cover)**

- <1
- >1-5
- >5-7
- >7-10
- >10

Population Density (# people/km²)

- 0 - 1
- >1-5
- >5-25
- >25-250
- >250-1000
- >1000

Figure 30. Map of *S. edmondsoni* abundance on Kaua'i (left) and O'ahu (right) with population density (# of people/km²) provided by NASA's Socioeconomic Data and Applications Center (SEDAC 2015). Inset map shows extent of mapped area delineated in red.

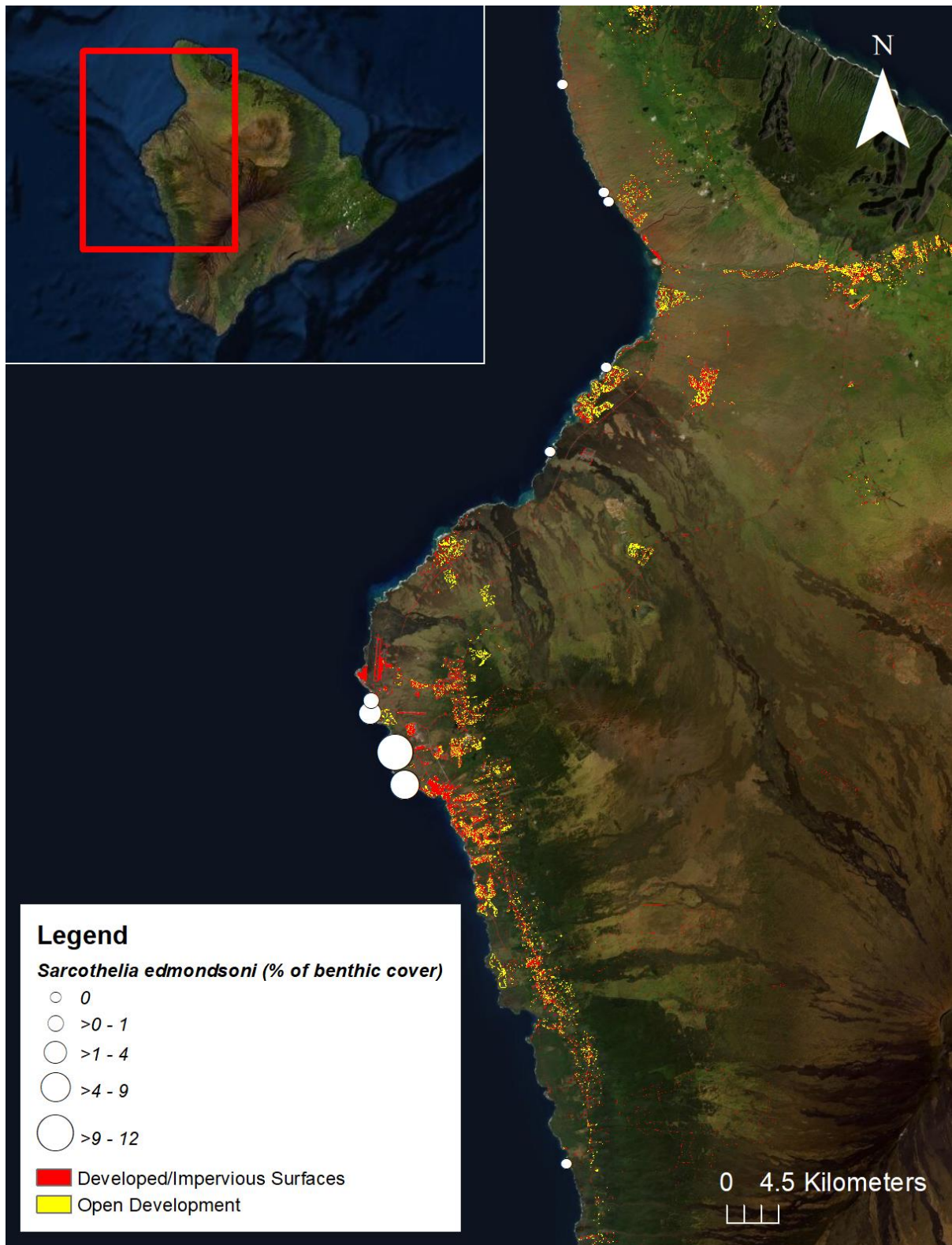
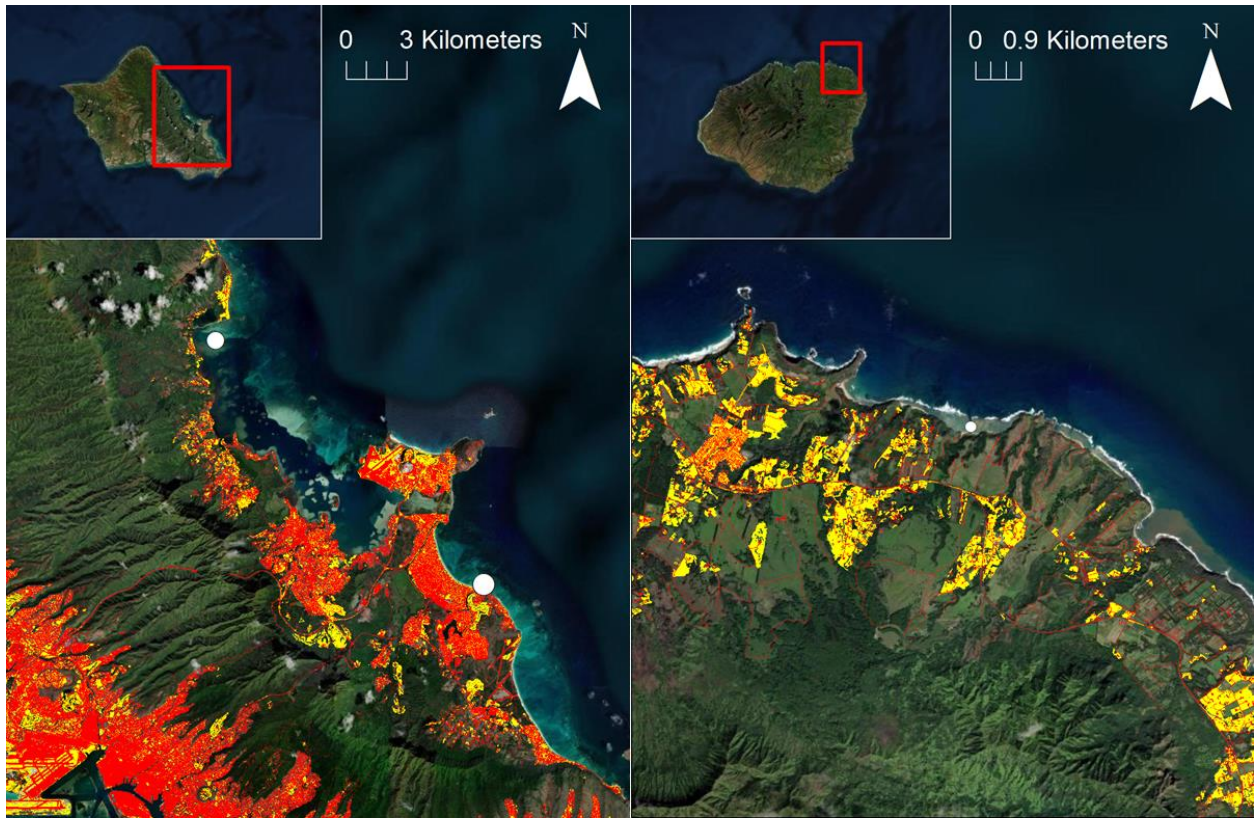


Figure 31. Map of *S. edmondsoni* abundance on West Hawai'i with land cover layers (impervious surfaces and open development) provided by the Coastal Change Analysis Program (2011). Inset map shows extent of mapped area delineated in red.



Legend

Sarcothelia edmondsoni (% of benthic cover)

- 0
- >0 - 1
- >1 - 4
- >4 - 9
- >9 - 12

■ Developed/Impervious Surfaces

■ Open Development

Figure 32. Map of *S. edmondsoni* abundance on O'ahu (left) and Kaua'i (right) with land cover layers (impervious surfaces and open development) provided by the Coastal Change Analysis Program (2011). Inset map shows extent of mapped area delineated in red.

5.6 Bioindicator Evaluation

A qualitative assessment was performed to evaluate how well *S. edmondsoni* met bioindicator criteria and guidelines that were previously established by the U. S. EPA and other researchers. Here I review the strengths and weaknesses of *S. edmondsoni* as an indicator of anthropogenic influences.

5.6.1 Conceptual Foundation

Questions that are addressed in this section are as follows:

- Is the indicator relevant to the assessment question or management concern?
- Does the indicator have an ecological function or is it linked to the critical resource?

An assessment question is a question that can be directly answered through quantitative methods. For example, an assessment question in this situation may include how much of this reef is covered by octocoral? By quantifying the abundance of *S. edmondsoni* through surveys, one can directly address the question of how much octocoral there is in an area, and if thresholds are later established (discussed in 5.6.4), one can furthermore determine whether a reef is healthy or degraded after benthic surveys. The presence and abundance of *S. edmondsoni* can also be linked to the common management concern of whether an ecosystem is exposed to human influences or land-based pollution, as higher populations were found in areas that were highly developed or subjected to stronger anthropogenic effects. The octocoral species is capable of being the most dominant benthic species, highlighting its ecological role in coral reef ecosystems. Significant correlations were found with hard coral cover, where higher abundances of *S. edmondsoni* are associated with low scleractinian coral cover (Table 11, Fig. 20). Reefs comprised of hard or stony corals in Hawai'i are a critical resource, and the abundance of the octocoral species is clearly linked to hard coral cover as evidenced by the significant negative correlation found (GLM; $p < 0.001$). *S. edmondsoni* may directly compete for space with scleractinian corals, and may have the capability to overgrow other benthic marine organisms and become dominant in degraded reef habitats.

5.6.2 Feasibility of Implementation

To examine the practicality of implementing *S. edmondsoni* as an indicator in monitoring methodologies, the following questions were investigated:

- Are the methods for sampling and measuring the environmental variables technically feasible, appropriate, and cost-efficient for use in a monitoring program?
- Is the indicator species relatively abundant and easily quantified?
- Can the species be identified by non-specialists?
- Does the indicator species have a stable taxonomy?
- Is it a sessile organism that is chronically exposed to local environmental conditions?

While transect surveys were used to quantify *S. edmondsoni* abundance in this study, other methodologies that can be employed include quadrat surveys or rapid assessments of presence/absence. All techniques are appropriate and cost-efficient as tools and equipment needed for transect and quadrat surveys are comparably low-cost. The purchase and use of expensive computer software are not needed, as CoralNet is now widely used as a coral reef benthic image analysis program and is available free of charge. Percent cover in quadrat surveys can be estimated by the surveyor in-situ, or a photograph can be taken and analyzed later. Furthermore, most coral benthic surveys already follow the transect method or utilize quadrat surveys to estimate coral cover (Walsh et al. 2010; Thompson et al. 2021), and therefore would not require additional time or analysis to calculate octocoral cover. Moreover, rapid assessments simply documenting the presence/absence of *S. edmondsoni*, or for example quickly estimating percent cover of the octocoral species within a five-meter diameter circle prior to starting a survey, would only take at most a couple minutes and would not be difficult or time consuming to incorporate into existing monitoring methodologies.

The octocoral species is also a sessile organism that is constantly exposed to local environmental conditions, and can be identified by non-specialists. Although at first glance the brown morphology of the octocoral can commonly be mistaken for algae, a closer inspection allowing the recognition of polyps assuredly provides positive identification of *S. edmondsoni* (Fig. 33). There are no other known species of coral here in Hawai‘i that are physically similar to

the blue octocoral. Nevertheless, there is some level of ambiguity regarding the taxonomy of this species. Taxonomy of *S. edmondsoni* and the possibility of the different color morphs representing divergent species is widely debated. Color variations in the octocoral species are broad, ranging from blue, purple, brown, to even pinkish brown and a mix of said colors. The brown color morph was recorded on my benthic transects conducted on O‘ahu and Kaua‘i. For the West Hawai‘i sites, morphologies recorded on transects include blue/purple, brown, and pinkish brown (A. Pugh, personal communication, November 23, 2020; M. Leatherman, pers. comm., November 23, 2020; L. Kramer, pers. comm., November 30, 2020). While currently it is considered the same species, there has been some speculation on whether the color morphologies may be distinct as they are found in different habitats and conditions.



Figure 33. The brown morphology of *S. edmondsoni* at Kualoa, O‘ahu, and a close-up of the polyps visible to the naked eye (right).

5.6.3 Response Variability

An appropriate indicator must meaningfully respond to stressors, and specific questions examining response patterns of *S. edmondsoni* were:

- Is the temporal variability within field season and across years understood?
- Is spatial variability understood and does it show gradations in response relative to level of stress?

- Does it respond to same stressors as other organisms within same habitat, but in a more sensitive manner?
- Does it respond specifically to a small number of stressors, or contrarily, show a generalized response to a wide range of stressors?
- Is it a long-lived organism that can provide signals of historical stress in the environment, or a species with short generation times that can respond quickly to changes?

Temporal variability within field season or across years is not yet well understood, as no long-term studies on *S. edmondsoni* have been conducted. My benthic transects established on O‘ahu only encompassed a nine-month period, and while the Pila‘a, Kaua‘i data were recorded over a four-year period, surveys were annually conducted in the summer, and therefore did not capture any seasonal patterns that *S. edmondsoni* may exhibit. In addition, Pila‘a transects were not established to specifically address octocoral abundance, and therefore is not adequate to be representative of true populations. For example, high concentrations were anecdotally recorded at Pila‘a in 2016, however, transect surveys reported only 0.07% of the blue octocoral (Rodgers et al. 2017b). The brown morphology of *S. edmondsoni* at Pila‘a was only found in nearshore areas near the stream mouths. Because original transects were randomized to cover and represent the entire reef area (original purpose was to document recovery from a sedimentation event), there was a lack of transects that were closer to shore, which would have been needed to more accurately track changes in octocoral abundance through time. Statewide data for *S. edmondsoni* abundance is also insufficient, due to either underestimation and its obscurity, or a complete negligence of recording octocoral presence. The longest dataset of *S. edmondsoni* abundance was from West Hawai‘i monitoring surveys from 2003-2016, but representative data from additional sites around the main Hawaiian Islands should be investigated before attempting to understand temporal variability.

My spatial analysis results shed light on spatial variability, showing a gradient response relative to environmental stress. *S. edmondsoni* is more concentrated nearshore where the effects of human influence and freshwater input are more pronounced, and a distance gradient further offshore where the impacts are less severe show a decreasing abundance. This supports the anisotropic properties of the octocoral, and reveals the spectrum of response relative to the level

of stressors. Heavier populations of the octocoral species are also found in areas that are more developed and populated (Kailua and Honokōhau Harbor), further supporting the spatial variability of *S. edmondsoni* to anthropogenic influence.

Although the octocoral species does not seem to exhibit increased vulnerability towards certain stressors compared to other organisms within the same habitat, *S. edmondsoni* does display faster response times. Other benthic organisms that may react to anthropogenic stressors include hard corals and macroalgae. Loss of coral cover or bleaching can be caused by several different stressors such as increased temperatures, sedimentation, irradiance levels, and nutrient input (Brown 1997; Philipp & Fabricius 2003; DeCarlo et al. 2020). Macroalgae can also exhibit blooming tendencies similar to the blue octocoral due to excess nutrients (Smith et al. 1981; Cooper et al. 2009). When examining benthic composition at Pila‘a from 2016-2019, hard coral cover remained stable throughout, ranging from 1.3 to 2.1%. Macroalgae and bleached coral cover, however, do fluctuate, reflecting their sensitivity to changing ecological conditions similar to *S. edmondsoni*. Bleached coral cover ranged from 0 to 20.3% of total coral cover, with the highest bleaching recorded in 2018, the year of the freshwater event in which the octocoral bloom was also recorded. The increase in coral bleaching at Pila‘a that year can most likely be attributed to the freshwater and nutrient input, as temperature records did not reach the upper thermal tolerance of corals that summer (Rodgers et al. 2021). Macroalgae also showed an increase following the storm event, which brings an influx of land-based nutrients, however, it appears to react slower as a higher abundance of macroalgae was not evident until the year following the event (2019), increasing from 3.2 to 7.9%. Response sensitivity of *S. edmondsoni* may be similar to macroalgae and coral bleaching, but the octocoral species does appear to react more quickly to increased temperatures, as evidenced by the disappearance in West Hawai‘i and Kualoa, O‘ahu during the 2015 and 2019 bleaching events, and lowered salinity/nutrient input as indicated by the rapid bloom detected at Pila‘a, Kaua‘i.

S. edmondsoni's generalized response to a wide range of stressors also meet bioindicator response criteria, however, not enough is known about generation times of the species. Increased abundances of the octocoral are correlated with a variety of stressors that are all related to anthropogenic influence: development, impervious surfaces, and population. The higher presence of *S. edmondsoni* detected in areas that are impacted by these pressures meets the indicator

response criteria, yet we currently have no knowledge on the lifespan of this species. Organisms with either short or long-term lifespans are recommended characteristics for strong bioindicators, but currently there are no studies that have examined generation times of *S. edmondsoni*.

5.6.4 Interpretation and Utility

The interpretation and utility of using *S. edmondsoni* as an indicator was examined addressing the outlining questions below:

- Will the indicator convey information on ecological condition that is meaningful to environmental decision-making?
- Does it have a direct linkage to management action?
- Will it provide information to support a management decision or quantify the success of past decisions?

S. edmondsoni meets all of the bioindicator criteria above, as the presence/abundance of the species conveys information on the health of the reef and changes that are occurring in the ecosystem, thus supporting management actions and decision-making. The presence and quantity of the octocoral species generally indicates a degraded reef that is impacted by anthropogenic influences. This provides a direct link to management action and decisions, providing the knowledge to directly identify and mitigate negative influences, or support decisions to possibly establish the zone as a protected or marine managed area. Furthermore, it can be used to quantify the success of actions or regulations.

Unusual high abundances of *S. edmondsoni* detected during monitoring surveys can prompt researchers and managers to investigate the cause or source. The octocoral species reacts and responds faster to stressors, thereby providing an early warning to managers before more severe degradation occurs. Once the source of the problem is identified, direct efforts can be implemented to address the issue or mitigate damage. This may include identifying sewage leaks, pollution input, freshwater seeps, or halting and re-evaluating development plans in sensitive, critical areas. Subsequent continued monitoring of *S. edmondsoni* may then determine the success of management efforts. A decrease or complete disappearance of the octocoral would

support the success of regulations or actions taken, or alternatively, a continued persistence and presence of the species may suggest the inadequacy of management actions and the need for adaptive management. Additionally, a quantitative baseline of *S. edmondsoni* cover may be established, representing what might be an acceptable condition for coral reef health prior to exceeding the abundance threshold. For instance, a reef with less than 5% *S. edmondsoni* cover may be regarded as a normal, healthy reef. However, once benthic surveys reveal an increase above the established threshold level, managers may employ this data to recognize an impacted reef and initiate action to identify the source and mitigate further damage.

6.0 DISCUSSION

The main objectives of this research were to examine temporal and spatial variations of *S. edmondsoni* populations, explore potential environmental and anthropogenic drivers that may influence changes, and assess the utility of *S. edmondsoni* as a bioindicator. Significant correlations of the octocoral species abundance were found with human population, impervious surface coverage, open development, and distance from shore which represented the extent of human influence. *S. edmondsoni* abundance was also lower in areas with high hard coral cover. An evaluation assessment of indicator performance following the U. S. EPA guidelines showed support for the use of *S. edmondsoni* as a bioindicator, as the species adequately met most of the criteria established.

6.1 Temporal Analysis

A temporal analysis of *S. edmondsoni* populations revealed distance from shore and hard coral cover as significant predictors of octocoral abundance. Each variable collected (distance from shore, coral cover, temperature, water quality, rainfall, and stream discharge) and their significance is discussed in the following sections.

6.1.1 Distance from Shore

Distance from shore was a significant predictor of *S. edmondsoni* abundance, with results showing a decrease in octocoral cover as distance from the mainland increases (Table 11 & Fig. 19). This is consistent with my hypothesis, and is likely due to the greater exposure of nearshore areas to anthropogenic stressors and freshwater input from river or stream mouths.

Terrigenous sedimentation increases turbidity on inshore reefs, and sediment storage, export, and flushing periods are dependent on tidal changes, shelf depth, and wave energy, with wave and tidal-driven sediment resuspension more pronounced at shallow depths (Ryan et al. 2018; Wang 2002; Larcombe et al. 2001; Larcombe & Woolfe 1999; Hoeksema et al. 2019). Distance from land describes the extent of terrigenous impact, which can be clearly evident through the presence of river plumes (Tarya et al. 2018). In addition, fluctuations in salinity and nutrient input also add to the chronic stress nearshore reefs experience. Marked declines in salinity have been observed closer to shore, with stronger declines in the presence of river or

stream mouths (Basterretxea et al. 2018). Studies have also shown significant differences in cross-shelf nutrient levels, where average nearshore concentrations can be up to six times higher than offshore values (Flo et al. 2011; Basterretxea et al. 2018). Due to these chronic stressors nearshore reefs are subjected to, community disassembly after a disturbance and overall reef degradation is exacerbated on inner-shelf reefs (Mellin et al. 2019). Coral recovery takes more time and energy in nearshore reefs, taking up to 11 years to reach the same level of reassembly on outer reefs (Johns et al. 2014).

Outer reef-shelves are often subject to less variable and reduced chronic stress (Mellin et al. 2019), which may explain the decreased abundance of *S. edmondsoni* further offshore. Increasing water clarity, wave exposure, and depth, along with decreasing terrigenous impacts affect community composition across a distance gradient from near to offshore (Hoeksema et al. 2019; Mellin et al. 2019; Cleary et al. 2005; Emslie et al. 2010). While it can be difficult to confidently separate the influence of each variable, depth in this study can most likely be ruled out as a predictor variable because depths across all established transects were similar (1-3 m) and therefore not tested. This further supports the idea that anthropogenic and freshwater influences are contributing to *S. edmondsoni* abundance patterns. The gradient of octocoral proportion from high to low as a measure of distance from shore was highly predictable, and a clear, distinct pattern was evident at all three sites (Fig. 19). Higher concentrations of the octocoral species found closer to shorelines as opposed to offshore areas less exposed to anthropogenic effects corroborate the idea that *S. edmondsoni* abundance is positively correlated with human and freshwater impacts.

6.1.2 Coral Cover

Hard coral cover was significantly correlated with *S. edmondsoni* abundance in the strongest GLM (Table 11). A decline in scleractinian coral cover was correlated with an increase in the octocoral species abundance (Fig. 20).

Hard coral cover can be indicative of reef health and status (Brodie & Waterhouse 2012). Higher scleractinian coral cover is generally found in healthier reefs or marine protected areas, and anthropogenic stressors such as climate change, terrestrial pollution, and/or development

have caused dramatic declines in coral cover worldwide from approximately 60% more than 50 years ago to nearly 20% today (Walton 2013; Mumby et al. 2007; Norström et al. 2009; Hughes et al. 2010). Decreasing coral cover also results in a reduced abundance of reef fishes, and fish assemblage and growth rates can also be negatively affected by reef degradation (Feary et al. 2009; Halford et al. 2004; Jones et al. 2004; Wilson et al. 2006). An increase in the abundance of *S. edmondsoni*, associated with a decline in hard coral cover, can therefore be indicative for management, revealing a degrading reef system and subsequently less fishes for subsistence, which is important here in Hawai'i. However, it is currently not known whether the octocoral species may be a strong competitor against hard corals.

S. edmondsoni is commonly seen growing on dead coral (Fig. 34), rubble, or other hard substrate, which is in agreement with other published studies on soft coral presence and settlement (Chandran et al. 2015; Fox et al. 2003). Yet it is not yet understood whether the octocoral is competitive with hard corals for space. According to personal observations, it appears to settle and colonize after hard corals die, which suggests a natural succession pattern following reef degradation. This successional pattern of soft coral dominance following declines in hard coral cover is also evidenced in other studies (Baum et al. 2016; Chandran et al. 2015; Fox et al. 2003), thus supporting the use of *S. edmondsoni* as an indicator of poor reef health. If hard coral cover continues to decline in the future, this may provide additional habitat and substrate for the octocoral species to settle and expand. Furthermore, if *S. edmondsoni* exhibits chemical defenses similar to other octocoral species, this presents a concern as the octocoral would be a strong competitor against hard corals, allowing dominance in benthic composition and further reducing scleractinian coral cover and diversity. Research examining *S. edmondsoni* interactions with other hard corals should be conducted to determine the competitiveness of the octocoral species.



Figure 34. *Sarcothelia edmondsoni* growing on a dead *Porites compressa* colony. Photo taken at the Kailua study site on August 12, 2020.

6.1.3 Rainfall and Stream Discharge

Precipitation and stream discharge were examined for effects on *S. edmondsoni* abundance, as they can be a source of freshwater and nutrient input. Stream discharge had a statistically significant negative correlation with octocoral cover in the strongest GLM for Kualoa ($p < 0.001$; Table 13), which was contradictory to my original hypothesis. Rainfall appeared in the strongest GLM models, however, varying patterns displayed between sites (interactive effect) prevents a conclusive interpretation.

Rainfall and stream discharge are strongly correlated variables, with higher precipitation generally leading to greater discharge rates and volumes (Adji & Bahtiar 2016; Gashi et al. 2011; Zoch 1934). However, both variables were explored for influence on octocoral populations due to differences in stream input at study sites. While all three sites (Kailua, Kualoa, and Pila‘a) contained perennial streams within their corresponding watersheds, the Ka‘elepulu stream in

Kailua is normally blocked by a sand berm year-round, preventing oceanic/freshwater exchange. During the course of this research, the stream mouth was opened only once within the 8-month study period, and was closed again within subsequent days. This indicates the lack of freshwater input from streams at Kailua. The Pila‘a stream did not have historical stream discharge records available, and does not currently have operating gauges; therefore stream discharge was examined and only modeled for the Kualoa study site.

I originally hypothesized that higher abundances of *S. edmondsoni* would be positively correlated with rainfall and stream discharge, however, the significant negative correlation with discharge suggests that the octocoral species may have salinity thresholds to freshwater input, similar to most scleractinian corals and other marine organisms (Rodgers et al. 2021; Banner 1968; Jokiel et al. 1993; Jones & Berkelmans 2014; Bahr et al. 2015). While *S. edmondsoni* may have salinity thresholds, the octocoral species could potentially have higher tolerance levels to decreased salinity as significantly higher abundances were detected at Pila‘a after the huge rainstorm and flooding event in 2018 (Fig. 18). Because precipitation had a positive (albeit insignificant) relationship with octocoral abundance at Kailua and Pila‘a, other complex, interactive effects may be occurring.

Rainfall was not a statistically significant predictor for octocoral abundance, however, it did have an interactive effect with site and consistently appeared in the top five strongest GLMs tested (Table 11; Appendix A). This implies that precipitation does play a role in *S. edmondsoni* abundance, yet it is hard to distinguish the relationship as patterns vary between sites. Positive correlations of octocoral cover with rainfall were found at Kailua and Pila‘a, and a negative correlation was found at Kualoa. This may be a result of nutrient loading occurring concurrently with increased rainfall from Kailua and Pila‘a due to the level of human influences, while Kualoa is less affected by anthropogenic impacts. The Kailua watershed is the most populated and developed of all three study sites, and while Pila‘a is significantly less populated and developed as compared to Kailua, over half the land cover is classified as agricultural (55%; Appendix B). This suggests the influence of fertilizers as agriculture is a main source of eutrophication in coastal reefs (Adam et al. 2021; Boesch 2002; Erler et al. 2018). The higher level of human influences may explain the general positive trend of rainfall on octocoral cover at Kailua and Pila‘a due to land-based inputs and ameliorating effects it may have on lowered salinity levels (Table 11, Fig. 21).

Concurrent nutrient loading along with rainfall and stream input in developed areas may have mitigating effects on lowered salinity levels, as a wide variety of research supports the attenuation of salinity stress with nutrient inflation. High nitrogen enrichment mitigated the negative effects of reduced salinity on biomass of the green macroalgae, *Enteromorpha intestinalis* in California (Kamer & Fong 2001). Enhanced total organic carbon and nitrogen concentrations in saline lakes alleviated salinity impacts to microbial primary producer abundance and diversity (Yue et al. 2019). Even terrestrial studies show nutrient uptake reduces salinity stress effects on growth and yield of wheat crops (Merwad 2020). It is likely that moderate nutrient loading may reduce the negative impacts of decreased salinity levels in marine ecosystems, explaining the positive relationship rainfall had on *S. edmondsoni* abundance in areas more heavily influenced by human impacts and development. It is difficult nonetheless, to separate precipitation effects from other factors such as nutrient and sediment loading that comes with storm events. This suggests more complex interactions are occurring with runoff and pollution inputs from heavy rainfall and discharge. Alternatively, *S. edmondsoni* may not be responding directly to freshwater/nutrient input, but instead be indirectly responding in a successional pattern by settling on available substrate after the death of scleractinian corals. The octocoral species may have greater resiliency towards changing levels of salinity and nutrients as compared to most hard corals, thereby allowing them take over unoccupied space. Further research should be conducted on exploring salinity thresholds of *S. edmondsoni*. Due to the insignificance of rainfall on octocoral abundance and the significant negative correlation found with stream discharge at Kualoa, there is not enough evidence to support the use of *S. edmondsoni* as an indicator of freshwater input.

6.1.4 Temperature

While temperature data did show up in the strongest model as an additive effect along with distance from shore and coral cover, it was excluded in the final model because it was not statistically significant and did not markedly improve model results (delta of next ranked model: 0.17; Appendix A). Concerns with pseudoreplication and the possibility of overfitting the model also precluded temperature from being incorporated into the final selected GLM.

Temperature loggers were not installed at every transect station. As a result, multiple stations were associated with the same temperature data (transect station temperatures were matched with the nearest temperature logger) which leads to pseudoreplication. Including too many predictor variables may also lead to overfitting the model, which can provide results that do not truly exist in the population and are nonreplicable (Babyak 2004). In general, selecting models that follow the principle of parsimony, or the simplest model containing only the variables that are necessary, is the best method for model selection (Hawkins 2004). The more predictors you add in a model, the more likely you will get predictors that look important but do not accurately represent what is going on in the population (Babyak 2004). It is widely accepted for linear models to contain a minimum of 10-15 observations per predictor variable to allow reasonable estimates, and this study had a total of 75 observations with four predictors (two independent variables: distance from shore and hard coral cover, and one predictor with an interactive variable: rainfall with an interactive effect of site) in the final model, which meets the criteria. In addition, including temperature in the model did not significantly increase model performance, and was therefore excluded in the final model. However, it is important to note that there may be a correlation of *S. edmondsoni* abundance with temperature.

There have been several anecdotal records suggesting the susceptibility of *S. edmondsoni* bleaching due to higher temperatures. In West Hawai'i, stable high abundances of the octocoral found around urbanized areas of Kailua-Kona from 2003-2014 virtually disappeared in 2016 (0% detected on transects), most likely due to the 2015 statewide bleaching event (Walsh et al. 2010; William Walsh & Lindsey Kramer-pers. comm.). Surveys conducted by The Nature Conservancy, NOAA, and DAR showed up to 92% of coral colonies on the west side of Hawai'i Island partially or fully bleached by early October 2015, with an average of about 60% bleached across all sites (The Nature Conservancy 2017). It is likely that *S. edmondsoni* bleached as well, but bleaching and mortality of this species has been difficult to document as soft corals disintegrate after death (Slattery et al. 2013; Strychar et al. 2005). A disappearance of the octocoral species was also anecdotally noted by my own reconnaissance surveys at the Kualoa site. Prior to establishing my transects at Kualoa, high abundances of *S. edmondsoni* that had existed around the area were not found during swim surveys in January of 2020. Preliminary surveys were conducted during that time to determine placement of my study transects, however, all the octocoral had virtually disappeared and were not found anywhere. This may again be due

to the bleaching event that impacted the Hawaiian Islands in late summer of 2019. While less severe than the 2015 event, up to 50% of corals were reported as bleached in Kāneʻohe Bay on patch reefs near my study site, and 55% were bleached at Lanikai adjacent to the Kailua study site (DLNR 2019). Nonetheless, the octocoral species reappeared sometime between February to June of 2019.

While the bleaching of soft corals has been documented worldwide (Strychar et al. 2005; Smith 2000; Obura 2000; Rajasuriya et al. 2000; Marshall & Baird 2000), information regarding temperature-induced bleaching of alcyonacean corals is limited, and no descriptions or research has been conducted on the bleaching and thermal tolerance of *S. edmondsoni*. Several studies suggest that Alcyonacean corals may actually be more susceptible to bleaching than hard corals, as countries such as Australia, Africa, and South Asia reported higher severity of bleaching in soft corals than scleractinians during bleaching events (Marshall & Baird 2000; Obura 2000; Rajasuriya et al. 2000). In Australia, the soft coral genus *Xenia* showed a higher sensitivity to elevated temperatures than the hard coral *Acropora* spp., which was previously known to be the most vulnerable species to temperature-induced bleaching (Strychar et al. 2005). Soft corals, however, have been reported to recover relatively quickly and can rapidly recolonize reefs as opposed to hard corals (Smith 2000; Obura 2000; Rajasuriya et al. 2000), which is congruent with my personal observations. Although coral recovery rates from bleaching are variable by species and influenced by community dynamics and other stressors, scleractinian corals can take anywhere from eight months to several years or more to fully recover (Burt et al. 2008; Rodrigues & Grottoli 2007; Obura 2000). Further exploration into the thermal tolerance of this species should be investigated to examine whether *S. edmondsoni* may be susceptible to increased temperatures similar to hard corals.

6.1.5 Water Quality

Water quality samples were collected and analyzed to examine any marked differences between survey sites and distance from shore. Nutrient data were not used in statistical analyses, as water quality constantly changes based on physical, chemical, or biological factors such as stream flow conditions and water motion (Feng et al. 2016; Ho et al. 2011; Abal & Dennison 1996; Parchure et al. 1996). To truly capture water quality characteristics within an area,

frequent and consistent measurements are needed, with continuous monitoring that would allow a more accurate representation of nutrient dynamics within an ecosystem (Ringuet & Mackenzie 2005). Due to time constraints and funding limitations for nutrient analyses, adequate samplings were not possible for this study. Therefore, nutrient data was simply used to provide a snapshot of coastal water quality at the Kailua and Kualoa study sites, and to assess any differences between nearshore vs. offshore transects.

Nutrient concentrations at Kailua and Kualoa were similar and remained well below nutrient thresholds (4.51 $\mu\text{mol/L}$ for nitrate and 0.63 $\mu\text{mol/L}$ for phosphate) for coral reefs throughout the study period. Total N+N values show seasonality patterns, with increases detected during the wet seasons at both sites. This is congruent with other studies that show higher nutrient loading following rain events due to terrestrial runoff (Fong et al. 2020; King et al. 2007; Ringuet & Mackenzie 2005). Total N+N concentrations at the Kualoa site were notably lower in July 2020 (Average = 0.07 $\mu\text{mol/L}$), a drier summer month, as compared to the December and March sampling periods (0.91 and 0.98 $\mu\text{mol/L}$, respectively). A significant increase in *S. edmondsoni* was detected from July to December ($p= 0.013$), increasing from a proportion of 0.37 to 0.83 of total coral cover (Fig. 16) which may be attributed to this nutrient increase. While total N+N at Kailua did show a similar increase as well during wet seasons (0.27 to 0.99 $\mu\text{mol/L}$), the difference was not as dramatic as the Kualoa site, which may explain why octocoral cover at Kailua did not significantly change throughout all survey periods (Fig. 17).

Water samples were also specifically collected to examine whether considerable differences were found at transects nearshore vs. offshore based on severity of runoff impacts. No substantial differences in water quality were found between nearshore and offshore transects at Kailua, however, Kualoa sampling stations reveal a slight difference. The offshore water sampling transect at Kualoa (Kua 8, Fig. 4) shows higher concentrations of total N+N during the December survey period (0.21 vs. 1.60 $\mu\text{mol/L}$), and higher levels of phosphate during the March sampling period (0.06 vs. 0.23 $\mu\text{mol/L}$, Table 10). Although the offshore sampling station is only separated by approximately 0.7 km to the nearshore station, the increased levels of N+N and phosphate may be contributed by the nearby Waikāne and Waiāhole streams (located 1.9 km away), which are much larger streams and have higher flow rates as compared to Hakipu‘u stream.

Results do appear to show a positive correlation of *S. edmondsoni* abundance and total N+N concentrations, as evidenced by the statistically significant increase in octocoral cover at Kualoa in concurrence with increased N+N levels. However, this is contradictory to other studies where enhanced nitrate levels led to decreased growth rates of *S. edmondsoni*.

Previously conducted laboratory experiments showed nitrate enrichment negatively affecting *S. edmondsoni* growth (Pugh 2019), but it may still be more resilient as compared to scleractinian corals under similar nutrient conditions. Soft coral dominance has been recorded in areas of poor water quality, and it has been suggested that greater soft coral coverage compared to hard coral cover could be a result of reduced competition from stony corals (Baum et al. 2016; Parsons et al. 2008). Successional dominance may also be a result of hard coral cover decreasing due to sedimentation and/or eutrophication, providing new substrate and habitat for octocoral settlement. Furthermore, *S. edmondsoni* abundance was found to have a positive relationship with diseased scleractinian corals in Honokōhau (Parsons et al. 2008), reiterating the theory that the octocoral species can tolerate and therefore become a significant competitor in degraded conditions. Future manipulative experiments looking at *S. edmondsoni* and scleractinian coral growth simultaneously under inflated nutrient levels can reveal the successional dynamics and differences in soft and hard coral resiliencies.

6.2 Spatial Analysis

A spatial analysis of *S. edmondsoni* abundance on O‘ahu, Kaua‘i, and West Hawai‘i revealed significant positive correlations with impervious surfaces, open development, and human population. Higher abundances of the octocoral species were found in areas with greater coverage of impervious surfaces. Hardened landscape increases and accelerates runoff, and also contributes to excess nutrient inputs, contaminants, and debris from residential, agricultural, and industrial sources (Chithra 2015; Frazer 2005). *S. edmondsoni* populations were also amplified in more heavily populated and developed areas, indicative of human influences.

6.2.1 Impervious Surfaces and Open Development

Significant correlations of *S. edmondsoni* cover were found with impervious surfaces (GLM; $p= 0.010$) and open development (GLM; $p= 0.013$). Large areas of impervious surfaces and paved roads due to urbanization contribute to greater quantities of runoff and negatively affects coastal water quality (Stoner & Arrington 2017; Guan et al. 2016; Ren et al. 2014; Chormanski et al. 2008). Soils and other natural porous surfaces absorb small particulate matter and other pollutants where communities of microorganisms can break them down, however, these contaminants are not able to penetrate impervious surfaces, and therefore runoff carrying these contaminants eventually ends up in our coastal waters (Frazer 2005). Pollutants may include sediments, pesticides, fertilizers, and bacteria and other disease-causing organisms from septic systems and wastewater treatment plants. Many studies have shown that increases in impervious surfaces lead to significant changes in the quantity and quality of rainwater runoff, resulting in degraded watershed health and coastal ecosystems (Morisawa & LaFlure 1979; Arnold et al. 1982; Bannerman et al. 1993). If more than 10% of a watershed is converted to impervious surfaces, stream quality begins to degrade, affecting watershed health and its adjacent coral reef communities (Schueler 1994; Rodgers et al. 2012). Furthermore, higher impervious cover generally leads to a decrease in groundwater recharge and an increase in storm flow and flood frequencies (Brun & Band 2000). Impervious surface coverage is widely accepted as a key indicator for the health of aquatic ecosystems and water pollution, and reducing runoff from these surfaces can improve stream and watershed health in urban areas (Arnold & Gibbons 1996; Ladson et al. 2006).

Larger populations of *S. edmondsoni* were found in areas that had a higher concentration of impervious surfaces (Figs. 31 & 32). On O‘ahu and Kaua‘i, the Kualoa and Pila‘a sites had lower coverage of impervious surfaces and therefore lower abundances of *S. edmondsoni*, while Kailua, which had the highest proportion of octocoral cover, had the highest coverage of impervious areas (Appendix B). In West Hawai‘i, many sites that had zero presence of *S. edmondsoni* were adjacent to regions that had low or no impervious surface cover (Fig. 31). High concentrations of the octocoral species were found in the Honokōhau area, which had a high density of impervious surfaces. A significant positive relationship with percent coverage of impervious surfaces and the octocoral species abundance indicates environmental impacts of

urbanization, and supports the use of the *S. edmondsoni* as an indication of anthropogenic influence.

Open development refers to low to medium intensity levels of development, and is a mixture of constructed materials (asphalt, brick, etc.) and mostly managed grasses and vegetation planted in developed areas for recreation and aesthetic purposes. Constructed/impervious surfaces account for less than 20% of total land cover in areas classified as open development, and these areas commonly include suburban neighborhoods and parks. While open development areas are not as severely modified by human influences compared to impervious surfaces/high intensity developed regions, these zones are still impacted by human activities mainly due to fertilization and irrigation. The statistically significant positive correlation of *S. edmondsoni* with open development land shows that even lower levels of development can cause increased abundances in octocoral populations.

6.2.2 Human Population

Human population had a statistically significant correlation with *S. edmondsoni* abundance (GLM; $p= 0.003$), where increased concentrations of the octocoral were found in heavily populated areas. This indicates the level of anthropogenic-induced stress, and presents an additional concern regarding the growing human population and subsequent environmental degradation in the future.

There are currently over 7.8 billion people living on Earth, with approximately half of the population living within 200 km of a coastline (Creel 2003). This places a disproportionate stress on coastal marine ecosystems, and many studies do recognize the size and growth of human population as the key threat to biodiversity and environmental declines (Mora et al. 2011; McKee et al. 2004; Cincotta et al. 2000). Human population density has been used as a proxy for anthropogenic impacts in coastal regions, and coral reef diversity and even biomass of resource fishes have been shown to negatively correlate with human population (Mora et al. 2011; Sale et al. 2014; Friedlander et al. 2018). As human population is projected to continue to increase, the deterioration of coastal environments will subsist if not effectively managed. Four billion people have been added since 1950 (Bongaarts 2009), and by 2100 the world's population is estimated to reach about 10.9 billion (Cilluffo & Ruiz 2019). Substantial human-induced environmental

changes will likely continue, and demographic change will also be an important factor in coral reef conservation and management. Significant positive correlations of *S. edmondsoni* cover with human population density and related anthropogenic stressors suggest that octocoral cover may persist and continue to increase in the coming years as human population will continue to grow.

6.2.3 Underground Injection Wells and Kaloko-Honokōhau

While underground injection wells were not a significant predictor of octocoral abundance, it does have a positive correlation and relatively large effect size on *S. edmondsoni* populations (Table 14). Underground injection wells that can leak into groundwater systems may play a large role contributing to the high abundances found in Honokōhau, Papawai, and Wawaloli on Hawai‘i Island (Fig. 10). Several water quality studies showed complex water quality issues and interactions along the shoreline due to increasing development and natural submarine groundwater discharge. For instance, intensive water sampling revealed brackish water within the Kaloko-Honokōhau National Historical Park, and lower nearshore water temperatures along with elevated tracers of groundwater input were found along the leeward coast of Hawai‘i Island (Street et al. 2008; Hunt 2014; Grossman et al. 2020). While groundwater discharge in Hawai‘i can vary in nutrient composition due to natural sources and land-use activities, it can play a substantial role in coastal water quality as it contributes to contaminant inputs from industrial, agricultural, urban, and wastewater disposal systems such as underground injection wells (Johnson et al. 2008; Street et al. 2008; Knee et al. 2010). When these pollutants from human sources inflate natural groundwater nutrient loads, submarine groundwater discharge significantly contributes to eutrophication and leads to the degradation of coastal reefs (Lapointe & Connell 1989; Lapointe 1997; Valiela et al. 1990).

The Kaloko-Honokōhau National Historical Park, which encompasses the Honokōkahu study site and is adjacent to the Wawaloli and Papawai sites that had high concentrations of *S. edmondsoni*, was established in 1978 with a goal to preserve and protect natural resources important to Native Hawaiian culture. At that time, lands surrounding the park were undeveloped, but within subsequent decades, urbanization of the Kailua-Kona area had dramatically expanded. Today most of the area is either developed or designated for industrial, commercial, or residential use, which includes golf courses, industrial parks, resorts, and

condominiums. Due to the rapid development in recent decades, anthropogenic nutrient input has undoubtedly increased as evidenced by elevated nitrogen levels detected in water sampling during the construction of a new golf course (Hunt 2014), and suspected reports of sewage discharge from the Kealakehe Sewage Treatment Plant just south of the park boundaries. Reef condition within the Honokōhau area appears to be degraded as high populations of *S. edmondsoni* and coral disease prevalence have been captured in previous benthic surveys (Walsh et al. 2010).

Contaminated groundwater discharge detected along West Hawai‘i’s coast is affecting coral reef condition, and septic contamination from underground wells may also be influencing ecosystem health. Past surveys along the leeward shoreline of Hawai‘i Island have uncovered a positive correlation of coral disease prevalence with size of submarine groundwater discharge plumes (Walsh et al. 2010), and abnormally high phosphorus concentrations have been recorded in groundwater discharge likely from industrial and septic leaks (Hunt 2014). It is well known that leaks from injection wells can end up in coastal waters, contributing to nutrient loading and deteriorating water quality (Paul et al. 1997; Hunt & Rosa 2009). Evidence of septic leachate detected in monitoring wells included not only magnified levels of nitrogen and phosphorus, but also certain pharmaceuticals at subtle levels (Hunt 2014). While the number of injection wells did not result in a statistically significant relationship with *S. edmondsoni* abundance when combining datasets with O‘ahu and Kaua‘i, it did have a significant positive correlation with octocoral abundance when examining only West Hawai‘i data (GLM; $p = 0.03$; pseudo $R^2 = 0.46$). Underground injection wells on the Big Island were only present at the Honokōhau, Papawai, and Wawaloli sites (Appendix B), which were precisely the sites that had notable abundances of *S. edmondsoni*. The Kailua and Pila‘a study sites did not contain injection wells, and therefore most likely resulted in a non-significant relationship with octocoral abundance when combining statewide data.

Human population, impervious surfaces, and development are all indicative of level of human influence, and significant positive relationships with *S. edmondsoni* populations support the use of the octocoral species as an indicator of anthropogenic influence. Moreover, prominent inputs of groundwater seeps from injection wells that degrade coastal water quality specifically in West Hawai‘i verify the severity of human impacts on the environment. While the Keawaiki

site on Hawai‘i Island is also strongly influenced by groundwater input (Grossman et al. 2020), it is isolated from urban influences (i.e. low population, low cover of impervious surfaces, zero open development), and zero presence of *S. edmondsoni* at that site further reinforces the strong role that urbanization clearly plays in groundwater quality and influence. Kailua and the Honokōhau areas are the most populated and developed study sites, and associated high abundances of the octocoral as compared to the rest of the sites corroborate the use of *S. edmondsoni* as a bioindicator of anthropogenic influence.

6.3 Indicator Evaluation and Assessment

A bioindicator assessment guided by the U. S. EPA’s recommendations for ecological indicator selection showed preliminary evidence that *S. edmondsoni* could serve as an indicator for anthropogenic influence in coral reef ecosystems. Performance of *S. edmondsoni* was adequate across all four phases within the guidelines (Conceptual Foundation, Feasibility of Implementation, Response Variability, and Interpretation and Utility). The octocoral species is relevant to management concerns, is easy to incorporate into existing monitoring methodologies, displays a response gradient relative to level of stress, provides a direct linkage to management decisions, and is linked to scleractinian coral cover which is a critical resource.

Connections between *S. edmondsoni* and hard coral cover should be further explored as linkages between bioindicators and critical resources ought to be understood. The significant negative correlation of *S. edmondsoni* abundance with hard coral cover suggests habitat competition, however, we currently have no knowledge on how *S. edmondsoni* interactions may affect hard corals here in Hawai‘i. The correlation between soft corals and hard corals have been identified in other studies elsewhere, where a decline in scleractinian coral cover was linked with an increase in octocorals (Chandran et al. 2015; Lasker et al. 2020; Tsounis & Edmunds 2017). Octocorals are known to rapidly cover degraded reefs, and recolonization of soft corals was among the first steps in ecological succession (Nishihira & Yamazato 1974; Chandran et al. 2015). *S. edmondsoni* show highly similar characteristics here in Hawai‘i, as elevated concentrations are found in degraded reefs that are near heavily developed areas. While there are currently no long-term studies examining the successive role of *S. edmondsoni* on coral reefs here in Hawai‘i, the blue octocoral is demonstrably linked to hard coral cover. If human-

mediated disturbances continue to contribute to the decline of scleractinian coral cover, this poses a concern for management as octocorals may continue to persist and expand.

A major gap yet to be explored also includes understanding the taxonomy of the species and temporal responses. While coral plasticity is a well-known phenomenon (Todd 2008; Muko et al. 2000; West 1997), further genomic investigations would determine the possible separation of the color forms, as it is important for an indicator species to exhibit a stable taxonomy. Long-term surveys should also continue to assess possible seasonal changes and temporal variability of the octocoral species. *S. edmondsoni* appears to be able to respond quickly to changes, and may reproduce and spread rapidly as evidenced by the blooms documented. While the spatial variability and response patterns that depict a gradient dependent on the level of stress has now been revealed, temporal variability, the range of environmental tolerances, and the lifespan of *S. edmondsoni* is not yet fully understood.

In summary, while knowledge on *S. edmondsoni* will advance our understanding and help reinforce its appropriateness as a bioindicator, the endemic octocoral species is well-supported to serve as a bioindicator of anthropogenic influence. Octocoral cover may be used in coral reef health classifications, as reef condition thresholds can be established using information collected on *S. edmondsoni*'s abundance and temporal and patterns. Creating and utilizing assessment thresholds in monitoring surveys are a simple and direct strategy that allows managers and researchers to identify and describe the extent of human impacts occurring in an ecosystem. *S. edmondsoni* has predictable spatial patterns, is easily quantifiable, has anticipated responses towards a wide range of anthropogenic stressors, clearly relays information on ecological changes that are meaningful to environmental decisions, provides a direct linkage to management action, and can be used to support and quantify the success of management efforts. These characteristics make *S. edmondsoni* a suitable candidate as a bioindicator of anthropogenic influence.

6.4 Conclusions

While further research should continue to explore *S. edmondsoni*'s life history patterns and environmental threshold limits, enough evidence has been revealed in this research to support the use of this octocoral species as a bioindicator of anthropogenic influence. Spatial analyses showed statistically significant positive correlations of *S. edmondsoni* with three of the strongest indicators of anthropogenic influence: human population, impervious surfaces, and open development. *S. edmondsoni* abundance also had a significant negative correlation with distance from shore, representing the severity and extent of human influence as a gradient from nearshore (strongest) to offshore. In addition, the octocoral species abundance was significantly and negatively correlated with hard coral cover, indicating a degrading reef system and highlighting the concern of *S. edmondsoni* persisting in the future and capable of monopolizing reefs.

S. edmondsoni meets bioindicator criteria and guidelines established by the U. S. EPA. The species performs strongly in the Conceptual Foundation, the Feasibility of Implementation, and Interpretation and Utility phases, however, the Response Variability phase necessitates continued research to understand temporal variation of *S. edmondsoni*. Strengths of using the octocoral as an indicator include how the presence and abundance of *S. edmondsoni* can be linked to the common management concern of ecosystem degradation, its efficiency of use, relative abundance, ability to depict a gradient based on level of stress, and the means to provide a direct linkage to management action. Knowledge gaps that should be addressed and further explored for response and temporal variability include life history patterns of the octocoral and environmental thresholds for salinity and temperature.

This research supports the use of *S. edmondsoni* as a bioindicator of human influence, providing a useful tool for natural resource managers and truly emphasizing the need for holistic coastal resource management. Many land-based anthropogenic factors upstream affect coastal reefs downstream as evidenced by this study, and successful management incorporates and acknowledges adjacent watershed health and upstream activities. "Ridge to reef", or catchment to sea connections have been recognized in many studies (Wolanski et al. 2009; Stock et al. 2011; Shelton III & Richmond 2016). Rodgers et al. (2012) established significant overall positive relationships with health of watersheds in Hawai'i and adjacent reef environments, further reinforcing the strength of these connections. Ecosystems have complex biotic and

abiotic interactions, and are connected through terrestrial, freshwater, and marine habitats. Resource managers need to consider these relationships and linkages, as accounting for connectivity among habitats will aid in properly locating and selecting areas with high conservation value (Tsang et al. 2019). Successive upstream solutions to coral reef conservation can also involve cooperating with landowners to reduce sediments and other land-based source pollutants using alternative land management strategies (Oleson et al. 2017). Combined land and sea management actions have been proven to be more successful, maximizing ecosystem returns and economic profits (Oleson et al. 2020). Statistically significant relationships with *S. edmondsoni* abundance and human influences including population, development, and impervious surfaces reiterates the strong linkages between land-based activities and coastal reef health. Incorporating the use of anthropogenic bioindicators such as *S. edmondsoni* will assist researchers and managers in detecting environmental changes early on, and the utilization of an integrated ecosystem approach will be pivotal to the conservation and management of coral reefs.

APPENDICES

Appendix A. Table of GLM outputs testing different combinations of simple and additive predictor variables and interactive effects of site on *S. edmondsoni* abundance. Model estimates are shown with degrees of freedom (df), log-likelihoods, AICc scores, delta, and model weights.

Model	(Intercept)	Distance	Rainfall	Coral Cover	Temperature	Rainfall:Site	Distance:Site	Coral Cover:Site	df	logLik	AICc	Delta	Weight
1	-2.579	-0.008	0.035	-0.331	0.256	+	NA	NA	10	27.4	-31.4	0.00	0.521
2	4.149	-0.008	0.022	-0.328	NA	+	NA	NA	9	26.0	-31.2	0.17	0.479
3	1.901	-0.005	0.022	NA	NA	+	NA	NA	8	17.0	-15.8	15.53	<0.001
4	1.428	NA	0.008	-0.171	NA	+	NA	NA	8	13.3	-8.5	22.90	<0.001
5	4.591	-0.007	0.004	-0.393	NA	NA	NA	+	9	7.0	6.7	38.11	<0.001
6	3.681	-0.005	NA	-0.296	NA	NA	+	NA	8	4.6	8.9	40.27	<0.001
7	4.437	-0.006	NA	-0.380	NA	NA	NA	+	8	2.7	12.7	44.07	<0.001
8	2.258	-0.004	0.002	NA	NA	NA	+	NA	8	-0.2	18.5	49.90	<0.001
9	2.529	-0.005	0.003	NA	NA	NA	NA	NA	6	-3.6	20.5	51.85	<0.001
10	2.065	NA	0.004	-0.298	NA	NA	NA	+	8	-1.4	21.0	52.42	<0.001
11	1.025	NA	0.003	NA	NA	NA	NA	NA	5	-9.6	30.1	61.48	<0.001
12	-0.706	0.002	NA	NA	NA	NA	NA	NA	3	-32.0	70.4	101.74	<0.001
13	-0.560	0.002	NA	-0.089	NA	NA	NA	NA	4	-31.3	71.2	102.59	<0.001
14	-0.339	0.002	-0.002	-0.078	NA	NA	NA	NA	5	-30.7	72.3	103.69	<0.001
15	-0.037	NA	-0.002	NA	NA	NA	NA	NA	3	-33.8	73.9	105.30	<0.001
16	-0.181	NA	NA	-0.028	NA	NA	NA	NA	3	-34.3	75.0	106.36	<0.001
17	0.046	NA	-0.002	-0.031	NA	NA	NA	NA	4	-33.7	76.0	107.34	<0.001

Appendix B. Table of extracted natural and anthropogenic parameters compiled for spatial analysis. Note that total population numbers may not be accurate due to low resolution and/or loss of cell sizes in rasterization of datasets.

Site	Adjacent Watershed	Mean <i>S. edmondsoni</i> (% of total benthic cover)	Distance from shore (km)	Mean Annual Rainfall (mm/yr)	Impervious Surfaces (%)	Open Development (%)	Agriculture (%)	Underground Injection Wells (#/km ²)	Total Population within watershed
Anaehoomalu	Hopeaia	0.00	3.00	516.58	0.22	0.00	0.00	0.00	396
Honokohau	Kohanaiki	12.33	1.90	860.78	5.65	2.82	4.85	0.68	5170
Kalahiki	Kiilae	0.00	4.90	1209.51	0.72	0.18	1.45	0.00	304
Kamilo	Pohakuloa Gulch	0.00	0.40	1318.13	1.21	0.63	65.05	0.00	123
Keawaiki	Puuwaawaa	0.00	4.50	578.55	0.29	0.00	3.88	0.00	19
Lapakahi	Lapakahi	0.00	2.10	735.35	0.59	0.00	81.05	0.00	0
Papawai	Honuaula	9.16	3.60	1169.96	3.83	1.94	5.05	0.43	5121
Waiakailio	Keawewai Gulch	0.05	0.70	893.01	2.81	2.09	40.47	0.00	353
Wawaloli Open	Kohanaiki	0.68	3.20	860.78	5.65	2.82	4.85	0.68	5170
Wawaoli FMA	Kohanaiki	4.08	2.40	860.78	5.65	2.82	4.85	0.68	5170
Kualoa	Hakipuu	6.38	1.20	2020.49	1.95	0.69	0.59	0.32	412*
Kailua	Kaelepulu	12.69	0.40	1002.29	41.32	13.80	0.00	0.00	18232
Pilaa	Pilaa	0.54	0.25	1718.44	3.32	4.64	55.05	0.00	193

*Population number used for Kualoa was extracted from the Coral Reef Assessment and Monitoring Program watershed information

(http://cramp.wcc.hawaii.edu/Watershed_Files/Oahu/WS_Oahu_koolaupoko_hakipuu.htm) as the original calculated population number was extremely low compared to publicly available values (42)

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