

JUVENILE FISH HABITAT ASSOCIATIONS: THE INTEGRATION OF
ECOLOGICAL SURVEYS, REMOTE SENSING TECHNOLOGY, AND LOCAL
KNOWLEDGE TO INFORM COMMUNITY-BASED FISHERIES
MANAGEMENT IN HĀ'ENA, KAUA'I

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ABSTRACT

Nearshore fish populations are in decline in the main Hawaiian islands, and in recent years there has been greater emphasis on the value of ecosystem-based local management. This project integrates multiple knowledge sources to provide a basis for effective community-based resource management in a rural Hawaiian community. This study tests the hypothesis that juvenile reef fish are significantly influenced by seascape variables, such as composition of surrounding habitat types. Set in the context of existing local knowledge of nearshore resources, nursery habitats for juvenile reef fishes – areas of particular ecological value for sustaining fisheries resources – are assessed in a quantitative manner, supplementing the information upon which management initiatives were based. To better understand underlying ecological patterns and processes, I conducted fine-scale *in situ* ecological surveys in addition to applying a spatially-explicit approach based on detailed benthic habitat maps produced using GIS and remote sensing methods. Canonical correspondence analyses were used to assess fish-habitat relationships, and habitat metrics were found to be influential on juvenile reef fish abundances. Depth, macroalgal cover, coral cover, and distance to shore emerged as primary influential factors. Some fish species were more influenced than others by seascape factors. Habitat associations of two important food resource species in the study area of Hā‘ena, Kaua‘i, the convict tang (*Acanthurus triostegus*) and the redlip parrotfish (*Scarus rubroviolaceus*), were identified, providing spatial distribution information valuable for resource management planning. This quantitative ecological study played an important role in the successful approval of the Hā‘ena fishery management plan by the state governing agency. An ecosystem-based management approach, informed by multiple knowledge sources, will help to ensure the sustainability of fisheries and maintain the societal benefits provided by the ecosystem.

TABLE OF CONTENTS

ACKNOWLEDGEMENTS.....	ii
ABSTRACT.....	iii
LIST OF TABLES.....	vi
LIST OF FIGURES.....	vii
CHAPTER 1. INTRODUCTION.....	1
1.1 Research questions and objectives.....	3
CHAPTER 2. BACKGROUND.....	4
2.1 Fish-habitat associations.....	4
2.1.1 <i>Juvenile habitats.....</i>	<i>5</i>
2.1.2 <i>Nursery habitats.....</i>	<i>6</i>
2.1.3 <i>Place-based studies.....</i>	<i>7</i>
2.1.4 <i>Seascape assessments.....</i>	<i>8</i>
2.2 Local ecological knowledge.....	9
2.2.1 <i>Community-based resource management and integration of science.....</i>	<i>10</i>
2.3 Remote sensing and habitat mapping.....	14
2.4 Summary.....	16
CHAPTER 3. METHODS.....	18
3.1 Study site.....	18
3.2 Biological surveys.....	20
3.2.1 <i>Sample design.....</i>	<i>20</i>
3.2.2 <i>Fish surveys.....</i>	<i>21</i>
3.2.3 <i>Benthic surveys.....</i>	<i>23</i>
3.3 Habitat mapping.....	24
3.3.1 <i>Classification scheme.....</i>	<i>24</i>
3.3.2 <i>Training surveys.....</i>	<i>26</i>
3.3.3 <i>Interpretation and delineation.....</i>	<i>26</i>
3.3.4 <i>Habitat data extraction.....</i>	<i>27</i>
3.3.5 <i>Remote measures of depth and rugosity.....</i>	<i>29</i>
3.3.6 <i>Additional remotely sensed seascape metrics.....</i>	<i>30</i>
3.4 Statistical analysis.....	31
3.4.1 <i>Canonical correspondence analysis.....</i>	<i>31</i>
3.4.2 <i>Treatment of variables.....</i>	<i>32</i>
3.4.3 <i>Assessment of ontogenetic differences in habitat associations.....</i>	<i>35</i>

CHAPTER 4. RESULTS.....	36
4.1 Juvenile fish assemblages.....	36
4.2 Seascape.....	37
4.2.1 <i>In situ</i> transect surveys.....	37
4.2.2 Remotely sensed benthic map.....	38
4.3 Juvenile fish-habitat associations.....	42
4.3.1 <i>In situ</i> environmental data.....	42
4.3.2 Remotely sensed environmental data.....	45
4.4 Ontogenetic differences in strength of habitat influence.....	52
CHAPTER 5. DISCUSSION.....	54
5.1 Juvenile fish-habitat associations.....	55
5.1.1 <i>Influential variables.....</i>	56
5.1.2 <i>Variations between data collection methods.....</i>	59
5.1.3 <i>Habitat generalists.....</i>	62
5.1.4 <i>Ontogenetic variation in habitat relationships.....</i>	63
5.1.5 <i>Value of a seascape approach.....</i>	64
5.1.6 <i>Spatial scale.....</i>	65
5.1.7 <i>Limitation of temporal restriction: Only a snapshot.....</i>	68
5.2 Community-based ecosystem management.....	69
5.2.1 <i>Contribution to CBSFA efforts in Hā‘ena.....</i>	71
5.2.2 <i>Baseline studies.....</i>	72
5.2.3 <i>Future monitoring efforts.....</i>	74
CHAPTER 6. CONCLUSION.....	76
REFERENCES.....	78
APPENDIX 1 Benthic taxa observed in <i>in situ</i> surveys.....	90
APPENDIX 2 Classification scheme descriptions.....	92
APPENDIX 3 Observed juvenile species.....	94

LIST OF TABLES

Table 1	Examples of local knowledge.....	13
Table 2	Habitat classification scheme.....	25
Table 3	Explanatory variable transformations.....	34
Table 4	Total number of transect surveys.....	36
Table 5	Juvenile species included in CCAs.....	37
Table 6	Total percent cover by benthic cover type from <i>in situ</i> surveys.....	38
Table 7	Percent total area of habitat classes from remotely sensed data.....	42
Table 8	Comparison of spatial scales of remotely sensed habitat data.....	46

LIST OF FIGURES

Fig. 1 Study site.....	20
Fig. 2 Transect survey locations.....	21
Fig. 3 Process for extracting remotely sensed habitat data.....	28
Fig. 4 Delineated habitat boundaries.....	39
Fig. 5 Intraset correlations and response variable scores, <i>in situ</i> data.....	44
Fig. 6 Ordination biplot, <i>in situ</i> data.....	45
Fig. 7 Intraset correlations and response variable scores, remotely sensed cover data..	48
Fig. 8 Ordination biplot for CCA with remotely sensed cover data.....	49
Fig. 9 Intraset correlations and response variable scores, remotely sensed structural data.....	51
Fig. 10 Ordination biplot for CCA with remotely sensed structural data.....	52
Fig. 11 Size distribution of <i>A. triostegus</i> between reef zones.....	53

CHAPTER 1. INTRODUCTION

Nearshore marine ecosystems around the globe are under great pressure from environmental and anthropogenic stressors such as habitat destruction, overfishing, climate change, invasive species, nutrient runoff, and sedimentation (Hughes et al. 2003, Lotze et al. 2006, Hughes et al. 2007). As a result, marine resources are in decline worldwide (Jackson et al. 2001, Hilborn et al. 2003, Bellwood et al. 2004). In the state of Hawai‘i, nearshore resources are severely depleted (Friedlander and DeMartini 2002, Friedlander et al. 2005, Williams et al. 2008, Williams et al. 2009) and the development of effective management is critical. Long-standing ecosystem-based approaches to resource management, central to traditional Hawaiian practices, deteriorated with the privatization of lands and establishment of top-down governmental management (Johannes 1978b, Andrade 2008), but have recently been revitalized as the need for effective preservation of resources grows more urgent (Aswani 2010, Friedlander et al. 2013). Hawaiian communities have begun to explore the integration of customary and contemporary management approaches (Berkes et al. 2000, Johannes 2002), in hopes of developing community-based management systems that preserve cultural practices as well as implement nearshore marine resources (Friedlander et al. 2013).

On the north shore of Kaua‘i, the community of Hā‘ena has long sustained itself on local resources (Andrade 2008), employing traditional management practices that recognize the importance of ecological connections. Recent state legislation (HB Act 241) designated Hā‘ena as a Community Based Subsistence Fishing Area (CBSFA), which empowers the community to recommend a management plan to the Hawai‘i Department of Land and Natural Resources (DLNR), informed by local knowledge and based on local cultural practices. As part of the

proposed management plan, the community hopes to establish boundaries for a regulated *pu'uhonua*, or “place of refuge” (Antolini 2004), which would protect areas considered to be important for the growth and survival of juvenile reef fishes. Based on local knowledge of ecological patterns, the community has prioritized a location for such protection, an area well-known by community members to be critical for supporting fish in early life stages, allowing them to grow and later replenish adult populations.

As part of a larger project funded by the National Science Foundation that investigates ecosystem resilience under various management regimes and climate change scenarios, this project seeks to bolster the efforts of the Hā'ena community with information drawn from quantitative scientific studies, an important contribution in the endeavor to establish state-sanctioned management rules for the local fishery. Biological studies play an important role in the process of developing management laws, providing a foundation upon which assessment and legislation can be based (Lindeman et al. 2000, Beck et al. 2001, Botsford et al. 2009). In order to successfully achieve legislative protection of resources, it is critical that community-based management efforts bridge the gap between local knowledge and science (Tissot et al. 2009). The methods and approaches described herein provide an example of effective integration of local and scientific knowledge, and should be used as a template for similar efforts around the state and elsewhere.

1.1 Research questions and objectives

Question 1: Is the distribution of juvenile reef fishes influenced by surrounding habitat and seascape metrics?

Research Objective 1: Develop a spatially-explicit estimate of habitat association patterns of juvenile reef fishes in the Hā‘ena nearshore ecosystem to aid in identification of essential fish nursery habitat.

Question 2: How do remote sensing methods compare to *in situ* measures in the interpretation of ecological patterns?

Research Objective 2: Assess fish-habitat associations with a high resolution benthic habitat map of the Hā‘ena nearshore area at a scale that is ecologically relevant for development and assessment of local management efforts; compare these associations to assessments with data gathered from field methods.

Question 3: Can remote sensing methods be used to assess seascape variables that may otherwise be difficult to incorporate with field methods alone?

Research Objective 3: Incorporate additional spatial seascape metrics, quantified with remote methods and geospatial software, to assess whether these variables help explain juvenile fish distribution patterns.

CHAPTER 2. BACKGROUND

2.1 Fish-habitat associations

In the life cycle of reef fishes, an individual passes through an egg (zygote) stage, followed by a larval stage, then grows into juvenile and sub-adult stages, and ultimately reaches the adult stage (Richards and Lindeman 1987). For many species of fishes, different habitats are used across the various stages of the life cycle. Fish habitat use is largely determined by an interaction between the requirements of the fish at a given time and any constraints a fish faces in selecting habitats. These habitat requirements and associations shift with ontogeny, or according to life stage (Sale 1998, Lindeman et al. 2000, St. Mary et al. 2000, Appeldoorn et al. 2003). Particular habitats may provide protection from predation, enhanced foraging opportunities and thus contribution to faster growth, ideal reproduction or spawning conditions, or favorable abiotic conditions such as freshwater input or protection from waves and swell (Holbrook and Schmitt 1988, Hixon and Beets 1989, 1993, Adams and Ebersole 2002, DeMartini 2004).

Ontogenetic habitat shifting, or movement of fish from one habitat to another at certain life stages, is assumed to be a strategy that provides different advantages to individuals at different life stages, which in turn increases lifetime fitness (Dahlgren and Eggleston 2000, Grol et al. 2014). Thus, as foraging needs, predation risk linked to body size, and reproductive stages change over life stages, so do resource needs and habitat use (Johannes 1978a, Cocheret de la Morinière et al. 2003, Nemeth 2009). An understanding of fish-habitat relationships at certain life stages can help to identify areas that serve as essential fish habitats.

2.1.1 *Juvenile habitats*

In an early life stage, larvae move, either by passive or active transport, to juvenile habitats such as estuaries (Brown et al. 2005), mangroves (Mumby et al. 2004a, Nagelkerken et al. 2008a), and reef lagoons (Adams and Ebersole 2002). There, they settle, metamorphose, grow to sub-adult juvenile stages, and for many species, move to nearby adult habitats offshore or in outer reef areas (Parrish 1989, Beck et al. 2001). Early post-settlement mortality and growth affect variation in recruitment (Jones 1987, Forrester 1990). The ability of recruits to survive through predation intensity, food scarcity, and unfavorable abiotic conditions is often influenced by the surrounding habitat (Holbrook and Schmitt 1988), so juvenile habitat utilization patterns can impact the demography of post-settlement fish assemblages (Sale et al. 1984, Carr 1989, Tolimieri 1998). For example, in reef ecosystems where predation intensity on juvenile fishes is particularly high (Johannes 1978a, Parrish 1989, Hixon 1991, Hixon and Jones 2005, Dorenbosch et al. 2009), habitats that provide refuge from predation may support higher abundances of juveniles (Hixon and Beets 1989, Almany 2004). Refuge is often provided in the form of structural complexity by which small individuals can hide (Hixon and Beets 1993, Beukers and Jones 1998), therefore structurally complex habitats are likely to support higher abundances of fishes.

Factors which impact juveniles can also have indirect effects on adult assemblages. Juvenile fish recruitment is an important factor contributing to adult fish densities, and adult fish populations can fluctuate with variation in recruitment success (Sale et al. 1984, Victor 1986, Jones 1990). Studies have begun to illuminate the importance of juvenile habitats to local reef fish biomass (Friedlander 2001, Jones et al. 2010, Nagelkerken et al. 2012). Through the process

of ontogenetic migration, juvenile habitats supply recruits to adult populations and replenish fish populations on directly adjacent reefs (Verweij et al. 2008, Jones et al. 2010). For example, Mumby et al. (2004a) investigated the value of mangroves as juvenile habitat, and showed that reefs with nearby mangroves had higher fish density than reefs without nearby mangroves. This pattern points to the value of protecting juvenile habitats as a means of managing adult populations.

2.1.2 Nursery habitats

Some habitats serve the role of juvenile habitat more effectively than others, contributing greater abundances of individuals to adult populations. It is on the premise of disproportionate contribution to adult populations that the nursery-role concept is based (Beck et al. 2001). In an effort to strengthen future studies on the nursery-role of habitats, Beck et al. (2001) established a clearly defined and testable nursery-role hypothesis, stating that nursery habitat for a given species has a greater-than-average contribution per unit area of individuals to adult populations, as compared with other juvenile habitats in the system. The authors specify four factors by which ecological processes may support greater contributions to adult populations (density, growth, survival of juveniles, and movement to adult habitats), with the underlying value of a nursery habitat in that it successfully transfers higher biomass to adult populations (Gillanders et al. 2003).

Given that nursery habitats provide disproportionately high contribution of fishes to adult populations, they are important to the goal of managing and sustaining fish populations.

Focusing management efforts on these areas can be a time- and cost-efficient way to protect local fisheries resources, an important condition when such resources are limited, as they often are (Beck et al. 2001, Dahlgren et al. 2006). Nagelkerken et al. (2012) even found the effects of proximity of nursery habitats on fish assemblage biomass to far outweigh the effects of fishing restrictions on adult populations, underlining the ecological importance of nursery habitats and the value of protecting them.

Modern fisheries management approaches are now taking the importance of nurseries into account. The U.S. Magnuson-Stevens Fisheries Conservation and Management Act of 1996 set the stage for habitat-based management, recognizing that habitats that are ecologically important to fisheries should be conserved (Rosenberg et al. 2000). Largely in acknowledgement of the importance of nursery habitats, the act mandated more research on the identification of essential fish habitat, and subsequent conservation of such. This project contributes to a growing bank of knowledge about the habitat characteristics that are of critical importance to preserving natural ecological functions that support fisheries.

2.1.3 Place-based studies

Extensive research has been done in recent years on the value of mangroves (Mumby et al. 2004b), seagrass beds (Nagelkerken et al. 2000), and back-reef lagoons (Adams and Ebersole 2002) as nursery habitats. However, investigations of fish nursery habitat in Hawaiian reef systems are few (but see DeMartini 2004, DeMartini et al. 2010). Previous studies that have investigated nursery habitats of fishes in Hawai‘i have generally addressed a single species or genera, rather than a local assemblage (Leber et al. 1996, Leber et al. 1998, Smith and Parrish

2002, Friedlander and Ziemann 2003). In the tropical Pacific, there is still much to be understood about the ecological processes that sustain coastal fisheries (Bell et al. 2013).

The importance of location-specific investigations of nursery habitats is illustrated by the disparate and at times contradictory conclusions about the role of certain habitats as nurseries. For example, while some studies have indicated that seagrass meadows serve an important nursery role in the Caribbean (Nagelkerken et al. 2000), other studies in Australia have not found seagrass habitat to be particularly important as a nursery (Edgar and Shaw 1995). Additionally, recruitment patterns can be highly variable by location (Walsh 1987). Place-based studies of the ecological factors driving these variations can help to more accurately inform local management efforts.

2.1.4 Seascape assessments

Many studies that have investigated relationships between fish assemblages and habitat have assessed fish variables by individual habitat types, such as hard-bottom vs. unconsolidated sediment, or mangrove vs. rubble vs. patch-reef (Adams and Ebersole 2002, Friedlander et al. 2003b, Friedlander et al. 2007a, Grol et al. 2014). This stratification guides sampling design and accounts for variation in fish assemblage structure resulting from single habitat types (Wedding et al. 2011a). However, it is important to recognize that fish assemblages are influenced not simply by a single habitat type alone, but by the landscape of surrounding habitats, or more appropriately the “seascape” (Christensen et al. 2003a, Kendall et al. 2004, Pittman et al. 2004, Wedding and Friedlander 2008).

The composition and arrangement of habitats in a seascape influence the ecological dynamics within a system (Pittman et al. 2007b). Fishes are affected by their immediate habitat as well as direct or indirect interactions with other habitats in the area (Sheaves 2005). Sites otherwise similar in all respects but differing in the types of co-occurring habitats may differ in their capacity to support juvenile fishes. For example, Kendall et al. (2003) found the distribution of juvenile French grunt (*Haemulon flavolineatum*) in the Caribbean on hard bottom habitats to vary with spatial variation (distance and area) of surrounding soft bottom foraging habitats. Often, multiple habitat types are located within one small area, and species may use several different habitat types during a single life stage (Adams et al. 2006, Pittman et al. 2007b). The evaluation of suitable nursery habitat should thus incorporate the spatial characteristics of the mosaic of habitats, as opposed to assessing individual habitats.

2.2 Local ecological knowledge

To say that studies on nursery habitats in Hawai‘i are lacking is not to say that the knowledge does not exist. In traditional Hawaiian fishing practice, conservation was a way of life, as expressed in a published interview with *kūpuna* (elders): “...When I was growing up at Miloli‘i (Hawai‘i Island) before, I never heard of conservation, but when I heard it, I said, ‘Oh my goodness, we had that!’ We had all those things” (Maly and Pomroy-Maly 2003). Fishermen understood the ecological values of areas that supported high abundances of juvenile fishes (Maly and Pomroy-Maly 2003). In order to maintain the fish stocks that fed the community, traditional Hawaiians would designate known nursery areas as *pu‘uhonua*, or places of refuge. These were protected areas intended to allow for the growth and survival of juveniles, so that

they may contribute to the adult populations and allow fish stocks to replenish (Maly and Pomroy-Maly 2003, Higuchi 2008). These actions were based on knowledge that accumulated over many years of close connection with the land and sea, and which represents intimate, fine-scale information on the ecological dynamics of nearshore systems (Poepoe et al. 2003, Berkes and Berkes 2009).

2.2.1 Community-based resource management and the integration of science

Hawaiian communities have begun to explore the integration of customary knowledge and practices with contemporary management approaches (Berkes et al. 2000, Johannes 2002), in hopes of developing community-based management systems that preserve cultural practices as well as nearshore marine resources (Friedlander et al. 2013). There still exist areas of Hawai'i that have maintained cultural knowledge and belief systems, and continue to harvest and manage resources in a manner consistent with traditional practices (McGregor 2007). In published interviews with Hawaiian fishermen, one interviewee conveyed the value of *pu'uhonua* for the maintenance of food sources, stating, "For us, leave that *pu'uhonua* alone. That place of refuge, and let it feed us" (Maly and Pomroy-Maly 2003). Another interviewee addressed the importance of retaining cultural practices and passing them on through generations, affirming *aloha* (love) for the *'aina* (land) and stating that, "...the *heiau*, the *ko'a*, the *pu'uhonua*, they got to designate and take care of those places. Lucky today, the young people are getting educated about those things" (Maly and Pomroy-Maly 2003). Local knowledge and cultural practices are still intact in

many Hawaiian communities, and this source of information is of critical importance in the effort to *malama* (care for) local marine ecosystems.

On the north shore of Kauaʻi, the community of Hāʻena has retained much of this local knowledge, passed down through generations and maintained with continued observation and connection to the ecosystems that provide them with food and materials (Table 1). The community has long sustained itself on local resources, employing the traditional *ahupuaʻa* (watershed) system of resource management that recognizes the importance of ecological linkages, from the uplands to the sea (Andrade 2008). The rich source of knowledge held within the community guides resource harvesting practices, and is the foundation for current efforts to establish state-sanctioned rules to manage the local fishery.

In 2006, the community of Hāʻena successfully lobbied the Hawaiʻi State Legislature to pass HB Act 241 (Hawaiʻi Revised Statutes, Chapter 188-22.9), which established a Community-Based Subsistence Fishing Area (CBSFA) for the *ahupuaʻa* of Hāʻena. The act empowers the community to recommend a management plan to the Hawaiʻi Department of Land and Natural Resources (DLNR), enabling the development of management that espouses the *ahupuaʻa* system to protect local ecosystems and resources, such as fisheries that feed the community (Poepoe et al. 2003, Tissot et al. 2009, Friedlander et al. 2013). In the proposed fishery management plan for Hāʻena, the community outlined boundaries for a regulated *puʻuhonua*, based on local knowledge of the ecologically important areas of the nearshore reef systems. The proposed area is one of several areas well-known by community members to be critical for supporting fish in early life stages, allowing them to grow and later support adult populations.

One of the challenges that community-based management efforts must face is that of bridging the gap between local knowledge and legislative prerequisite for supporting quantitative data (Tissot et al. 2009). Thus, in order to successfully enact regulations in the current system of state-sanctioned management, there must be an integration of community and science. Biological studies play an important role in the process of developing management laws, and quantitative data describing fish distributions lend a foundation on which assessment and legislation can be based (Lindeman et al. 2000, Beck et al. 2001, Botsford et al. 2009).

The people of Hā‘ena have been working for many years to develop a CBSFA management plan. Rules were drafted based on knowledge of *kūpuna*, long-time resident families, and the traditional and customary practices of the local native Hawaiian community. As the community seeks increased collaboration with the state, their efforts are strengthened by the integration of ecological studies. This study was developed with the intent to contribute scientific knowledge to the efforts of the Hā‘ena community in managing their marine resources in a sustainable manner. The objectives of the original study were to assess juvenile fish abundances in the proposed *pu‘uhonua* management area relative to surrounding areas – a comparison of zones. The project described in this thesis stems from the original study, and expands the investigation of juvenile fish distribution to describe habitat characteristics particularly important to the local juvenile fish assemblage, addressing species-specific, spatially-explicit habitat associations.

Table 1. Examples of local knowledge represented in published interviews with Hā'ena community members and local fishermen.

Topic	Quote	Reference
Historical abundance of resources	"You know how much <i>kala</i> ¹ we caught? Ninety-two <i>kala</i> that was a record!"	Maly and Maly (2003); pg. 270
Changes in abundance of resources	"Throwing net in those days, had plenty fish, Hā'ena, the beach had plenty fish. Not anymore. It's really changed. Times have changed."	Andrade (2008); pg. 52
Fish behavior	"When they hit the <i>moi</i> ² in Lumahai, they going run over here. That I know."	Maly and Maly (2003); pg. 194
Distributions of resource species	"[Uncle Tom] knew right where to go whenever fish were needed to feed his family or to contribute to family celebrations of birth, graduation, marriage, or the passing of a loved one."	Andrade (2008); pg. 144
Introduced species	"Maybe it's not that. Maybe it's the time now and maybe how our reefs look. Like before, the reef used to be covered with all kind <i>limu</i> ³ . Now we get something like alien kind <i>limu</i> ."	Maly and Maly (2003); pg. 157
Response of resource to environment	"From what I learned in the past, where there is fresh water the <i>i'a</i> ⁴ is soft, and where there is no rivers like Ni'ihau the fish are tough. When you fry, as soon as you throw in the frying pan... [gestures curling up in the pan]."	Maly and Maly (2003); pg. 265
Seasonal patterns	"And over here during the summer, that's when it comes. I guess that's when the <i>manini</i> are born."	Maly and Maly (2003); pg. 258
Transmission of knowledge	"Year after year [Uncle Tom] accompanied his father, who always referred by traditional Hawaiian names of the locations where the fish were caught."	Andrade (2008); pg. 144
Cultural harvesting practices	"Only enough to eat, and that's how they used to fish before... you leave some back."	Maly and Maly (2003); pg. 271

¹ *kala* = *Naso unicornis* (bluespine unicornfish)

² *moi* = *Polydactylus sexfilis* (Pacific threadfin)

³ *limu* = algae, seaweed

⁴ *i'a* = fish

2.3 Remote sensing and habitat mapping

Remote sensing technology has become a powerful tool in the investigation of ecological dynamics within coral reef systems (Andréfouët et al. 2003, Mumby et al. 2004c, Wedding et al. 2011b). Technological advances in geospatial tools allow for quantitative studies of the correlations between the mosaic of habitats in an area and the assemblage structure of reef fishes (Kendall 2005, Pittman et al. 2007a, Friedlander et al. 2011). The combination of *in situ* fish census data with benthic mapping allows for a clear and robust evaluation of fish distributions in a seascape framework, which can inform ecosystem-based management (Kendall et al. 2004, Friedlander et al. 2011). By mapping the different habitats and surveying the associated fish assemblages, it is possible to establish relationships and identify the habitat characteristics that are most important to structuring fish communities (Christensen et al. 2003a, Pittman et al. 2007a), allowing for inference of fish distributions at larger scales (Mumby et al. 2004c, Wedding et al. 2008).

Furthermore, remote sensing technology allows for the investigation of the importance of spatial pattern metrics and seascape characteristics that might otherwise be difficult to quantify with field methods alone. For example, metrics of spatial configuration such as habitat area, patch-based connectivity, and proximity of features can be quantified from 2D categorical maps and used to assess ecological patterns (Turner 2001). Tools and metrics that facilitate the examination of spatial ecological dynamics have been commonly applied to terrestrial landscape ecology (Turner 1989) and landscape ecology as it applied to riverine systems (Wiens 2002), but the value of such tools in marine systems is still being explored and expanded (Wedding et al. 2011b).

Geospatial information on habitat and associated marine resources strengthens an understanding of species-habitat linkages and supports informed management practices (Pittman et al. 2007a, Wedding and Friedlander 2008, Wedding et al. 2011a). Knowledge of the spatial distributions of species relative to the mosaic of habitat types can be used to infer foraging and ontogenetic movement patterns, which can assist resource managers in preserve design and evaluation (Friedlander et al. 2007b, Pittman et al. 2007b, Wedding et al. 2011a). Given the substantial amount of time and resources necessary for *in situ* data collection (Wilson et al. 2007), remote sensing technology serves as a tool which provides information for coastal management that is cost-effective, time-efficient, and replicable (Purkis et al. 2008, Hamel and Andréfouët 2010, Wedding et al. 2011a).

In order to establish useful knowledge of fish distribution patterns in relation to habitat, maps must contain appropriate spatial and thematic detail, created at a scale that allows for the tracking of fish-habitat interactions in the system (Kendall et al. 2004, Mumby et al. 2004c, Purkis et al. 2008). The benthic habitat maps that are currently available for the Hā‘ena shoreline were created by the NOAA National Ocean Service Biogeography Branch in a national mapping effort, produced at a scale of 1:6000 with a minimum mapping unit of 1 acre (0.4 ha; Battista et al. 2007). Previous maps produced at this same scale (but with a slightly different classification hierarchy) (Coyne et al. 2003) have proven beneficial to the evaluation of region-level function of MPAs in Hawai‘i (Friedlander et al. 2007b). However, to assist management efforts at a local scale, higher resolution maps are necessary (Wedding et al. 2011a). Without highly resolved and accurate benthic habitat maps, the ability to understand fish-habitat dynamics is limited, as is the

capacity to apply such information towards management design and evaluation, and ultimately to the preservation of coastal ecosystems (Kendall et al. 2004).

Quantification of relationships between fish assemblages and fine-scale habitat features in Hā'ena provide an appropriate spatial context for management decisions (Eggleston et al. 2004, Kendall et al. 2004). By using seascape-scale measures of fish-habitat associations, resource managers can interpret areas of high juvenile fish abundance and design reserves for the protection of these areas (Pittman et al. 2004, Grober-Dunsmore et al. 2007). The ability to understand the linkages between fish and habitat and maintain the integrity of critical habitats in an ecosystem can be an important element to effective design of protected areas and preservation of biological communities (Appeldoorn et al. 2003, Grober-Dunsmore et al. 2007). Species-specific evaluation of critical habitats also provides a means of prioritizing reserve areas that may be particularly important for supporting economically or ecologically valuable species (DeMartini et al. 2010).

2.4 Summary

An ecosystem-based approach to management efforts in the Hawaiian Islands and elsewhere is crucial for the conservation of species and processes that maintain healthy coral reefs. As opposed to organism-oriented management plans, an ecosystem approach helps to protect the habitats and combinations of habitats critical for different species of fishes and different life stages (Nagelkerken et al. 2002, Pittman et al. 2007b). The design of management areas must take into account not only the functional importance of habitats such as those that serve a nursery

role, but also the spatial arrangement of these habitats and how it facilitates ecological processes (Appeldoorn et al. 2003, Pittman et al. 2004).

This project integrates multiple knowledge sources and tools to help better understand the ecological dynamics that impact marine resources. In the context of the Hā'ena nearshore ecosystem, identification of spatial patterns of juvenile fish assemblages and the seascape variables that support them provide information about local ecological mechanisms responsible for variations in fish distributions (Appeldoorn et al. 2003, Pittman et al. 2007b, Grober-Dunsmore et al. 2008). Local knowledge, spatial habitat mapping, and ecological surveys have helped to gather information on these distribution patterns, and have played a vital role in the establishment of ecosystem-based local management actions.

In the efforts of local Hawaiian communities to design management plans and sustain their nearshore resources, local ecological knowledge and traditional practices provide invaluable information, and are integral to the development of management tailored to the culture and resource needs of the community. The state of Hawai'i has taken important steps in recent years to empower communities to care for their own fisheries, but in order for management efforts to be successfully sanctioned by state agencies, there is a great need for information from ecological studies. The integration of science, technology, and local knowledge is necessary. With a knowledge base informed by multiple sources, local ecosystem-based management can be developed to address the needs of a community in a manner that is most appropriate for the ecological and cultural dynamics of the place. This project and the actions taken by the Hā'ena community serve as a template for future resource management efforts around the state of Hawai'i.

CHAPTER 3. METHODS

3.1 Study Site

The study to address research questions was conducted in Hā‘ena, located on the north shore of the Hawaiian island of Kaua‘i. Kaua‘i is the oldest of the six main Hawaiian islands (3.5 – 5.7 million years; Macdonald et al. 1983), located at the northwest end of the chain of inhabited high islands (Fig. 1). Hā‘ena is a small community located at the end of the Kuhio Highway, which runs along the coastline of the east and north shores of the island. Hā‘ena sits adjacent to the Na Pali Coast State Park, a 26 km stretch of rugged, sheer cliffs that stretch as high as 1200 m above the ocean surface. The deep, wind-eroded valleys of the region funnel rainfall, carried on the wet trade winds, into the mountains, creating one of the wettest spot on earth, Mt. Waealele at 11,531 mm annual rainfall (Nullet and Mcgranaghan 1988). The abiotic conditions of the region make the nearshore waters of the north coast of Kaua‘i a highly dynamic ecological setting. Large ocean swells and storms directly impact this coastline, particularly during winter months (ca. October to March; Bodge and Sullivan 1999). Additionally, there are a number of streams, rivers, and groundwater inputs that enter the ocean along this coastline, depositing freshwater, nutrients, and sediments into the nearshore ecosystems (Calhoun and Fletcher 1999, Knee et al. 2008).

Biological surveys in this study were carried out on two nearshore reefs, Kē‘ē and Makua, located adjacent to one another and divided by a channel approximately 500 m wide. The crest of these fringing reefs is several hundred m offshore, dividing them into distinct fore- and back-reef zones (Fig. 1). Fore-reef zones extend from the reef crest seaward, and are characterized by high

exposure to waves, wind, and swell energy, with depths of 5-15 m as the reef drops down to the deeper offshore waters. Back-reef zones, or reef flats, are the areas between the reef crest and the mean high-tide line on the shore. They are more protected from wave energy, with shallower depths (≤ 5 m) and water movement.

For the initial sampling in July 2013, boundaries of the fore-reef zones were based on the areas of hard-bottom, pavement habitat structure, as delineated by the previous NOAA benthic habitat mapping efforts (Battista et al. 2007). The seaward extent was limited to roughly the 8 m depth contour, as determined from LiDAR (light detection and ranging) bathymetry (Irish and Lillycrop 1999). Division of fore- and back-reef zones was based on visual interpretation of satellite imagery. Sampling strata were based on boundaries outlined in the proposed Hā'ena Community Based Subsistence Fishing Area, Hawai'i Administrative Rules documentation (HAR § 13-60.8-2 2013). This was due to the research stemming from an original project that addressed objectives regarding proposed fisheries management areas, which called for explicit comparisons of the fish assemblages of the proposed *pu'uhonua* area and nearby reef zones.

Additional nearshore areas were included in the second round of sampling in August 2014. These areas represented distinct habitats, with characteristics different from those previously included and with juveniles present, so it was determined that they should be incorporated in the analysis of juvenile habitats. The additional areas were between the beach and the reef flat zones, ca. 50-60 m from the shoreline (Fig. 1). Sections of this nearshore area are very shallow, low relief rock benches, which are often exposed at low tides. The Makua Reef nearshore zone also has sections of unconsolidated, sandy bottom surf zone adjacent to the shoreline, from 0 to 1.5 m

depth. Kē'ē Reef has a small nearshore lagoon (ca. 0.67 ha), characterized by sandy bottom and limited water circulation due to the reef crest just offshore.

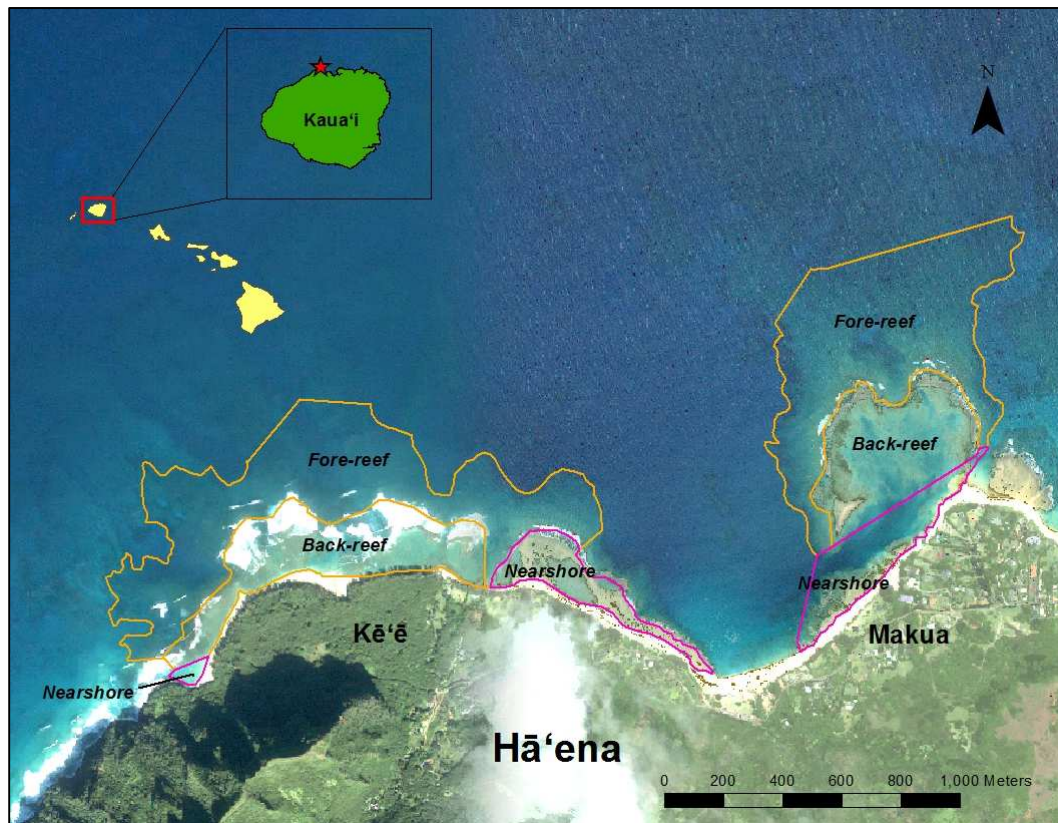


Fig. 1. Study site: Hā'ena, Kaua'i.

3.2 Biological surveys

3.2.1 Sample design

Transect start points were generated across the different zones (fore-reef, back-reef, and nearshore zones of Makua and Kē'ē Reefs), following a stratified random design using ArcMap 10.1 (ESRI 2011). To avoid potential overlap, survey locations were generated with a minimum

distance of 60 m between points. However, given the small sample area, this was applied only for locations within each sample year (2013 and 2014), not between sampling periods, as this would have severely limited the sample size. The number of transects sampled in the fore and back-reef zones of each reef was proportional to each zone's area, with a minimum of 11 transects per sampling period. Due to the small area of the additional nearshore zones, only seven and nine surveys were conducted at Kē'ē and Makua reefs, respectively (Fig. 2).

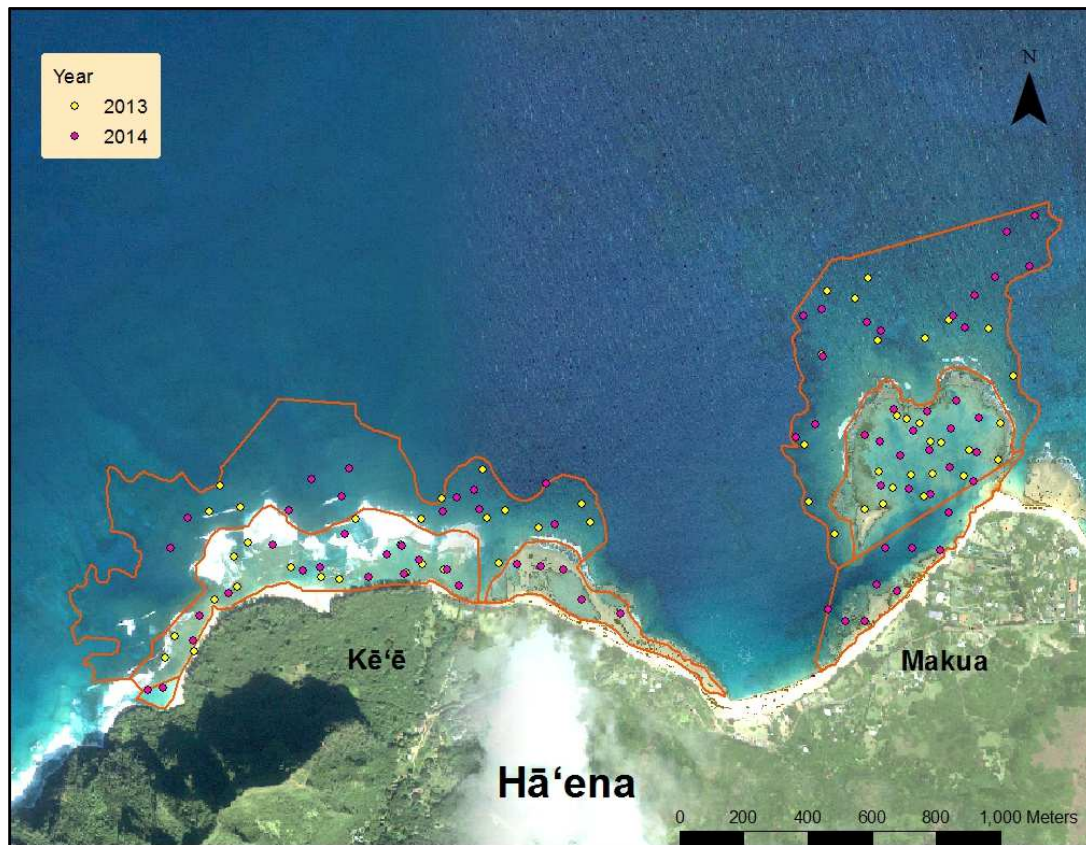


Fig. 2. Transect survey locations, by year.

3.2.2 *Fish surveys*

In order to investigate juvenile fish abundance and density in different habitats in the Hā'ena coastal environment, visual census fish surveys were conducted using underwater belt transect methods, along transects of 25×2 m (Brock 1954, Tolimieri 1998, Dahlgren 2009). A single diver swam the transect line from the start point, following a bearing that roughly followed the depth contour. Surveyors recorded all observed juvenile fishes (< 10 cm) within 2 m to the right of the transect line, identifying to the lowest taxon possible and estimating fork length to the nearest cm.

The focus of the research was on spatial rather than temporal patterns, therefore survey data were pooled across sampling periods (July 2013 and August 2014) after testing for similarity using analysis of similarities (ANOSIM) in PRIMER 6.1 (Clarke and Warwick 2001). ANOSIM applies a permutation-based test of significance, from which the output R statistic represents data that are well-separated ($R > 0.75$), overlapping but clearly different ($R > 0.5$), or barely different ($R < 0.25$) (Clarke and Gorley 2001). Juvenile assemblages were similar between years ($R = 0.05$), so the data were pooled.

Adult abundance data were used to assess ontogenetic differences in habitat relationships. Adult surveys were conducted along the same transect lines as juvenile surveys. However, adult surveys differed from juvenile surveys in that observations of adults (≥ 10 cm) were recorded within 2.5 m on either side of the center line (Brock 1954), resulting in a survey area of 25×5 m rather than 25×2 m used for juvenile surveys.

3.2.3 Benthic surveys

Benthic community composition was characterized along the same transect lines as the fish surveys, using quadrat point-intercept methods (Reed 1980). PVC quadrats of 0.5 m² were placed at 10 random locations along the right side of the transect line. Quadrats were randomized within 5 m segments with 2 quadrats per segment. Quadrats were strung with nylon line at every 10 cm along the frame to create a grid with a total of 16 intersection points. To avoid surveyor bias and eliminate parallax, a double-layered grid was strung on the PVC frame, and intersection points of the two layers were lined up when recording the underlying benthic component (Preskitt et al. 2004). At each of these intersection points, the underlying substrate (e.g., coral, algae) was identified to the lowest possible taxonomic level. While benthic cover data were recorded *in situ*, photos were taken of every quadrat for confirmation of species identification, and to provide a permanent archived record.

Depth was recorded at the start of each transect. Rugosity, an index of structural complexity, was measured using a chain-link method (Risk 1972). A 4 m chain was laid serially along the transect line for the entire length of the transect, ensuring that it followed the contours and features of the seafloor. The final distance covered by the length of the chain was recorded, and the ratio of that length to the linear distance of the transect (25m) provided a measure of rugosity (Friedlander et al. 2003c).

For *in situ* seascape data used in analyses, benthic survey point-intercept data were converted to percent cover for each transect. Taxa or substrate covers were pooled into five benthic cover types, coral, macroalgae, coralline algae, turf algae, or substrate (Appendix 1), which served as

the environmental variables used in analyses, along with *in situ* measurements of depth and rugosity.

Values for the Shannon-Wiener diversity index (SDI) were calculated based on the spatial proportion of benthic cover types represented in the transect area (Shannon and Weaver 1963, Coppedge et al. 2001). These measures were derived from the formula,

$$SDI = - \sum_{i=1}^{RS} p_i \ln p_i$$

where SDI is equal to the negative sum of the proportion of the i^{th} habitat type (p_i) multiplied by the natural log of the proportion of the i^{th} habitat type for all S habitats sampled. SDI was calculated for each transect, and used as an explanatory variable in analyses.

3.3 Habitat Mapping

The map produced for this project is available as an ArcGIS file (.shp), and was also converted for use and application in Google Earth (.kmz). This allows for the map to be more publicly shared and accessible, as specialized, purchased software is not required for Google Earth files.

3.3.1 Classification scheme

The benthic habitat classification scheme used for the mapping of the Hā‘ena coastal area was adapted from the hierarchical classification scheme developed by the NOAA National

Ocean Service Biogeography Program for coral reef mapping efforts in the main Hawaiian islands (Coyne et al. 2003, Battista et al. 2007). The scheme classifies benthic habitats by their geomorphological structure, as well as their biological cover (Table 2). Definitions of habitat classes were adopted from NOAA documentation, but were modified for appropriate application to the nearshore habitats of the north shore of Kaua‘i (Appendix 2). For example, the NOAA classification for “scattered rock and coral,” defined as scattered rocks or coral heads in a habitat of primarily unconsolidated sediment, was modified to describe scattered rocks and coral in a primarily pavement habitat. This is a characteristic habitat of the Hā‘ena study area, particularly of the Makua back-reef zone, for which there was no class in the original scheme.

Table 2. Habitat classification scheme for remotely sensed delineated habitats. Each habitat polygon was described by a structure class and a cover class.

Geomorphological structure	Biological cover
Aggregate reef	Coral
Artificial	Coralline algae
Individual patch reef	Emergent vegetation
Mud	Macroalgae
Pavement	Turf algae
Pavement with sand channels	Uncolonized
Rock and boulder	Unknown
Rubble	
Sand	
Scattered rock and coral	
Spur and groove	
Unknown	

3.3.2 *Training surveys*

On the initial site visit in May 2014, *in situ* habitat training point surveys were conducted in order to inform visual interpretation of remotely sensed images in the mapping process. Survey swims traversed a variety of habitat classes, conducted in a nearby area with a similar seascape to that of Hā‘ena, but outside of the study site so as not to bias the mapping of the study site habitats. Habitat classifications were recorded, following the same classification scheme used in the mapping process. Survey points were recorded using a Garmin 72 GPS. In ArcMap 10.1, waypoints were projected over the satellite imagery, as a means of photo interpretation training for the mapping process and to ensure accuracy of the classifications determined in the production of the map.

Habitat classifications for structure and cover (Table 2) were determined for a 5 m radius circular area around each training point. Notes were made for any points that appeared to be at a habitat boundary, describing the structure and cover classes for the adjoining habitat. A radius of 5 m was decided upon, as this equates to an area of 78.5 m², which is close to the minimum mapping unit of the habitat map (see below). In this manner, training point classifications were made at a spatial resolution consistent with that at which interpretations of remote imagery were to be made.

3.3.3 *Interpretation and delineation*

The habitat map of the Hā‘ena coastal area was created in ArcGIS 10.1 using visual interpretation of multispectral satellite imagery. Distinct habitat boundaries were digitized into

polygons, which were attributed according to the modified classification scheme. Visual interpretation was informed by training with NOAA benthic habitat maps, and by the *in situ* training surveys previously described.

The imagery used in the mapping process was from WorldView-2 panchromatic multispectral eight-band imagery, with a spatial resolution of 4×4 m. Remotely sensed data were projected in UTM Zone 4 NAD 1983. The map was created using the NOAA Habitat Digitizer extension for ArcGIS 10 (ESRI 2011), a tool developed to assist benthic mapping efforts carried out by the NOAA Center for Coastal Monitoring and Assessment. Polygons were delineated at a minimum mapping unit (MMU) of 100 m^2 . During the digitizing process, the scale was locked at 1:2000 to ensure a consistent level of detail in the delineation (Wedding et al. 2011a).

3.3.4 *Habitat data extraction*

Remotely sensed environmental data were extracted from the produced benthic habitat map using ArcMap 10.1 (ESRI 2011). Area (m^2) for each delineated habitat class was calculated within buffers of a given distance around transect midpoints. Habitat data were extracted for two different classification schemes: geomorphological structure and benthic cover (Table 2). Analyses using remotely sensed data were conducted at varying spatial scales in order to assess whether interpretations of juvenile associations with seascape variables differed with scale. Area of habitat classes were quantified within concentric circles of 20, 40, 60, and 100 m radii (arbitrarily defined areas) around transect centers (Fig. 3). SDI was calculated for each transect at

each spatial scale, based on the spatial proportion of habitat classes represented in the buffer area. In datasets with larger buffer areas, some spatial overlap of samples occurred. Analyses were conducted on the full datasets as well as reduced datasets, in which spatially overlapping samples were removed. Reported results are from the full datasets. A discussion of comparisons with reduced datasets is to follow (section 5.1.6).

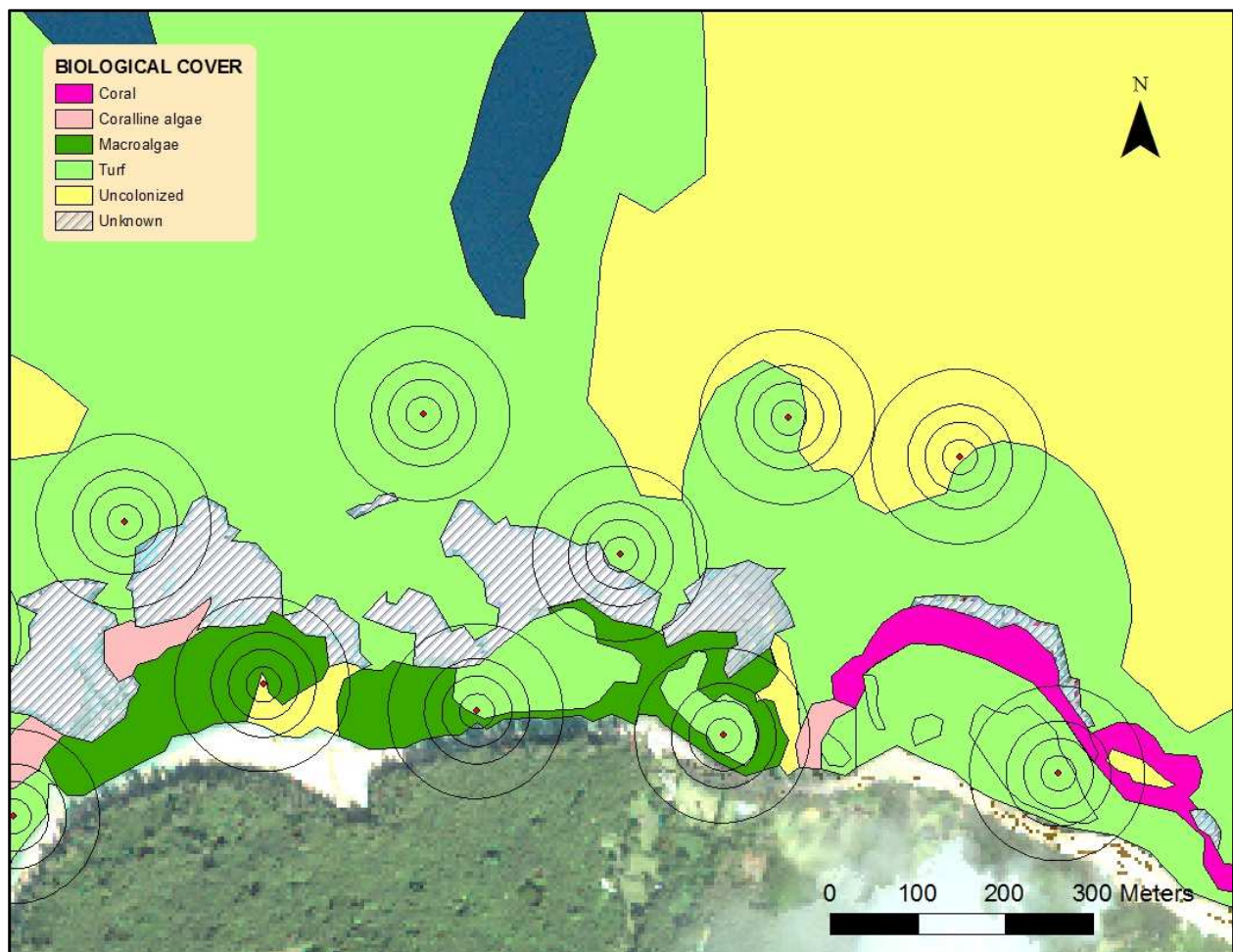


Fig. 3. Process for extracting remotely sensed habitat data. Cover area for each habitat class is quantified within transect buffer zones of 20, 40, 60, and 100 m radii.

3.3.5 Remote measures of depth and rugosity

Remote measures of depth and rugosity were obtained from LiDAR data collected by the Scanning Hydrographic Operational Airborne LiDAR Surveys (SHOALS; Irish and Lillcrop 1999). To obtain a measure of structural complexity from remotely sensed data, a slope of slope raster was created from LiDAR data using the Slope tool in the Spatial Analyst toolbox for ArcMap 10 (ESRI 2011). Slope of slope has been shown to have a strong relationship with various fish assemblage metrics in Hawai‘i (Wedding 2010) and the Caribbean (Pittman et al. 2009), and also showed to be more highly correlated with *in situ* measures of rugosity than other measures of structural complexity produced from Hā‘ena bathymetric data (e.g., surface area to planar area ratio). The Focal Statistics and Sample tools were then used to extract mean values of slope of slope for a circular area of a 20 m radius around each transect mid-point. This was the spatial scale of highest correlation with *in situ* measures, and as values at greater spatial scales appeared to lose much of their correlation with fine-scale measures. Mean values derived at the 20 m scale were used in all remote datasets, regardless of the scale of the extracted habitat classes.

Measures of mean depth were derived from bathymetric data using the Sample tool to extract values for six points along the transect survey lines – start point and every 5 m to the end of the transect. This measure showed higher correlation with *in situ* measures of depth than means derived from a circular area around the transect. Mean values of the six points at each transect were used for analyses at all spatial scales.

Gaps in the LiDAR bathymetric data resulted in missing values for depth and slope of slope at some sample sites. As remotely sensed measures of depth were highly correlated with *in situ*

measures ($r = 0.882$, $p < 0.05$), measures of depth were calibrated for missing values based on modelling *in situ* measures as a function of remotely sensed measures, and using the analysis to calibrate missing predictor values in CANOCO. There were no measures with which to produce reliable estimations of missing slope of slope data, so 12 sites were excluded from the analyses due to missing data (in addition to the 12 that were excluded for .

3.3.6 *Additional remotely sensed seascape metrics*

An advantage of remote sensing technology in the investigation of seascape variables that influence juvenile fish assemblages is the ability to easily obtain metrics of the spatial ecological context of observed fishes over a broad spatial scale. For example, in an assessment of remotely sensed environmental variables that drive distributional patterns of five Caribbean fish species, Pittman and Brown (2011) found distance to shoreline and distance to shelf edge to be important predictors of adult fish species distributions. In the examination of seascape variables that influence the juvenile fish assemblage in Hā'ena, Kaua'i, remote sensing technology was used to quantify distance to shore and distance to reef edge. Polygons for shoreline and reef edge were delineated in ArcMap 10.1, and the Generate Near Table tool was used to calculate the closest distance between each transect midpoint and shoreline or reef edge.

3.4 Statistical analysis

3.4.1 Canonical correspondence analysis

The objective of the analysis was to detect and describe the major ecological patterns in a set of response variables (e.g., biological community composition) explained by a set of explanatory variables (e.g., environmental measures). Ultimately, the goal was to quantify the strength of these relationships (Hair et al. 1998), and to define the habitat characteristics that maximize niche separation among juvenile fish species (ter Braak and Verdonschot 1995). Using CANOCO 5 statistical software (ter Braak 2012), we applied canonical correspondence analysis (CCA) to investigate multivariate associations between juvenile fish assemblages and their surrounding habitat.

CCA is an eigenvalue-based ordination method that assumes a unimodal response function of response variables. Principal ordination axes are constrained to be a linear combination of environmental descriptors, where the first axis is a linear combination that best explains variation in community data, and additional orthogonal axes explain the remaining variance (ter Braak 1986, ter Braak and Prentice 1988). CCA allows for the assessment of relationships between two sets of multivariate data, as opposed to multiple linear regression (or similar methods) where a single response variable is explained by a set of multivariate explanatory data.

CCA does not strictly assume multivariate normality, although normality is required for the statistical inference test of the significance of each canonical function (Hair et al. 1998). Therefore, each explanatory variable was evaluated for normality, and transformed as necessary (Table 3). For each analysis, statistical significance ($P < 0.05$) of the individual axes as well as of

the overall analysis was determined with Monte Carlo permutation tests (Coppedge et al. 2001). Environmental data were centered and standardized in CANOCO 5 to have zero mean and unit variance (Šmilauer and Lepš 2014).

In order to assess the relative importance of a particular explanatory variable to the axes, intraset correlations were calculated in CANOCO 5. Intraset correlations, or the correlation between CCA axis scores and seascape variables, are helpful in identifying environmental characteristics represented by ordination axes (ter Braak 1986, Coppedge et al. 2001). Intraset correlations were used instead of canonical correlations, as use of the latter assumes all variables are uncorrelated, which is often not the case (ter Braak 1986).

3.4.2 Treatment of variables

In the CCA analysis, the response variables were juvenile fish species abundance, square-root transformed to down-weight the contribution of a few highly abundant species on assemblage structure. In order to reduce the number of response variables (fish species) in the model, species that were observed in less than 11 (~10%) of the sample surveys were excluded from the analysis (cf. Lepczyk et al. 2008). Though juvenile abundance data were collected for all fish <10 cm, count data were further cleaned by applying post-hoc species-specific maximum size criteria. Of the species included in the analyses, *Coris venusta*, *Stegastes marginatus*, and *Macropharyngodon geoffroy* were limited at 5 cm, and a 3 cm limit was applied to *Gomphosus varius*, *Thalassoma duperrey*, *Stethojulis balteata*, *Plectroglyphidodon imparipennis*, and *Chromis vanderbilti*. A maximum size of 10 cm was retained for *Acanthurus leucopareius*,

Acanthurus triostegus, and *Scarus rubroviolaceus*. These size limits were applied to ensure that the data represented true juveniles, as some species reach the adult life stage at smaller sizes. This adjustment improves accuracy of interpretations of fish-habitat associations in the juvenile life stage.

Data for explanatory variables (seascape metrics) came from two sources: *in situ* benthic surveys and remotely sensed habitat class data from the produced benthic habitat map. Separate analyses were conducted for the different sources as a means of comparing fish-habitat relationships detected at different levels of habitat description resolution, i.e. coarse-scale resolution of remotely sensed data vs. fine-scale resolution of *in situ* data. Furthermore, comparisons between data collected in the field and data collected with remote sensing methods allows for the assessment of the relative importance of spatial predictors (only quantified in remotely sensed datasets) in the distribution of juvenile fishes.

Environmental variables for all datasets were examined for covariance, as removal of one variable in a set of environmental variables highly covaried in the same direction ($\rho \geq 0.8$) allows for more direct ecological interpretation of the species-habitat relationships. Additionally, habitat classes that occurred in less than 10% of the sample surveys were excluded from analysis.

Table 3. Explanatory variable transformations. The same transformations were applied to remotely sensed explanatory variables among all spatial scales. “Log” is log base 10.

Dataset	Explanatory variable	Transformation
<i>In situ</i>	Coral	$\text{Arcsin}(\sqrt{X})$
	Coralline algae	$\text{Log}(1000X + 1)$
	Macroalgae	$\text{Arcsin}(\sqrt{X})$
	Substrate	$\text{Log}(1000X + 1)$
	Turf algae	<i>(none)</i>
	Depth	$\text{Log}(X)$
	Rugosity	$\text{Log}(X)$
	Shannon-Weaver diversity index	<i>(none)</i>
Remotely sensed biological cover	Coralline algae	$\text{Arcsin}(\sqrt{X})$
	Macroalgae	$\text{Arcsin}(\sqrt{X})$
	Turf algae	$\text{Arcsin}(\sqrt{X})$
	Uncolonized	$\text{Log}(1000X + 1)$
	Shannon-Weaver diversity index	<i>(none)</i>
Remotely sensed geomorphological structure	Aggregate reef	$\text{Log}(1000X + 1)$
	Pavement	$\text{Arcsin}(\sqrt{X})$
	Sand	$\text{Log}(1000X + 1)$
	Scattered rock and coral	$\text{Log}(1000X + 1)$
	Shannon-Weaver diversity index	<i>(none)</i>
<i>(remotely sensed variables included in both cover and structure analyses)</i>	Depth	$\text{Log}(X)$
	Slope of slope	<i>(none)</i>
	Distance to shore	$\text{Log}(X + 1)$
	Distance to reef crest	$\text{Log}(X + 1)$

3.4.3 Assessment of ontogenetic differences in habitat associations

In order to examine ontogenetic shifts in fish-habitat relationships, I compared the influence of seascape variables on fish abundance between the juvenile and adult assemblages of *A. triostegus*. This species was selected based on its value as a food resource species for the community of Hā'ena, and because there were enough observations ($n = 40$ for each stage) for both juveniles and adults. Habitat relationships were assessed with generalized linear models, assuming a Poisson distribution and using a log link function based on the skewed distribution of the abundance data. Abundance data were transformed with a $\text{Log}(X + 1)$ function, and *in situ* seascape variables were used for explanatory variables, applying the same transformations as were used in the CCA (Table 3). Variables with significant effect on abundance were compared between juvenile and adult assemblages to describe the ontogenetic differences in habitat relationships of *A. triostegus*. Results are presented as means \pm standard deviation with a p-value of ≤ 0.05 considered significant, unless otherwise noted.

CHAPTER 4. RESULTS

A total of 126 independent transect surveys were conducted over two sampling periods (July 2013 and August 2014). Sampling of fore- and back-reef of Makua and Kē‘ē reefs occurred in both sampling periods, while nearshore sampling was conducted in August 2014 only (Table 4).

Table 3. Total number of transect surveys in each stratum, by year.

Reef	Zone	2013	2014	TOTAL
Kē‘ē	Fore-reef	12	11	23
	Back-reef	15	14	29
	Nearshore	-	7	7
Makua	Fore-reef	12	14	26
	Back-reef	16	16	32
	Nearshore	-	9	9
TOTAL		55	71	126

4.1 Juvenile fish assemblages

Across 126 transects, a total of 2,040 juvenile fish were observed, representing 54 species from 15 families. The most abundant species were *S. balteata* (27.3%), *T. duperrey* (21.0%), and *A. triostegus* (14.3%), together comprising 62.7% of the total number of individuals surveyed (Appendix 3). Based on a criterion of occurrence in at least 10% of the sample surveys, 11 species of juvenile fishes, accounting for 90% of total fish abundance, were selected for inclusion in the CCA (Table 5). Of these species, *A. triostegus*, *A. leucopareius*, and *S.*

rubroviolaceus are considered important food resource species, harvested by the local community and throughout Hawai‘i.

Table 5. Juvenile species included in canonical correspondence analyses. Frequency of occurrence (number of transects in which the species was observed) was quantified after post-hoc size maxima were applied to juvenile data.

Species	Common Name	Hawaiian Name	n	% total abund	Freq. of occur.
<i>Stethojulis balteata</i>	Belted Wrasse	‘ōmaka	557	27.33	66
<i>Thalassoma duperrey</i>	Saddle Wrasse	hīnālea lauwili	428	21.00	67
<i>Acanthurus triostegus</i>	Convict tang	manini	292	14.33	40
<i>Plectroglyphidodon imparipennis</i>	Brighteye Damsel fish		167	8.19	57
<i>Gomphosus varius</i>	Bird wrasse	hīnālea ‘i‘iwi	114	5.59	31
<i>Stegastes marginatus</i>	Pacific Gregory		89	4.37	48
<i>Macropharyngodon geoffroy</i>	Shortnose wrasse		50	2.45	24
<i>Scarus rubroviolaceus</i>	Redlip Parrotfish	pālukaluka	35	1.72	22
<i>Chromis vanderbilti</i>	Blackfin chromis		30	1.47	14
<i>Acanthurus leucopareius</i>	Whitebar Surgeonfish	māikoiko	27	1.32	18
<i>Coris venusta</i>	Elegant coris		23	1.13	13

4.2 Seascapes

4.2.1 *In situ* transect surveys

Among the 126 sample transects, 55 different taxa or substrate types were observed in the benthic surveys, and were pooled into six different benthic cover categories (Appendix 1). Turf

algae had the highest percent cover, accounting for 55.7% of total cover across all transects (Table 6). Scleractinian corals, macroalgae, unconsolidated substrate, and coralline algae had fairly even cover between them, ranging from 8.8 to 12.6% for each cover type. None of the habitat types were highly correlated ($|\rho| \geq 0.8$). Recorded depths ranged from 0.3 to 8.2 m, with a mean of 2.8 (± 2.4 sd) across all transects. Rugosity index values ranged from 1.00 to 1.87, with a mean of 1.20 (± 0.17 sd). SDI varied from 0 (indicating a single habitat class) to 1.436 (± 0.29 sd), with higher values representing more mixed and even habitats in the surrounding seascape.

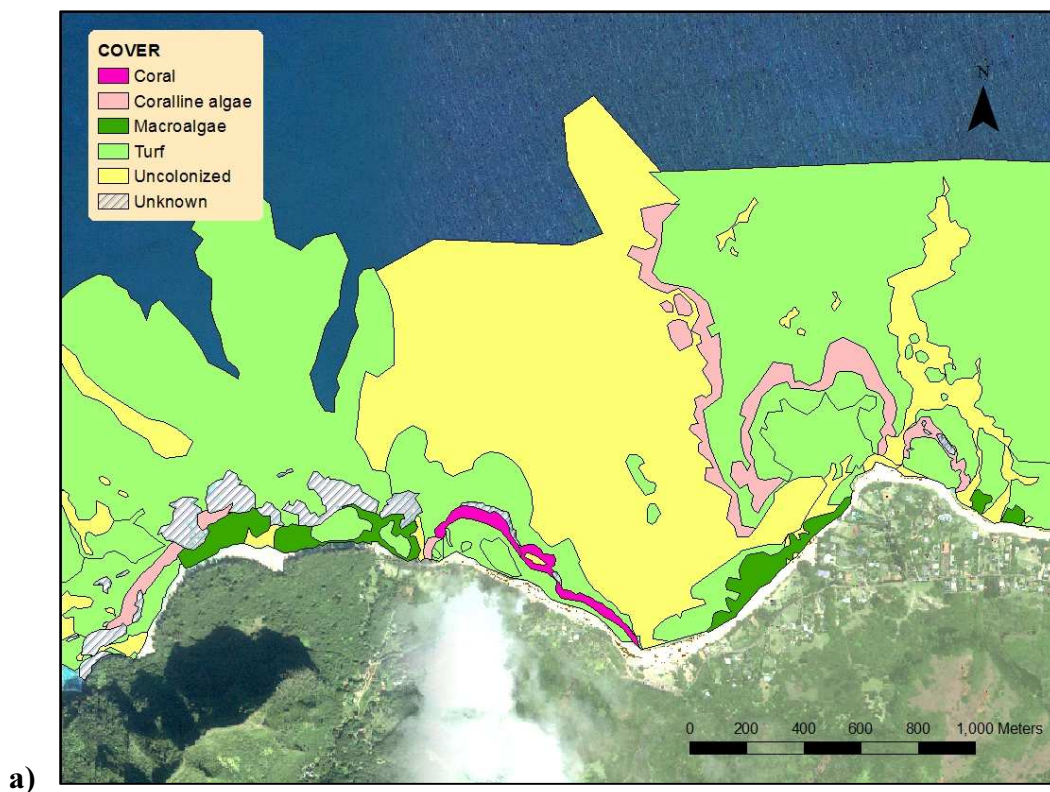
Table 6. Total percent cover by benthic cover type from *in situ* surveys. Note: values do not add to 100%, as invertebrates and unknown classes were not included in the habitat analyses. These excluded classes comprised $< 1.5\%$ of the total cover across all transects.

Benthic cover type	Total % cover
Turf	55.66
Coral	12.61
Macroalgae	11.32
Unconsolidated	10.10
Coralline algae	8.79

4.2.2 Remotely sensed benthic map

A total area of 5.24 km² of benthic habitat was visually interpreted, classified, and mapped for the coastal ecosystem of Hā'ena, along 5.6 km of coastline and extending up to 1.7 km offshore. Within the total mapped area, seven different structure classes and five different cover classes were delineated (Fig. 4a,b). For the analyses of biological cover data, turf algae again

represented the highest percentage of cover (73 to 80% among spatial scales; Table 7a). The remaining biological cover was primarily composed of macroalgae (8.6 to 10.4%), coralline algae (6.3 to 7.8%), and uncolonized benthos (3.7 to 9.8%; generally representing sand habitats). Coral habitat represented a very small proportion of remotely sensed habitat data (~1%), and was excluded from CCAs as it was present in <11 samples (~10%) at all scales.



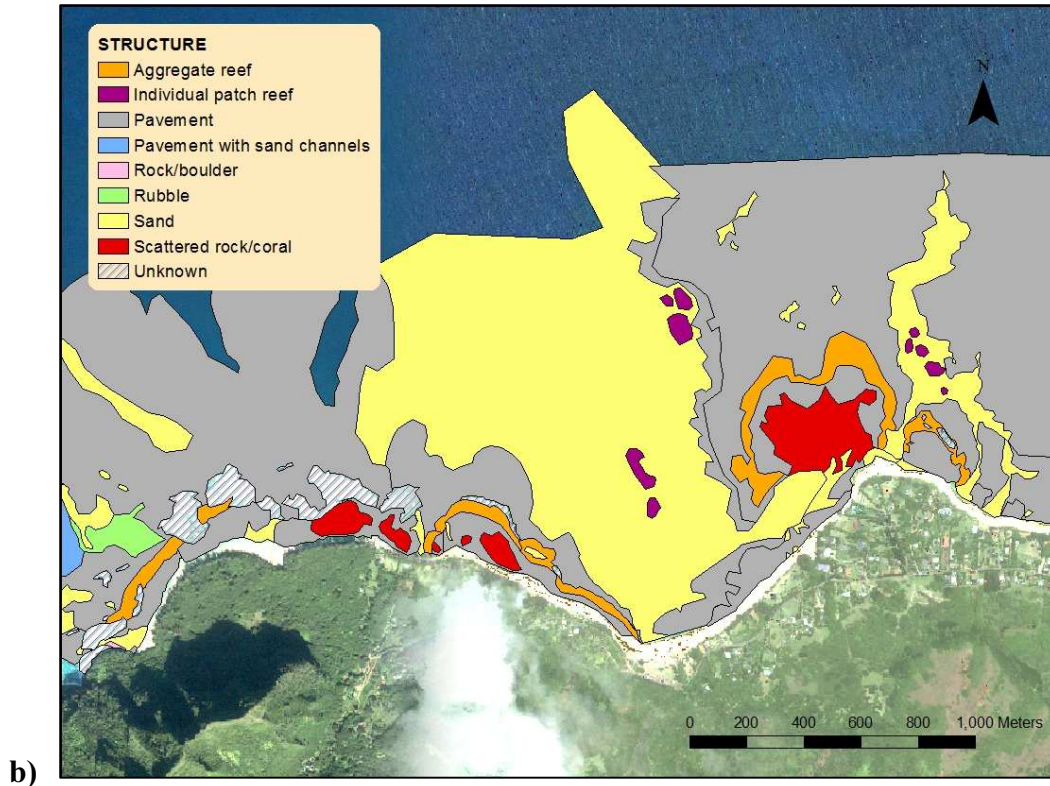


Fig. 4. Delineated habitat boundaries at the study site, based on visual interpretation of satellite imagery, for **a)** biological cover classes, and **b)** geomorphological structure classes. The final product of the produced map is available in .xml format (for ArcMap), and was also converted to .kmz format for use in Google Earth, a free program, so as to be more widely accessible to the public and resource managers.

LiDAR-derived measures of depth for transects ranged from 0 to 12.3 m, with a mean of 2.8 (± 2.7 m). Remotely sensed measures of slope of slope ranged from 0 to 52.1, with a mean of 17.5 (± 9.2). Sample transects were 0 to 864 m from shore, with a mean distance of 257 m (± 219.6 m). Distance of samples to the closet reef crest ranged from 0 to 483 m, with a mean of 103 m (± 86.9 m).

For geomorphological structure classes, pavement was the dominant class, with 62 to 67% of the total area among spatial scales (Table 7b). Scattered rock and coral, which primarily characterized the Makua back-reef (Fig. 4b) comprised most of the remaining cover (21 to 25%). Rubble, rock and boulder, and individual patch reef made up <1% of the area in extracted data, and were all excluded from CCAs at all spatial scales.

Table 7. Percent total area of each habitat class within data extracted for analysis at each spatial scale.

a) Biological cover classes

Cover Class	Spatial scale				Mean (\pm sd)
	20 m	40 m	60 m	100 m	
Turf	79.95	76.30	74.44	72.73	78.86 (\pm 3.09)
Macroalgae	9.75	10.39	10.29	8.55	9.75 (\pm 0.85)
Coralline algae	6.30	6.89	7.32	7.78	7.07 (\pm 0.63)
Uncolonized	3.65	5.64	6.89	9.83	6.50 (\pm 2.59)
Coral	0.35	0.78	1.06	1.11	0.83 (\pm 0.35)

b) Geomorphological structure classes

Structure Class	Spatial scale				Mean (\pm sd)
	20 m	40 m	60 m	100 m	
Pavement	67.21	65.76	64.37	61.81	64.79 (\pm 2.30)
Scattered rock and coral	25.09	23.15	22.08	20.63	22.74 (\pm 1.88)
Sand	3.84	5.74	6.99	9.89	6.62 (\pm 2.54)
Aggregate reef	3.49	5.19	6.28	7.18	5.54 (\pm 1.59)
Rubble	0.36	0.16	0.18	0.27	0.24 (\pm 0.09)
Rock and boulder	-	0.01	0.07	0.05	0.04 (\pm 0.03)
Individual patch reef	-	-	0.04	0.16	0.10 (\pm 0.08)

4.3 Juvenile fish-habitat associations

4.3.1 *In situ* environmental data

In the assessment of the relationship between juvenile fish assemblages and habitat data collected from *in situ* surveys, the linear combinations of seascape variables explained 26.0% of the juvenile fish assemblage data variance. The Monte Carlo permutation tests of the juvenile

species-seascape relationship found that the first CCA axis ($F = 16.4$; $P = 0.001$), the second ($F = 6.1$; $P = 0.007$), and the overall analysis ($F = 4.4$; $P = 0.001$) were all significant.

The variables most strongly correlated with Axis 1, which explained 14.12% of the variance in fish community data, were depth and coralline algae in the positive direction ($r = 0.887$, and $r = 0.620$, respectively) and unconsolidated substrate in the negative direction ($r = -0.561$; Fig. 5). The first axis could be described as a gradient from shallow, unconsolidated habitats (typically sand) to deeper, structurally complex habitats dominated by coralline algae. Axis 2 explained an additional 4.91% of the community variance and can best be described as a gradient of complexity of hard-bottom habitats, most strongly correlated with coralline algae ($r = 0.551$), coral ($r = -0.520$), and rugosity (-0.430 ; Fig. 5).

On Axis 1, *C. vanderbilti*, *M. geoffroy*, and *A. leucopareius* were associated with deeper, more rugose sites, while *A. triostegus* was associated with shallower sites. *S. rubroviolaceus* was most highly influenced by the second axis, associated with habitats of greater structural complexity (Fig. 5). The relationships between juvenile fishes and seascape characteristics were supported by the configuration of variables in bi-plot ordination diagram (Fig. 6). *A. triostegus* and *C. venusta* were shown to be negatively associated with depth, and positively associated with unconsolidated or macroalgal habitats. *S. rubroviolaceus* showed a close relationship with coral and rugosity. Furthermore, *S. marginatus* and *T. duperrey* were oriented near the bi-plot origin, indicating that they were relatively uninfluenced by habitat and seascape variables.

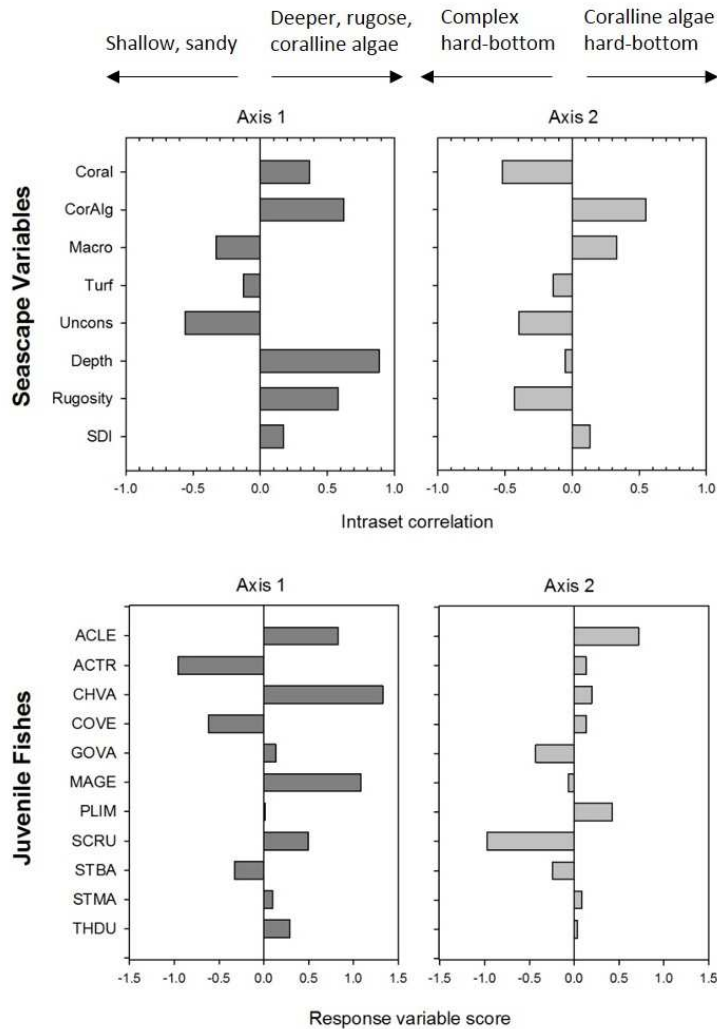


Fig. 5. Intraset correlations and response variable scores between variables and axes of the canonical correspondence analysis for *in situ* seascape data. Intraset correlations are the correlations between CCA axis scores and seascape variables, and help to describe the seascape characteristics represented by the axes. Analogously, response variable scores represent correlations between axes and juvenile fish variables, and can be compared with the seascape correlations to interpret associations between juvenile species and seascape characteristics.

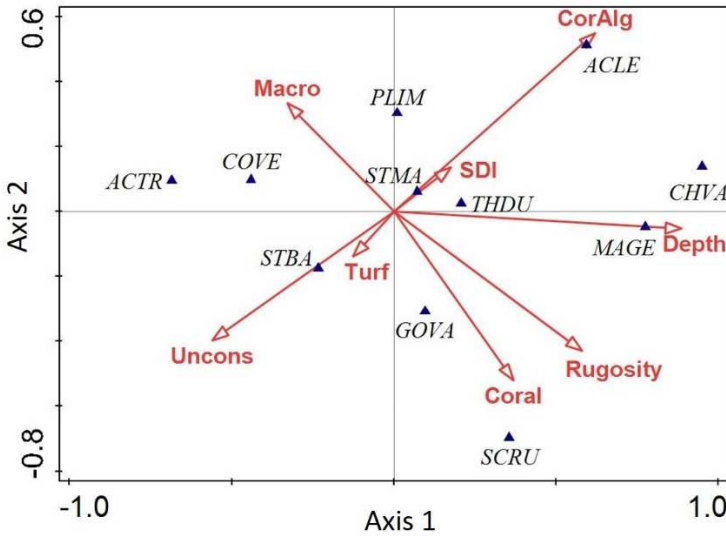


Fig. 6. Ordination bi-plot of relationships between juvenile fishes and benthic habitat types described with *in situ* survey methods. Seascape variables are represented by vectors, and species optima by dark triangles. ACLE = *Acanthurus leucopareius*, ACTR = *Acanthurus triostegus*, CHVA = *Chromis vanderbilti*, COVE = *Coris venusta*, GOVA = *Gomphosus varius*, MAGE = *Macropharyngodon geoffroy*, PLIM = *Plectroglyphidodon imparipennis*, SCRU = *Scarus rubroviolaceus*, STBA = *Stethojulis balteata*, STMA = *Stegastes marginatus*, THDU = *Thalassoma duperrey*.

4.3.2 Remotely sensed environmental data

Analyses at all spatial scales, for both biological cover and geomorphological structure habitat classes, showed significant relationships between juvenile fish assemblages and seascape characteristics (Table 8a, b). Across all analyses the percentage of variance in response data explained by explanatory variables ranged from 18.6 to 20.6% for cover variables (Table 8a), and 21.5 to 24.7% for structure variables (Table 8b). Based on the percent variance explained by seascape variables for each analysis, the strongest relationships were detected at the 40 m scale

for cover variables, and the 100 m scale for structure variables. Only results from these analyses in which relationships were strongest are reported.

The relationships between juvenile fish and habitat cover at 40 m radius was significant ($F = 2.6, P = 0.001$), but as was the case for all scales of biological cover, only the first axis was significant ($F = 13.2, P = 0.001$; Table 8a). The first CCA axis explained 12.59% of the juvenile fish assemblage data variance, and was most strongly correlated with distance to shore ($r = -0.895$), depth ($r = -0.794$), and macroalgae ($r = 0.799$; Fig. 7). This first axis can be described as a gradient from deep sites further from shore to shallow nearshore sites characterized by macroalgal cover.

Table 8. Comparison of spatial scales of remotely sensed habitat data. Significant results are in bold.

a) CCA with cover class dataset. Note: Axis 2 was not significant for biological cover variables at any spatial scale.

Spatial scale (radius)	Monte Carlo test (all axes)	Monte Carlo test (Axis 1)	Monte Carlo test (Axis 2)	% Variation explained by seascape variables	% Variation explained by significant axes
20 m	$F = 2.4, P = \mathbf{0.001}$	$F = 12.7, P = \mathbf{0.001}$	$F = 2.9, P = 0.475$	19.1	12.39
40 m	$F = 2.6, P = \mathbf{0.001}$	$F = 13.2, P = \mathbf{0.001}$	$F = 3.8, P = 0.215$	20.6	12.59
60 m	$F = 2.6, P = \mathbf{0.001}$	$F = 13.0, P = \mathbf{0.001}$	$F = 3.7, P = 0.202$	20.1	12.35
100 m	$F = 2.3, P = \mathbf{0.001}$	$F = 13.1, P = \mathbf{0.001}$	$F = 2.9, P = 0.503$	18.6	12.43

b) CCA with structure class dataset

Spatial scale (radius)	Monte Carlo test (all axes)	Monte Carlo test (Axis 1)	Monte Carlo test (Axis 2)	% Variation explained by seascape variables	% Variation explained by significant axes
20 m	$F = 2.8, P = \mathbf{0.001}$	$F = 13.3, P = \mathbf{0.001}$	$F = 4.3, P = 0.11$	21.5	12.66
40 m	$F = 2.9, P = \mathbf{0.001}$	$F = 13.5, P = \mathbf{0.001}$	$F = 5.3, P = \mathbf{0.02}$	22.0	17.56
60 m	$F = 3.0, P = \mathbf{0.001}$	$F = 13.4, P = \mathbf{0.001}$	$F = 5.9, P = \mathbf{0.009}$	22.7	17.96
100 m	$F = 3.3, P = \mathbf{0.001}$	$F = 13.5, P = \mathbf{0.001}$	$F = 6.3, P = \mathbf{0.006}$	24.7	18.35

At the 40 m radius scale, the relative abundances of *C. vanderbilti* and *M. geoffroy* were associated with negative Axis 1 scores, indicating association with deeper habitats further from shore. *A. triostegus* again showed an association with shallower habitats. It was also strongly associated with macroalgae, as was *C. venusta* (Fig. 7, 8). *S. rubroviolaceus* distribution was not strongly influenced by the first axis, yet it was associated with turf algae (Fig. 8). *S. marginatus* remained near the bi-plot origin, showing little influence from seascape characteristics. *P. imparipennis* also showed very little influence from seascape variables in this analysis. *T. duperrey* showed consistent habitat generalist patterns, influenced somewhat by distance to shore (Fig. 8).

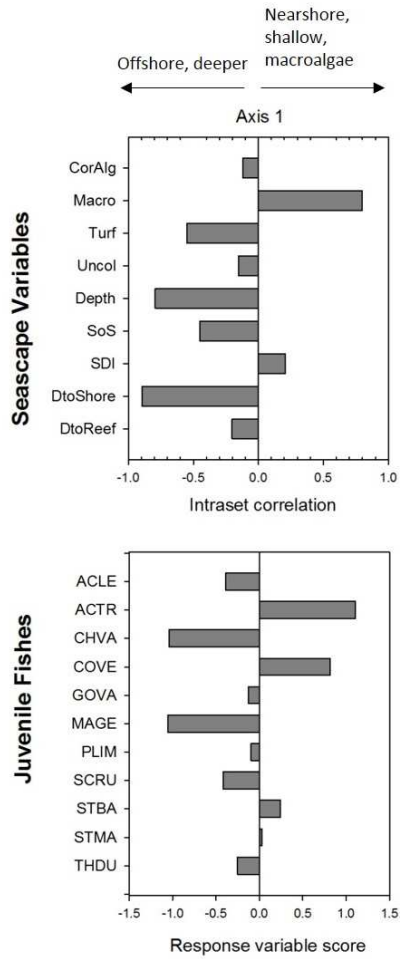


Fig. 7. Intraset correlations and response variable scores between variables and axes of the canonical correspondence analysis for remotely sensed biological cover seascape data, at a spatial scale of 40 m radius around transect centers.

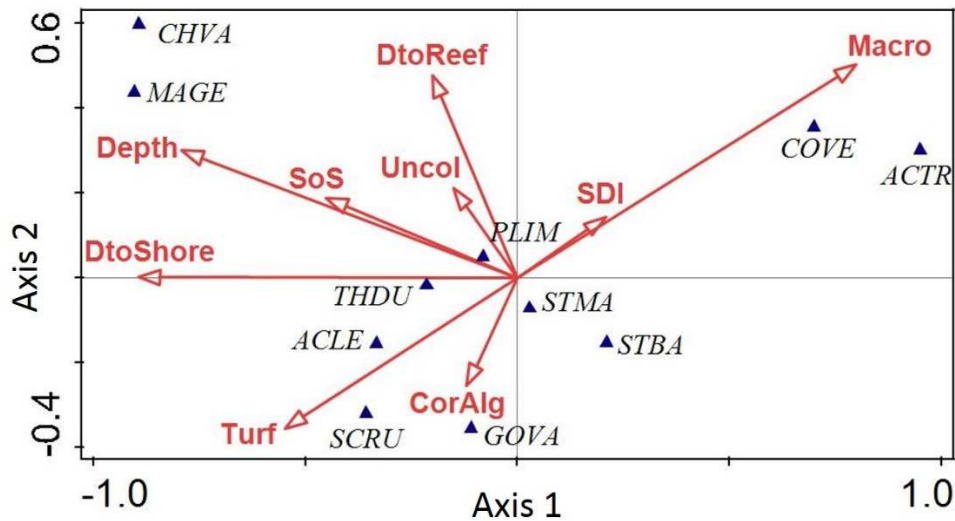


Fig. 8. Ordination bi-plot of relationships between juvenile fishes and remotely sensed biological habitat cover, at a seascape spatial scale of 40 m radius around transect centers. DtoShore = distance to shore, DtoReef = distance to reef edge, SoS = slope of slope, SDI = Shannon-Weaver diversity index.

In the analysis of relationships between structural habitat characteristics and juvenile fishes, the highest explained variance was at a seascape scale of 100 m radius, with 24.7% of the response variance explained by seascape variables (Table 8b). Both axes were significant (1st axis: $F = 13.5$, $P = 0.001$; 2nd axis: $F = 6.3$, $P = 0.006$), as was the overall relationship ($F = 3.3$, $P = 0.001$; Table 8b). The first two CCA axes explained 18.35% of the juvenile fish assemblage data variance. Specifically, axis 1 explained 12.80% of the variance in fish assemblage data. This axis defined a gradient of offshore habitat to heterogeneous habitat (scattered rock and coral habitat, and/or high diversity index) closer to shore, where distance to shore and scattered rock and coral had the strongest influences on juvenile fish assemblage ($r = -0.877$ and 0.478 , respectively; Fig. 9). Axis 2 explained an additional 5.55% of the community variance, and was

primarily influenced by flat pavement habitats ($r = 0.842$) and heterogeneous habitats of scattered rock and coral ($r = -0.672$). Depth had a much weaker relative influence in this analysis compared to the analysis with *in situ* data and with biological cover data.

The relative abundances of *C. vanderbilti* and *M. geoffroy* were associated with offshore habitats, and *A. triostegus* with nearshore habitats (Fig. 9). *S. rubroviolaceus* was most strongly influenced by scattered rock and coral, and *A. leucopareius* by pavement habitat (Fig. 10). *S. marginatus* and *T. duperrey* again showed weak associations with seascape variables, with weak influence of distance to shore on *T. duperrey*.

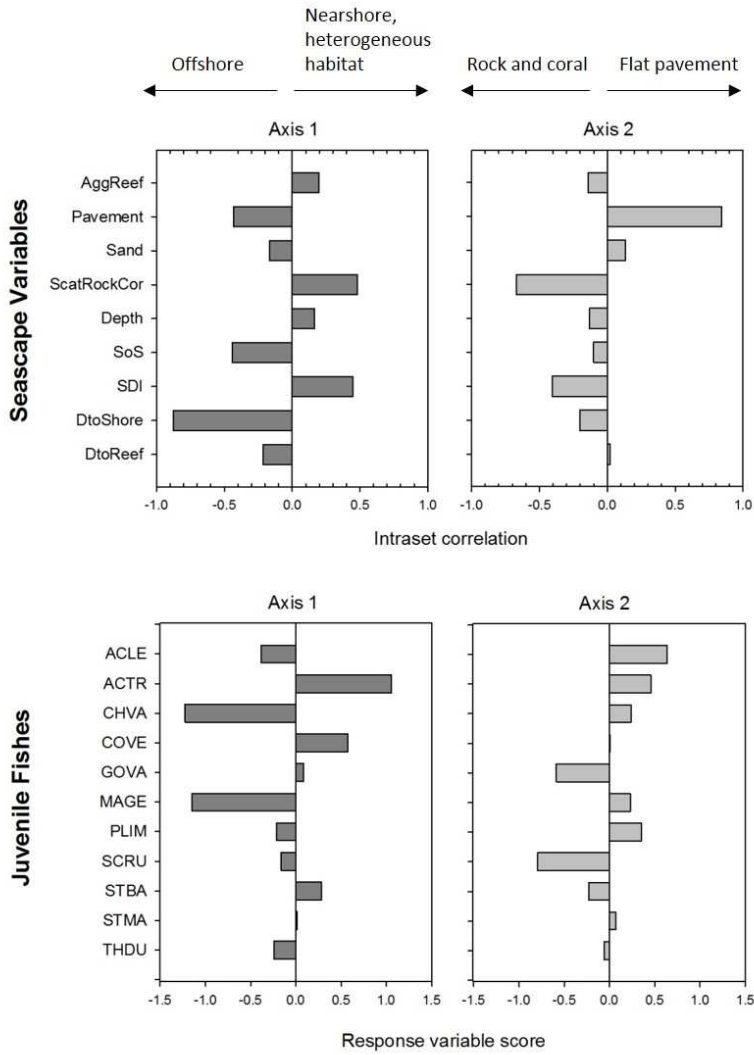


Fig. 9. Intraset correlations and response variable scores between variables and axes of the canonical correspondence analysis for remotely sensed geomorphological structural seascape data, at a spatial scale of 100 m radius around transect centers.

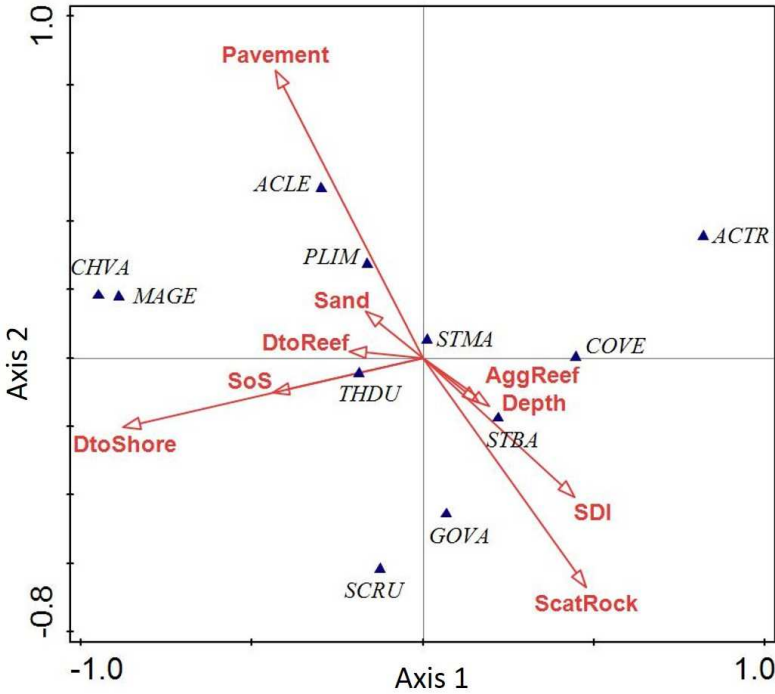


Fig. 10. Ordination bi-plot of relationships between juvenile fishes and remotely sensed geomorphological structure, at a seascape spatial scale of 100 m radius around transect centers.

4.4 Ontogenetic differences in strength of habitat influence

In the assessment of ontogenetic differences in habitat associations within a single species, the distribution of adult *A. triostegus* was associated with different seascape variables compared to juveniles. Both juvenile and adult *A. triostegus* had a significant relationship with fine-scale (*in situ*) seascape variables ($G^2 = 93.761$, $df = 7$, $P < 0.001$ and $G^2 = 35.408$, $df = 7$, $P < 0.001$, respectively). However, the variables within each analysis that were associated with fish abundance varied. For juveniles, unconsolidated substrate ($G^2 = 6.885$, $df = 1$, $P = 0.009$), macroalgae ($G^2 = 5.66$, $df = 1$, $P = 0.017$), and depth ($G^2 = 16.52$, $df = 1$, $P < 0.001$) were significant predictors with abundance, patterns which were consistent with those observed in the

results of the CCA with *in situ* data. Adult *A. triostegus* were also correlated with macroalgal cover ($G^2 = 21.94$, $df = 1$, $P < 0.001$), but rather than depth and unconsolidated substrate, coral was the only other significant predictor of adult abundance ($G^2 = 13.74$, $df = 1$, $P < 0.001$).

Furthermore, ontogenetic habitat shifting is demonstrated by the difference in size distributions between reef zone strata (fore-reef and back-reef) by which sampling sites were grouped (Fig. 11). It is apparent that while adults occurred in both the fore- and back-reef zones, juvenile *A. triostegus* were generally observed only in back-reef zones, suggesting a strong association with seascape characteristics that distinguish this zone from the fore-reef.

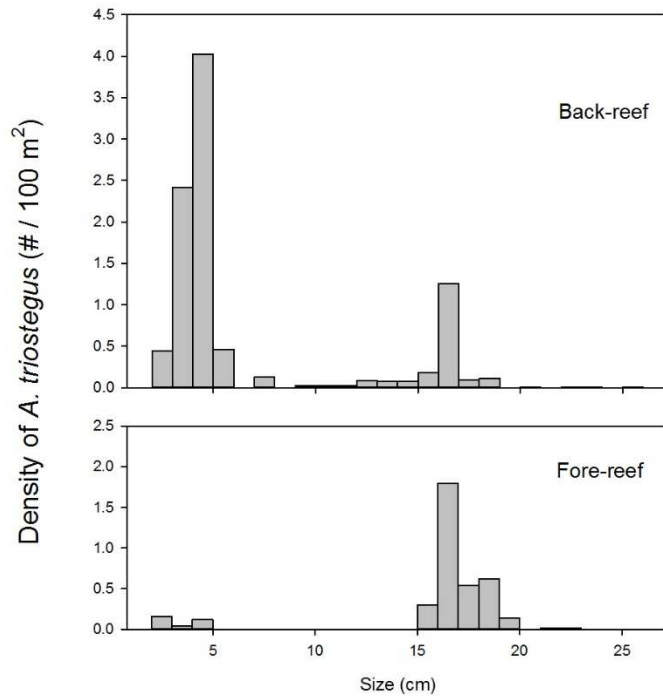


Fig. 11. Size distribution of *A. triostegus* between back- and fore-reef zones.

CHAPTER 5. DISCUSSION

This project integrated local knowledge, *in situ* surveys, and geospatial tools and technology to describe the patterns of distribution and abundance of juvenile fishes in the coastal marine environment of Hā'ena, Kaua'i, information which was applied toward the successful establishment of community-based marine resource management. Results demonstrated that different habitats types and measures of spatial configuration in the nearshore reef ecosystem of Hā'ena were associated at varying levels with the juvenile fish assemblage, with some species of juvenile fishes more highly correlated with seascape variables than others. The variation in combinations of these predictors across the local seascape presumably created spatial differences in habitat suitability for juvenile fishes (MacArthur and Levins 1964), leading to variation in juvenile distribution. With the application of CCA, I extracted from ecological data the combinations of environmental variables that best documented niche separation of different species of juvenile fishes (ter Braak and Verdonschot 1995). The described distribution patterns contribute to a depauperate body of literature on juvenile reef fish habitat associations in Hawai'i (DeMartini 2004, DeMartini et al. 2010), and informed management decisions for a small Hawaiian community fishery.

The capacity to describe fish-habitat associations and to map presumably influential seascape variables across the study site provided a valuable tool in the identification of likely essential fish habitat for a number of species of juvenile fishes, some of which have important commercial and cultural value. In the Hā'ena nearshore fishery, *S. rubroviolaceus* and *A. triostegus* are important food resource species, and both consistently showed strong associations with various habitat variables. These patterns provided important information on juvenile distributions, and the

contribution of such knowledge helped to inform the management of marine resources, taking into consideration the importance of multiple seascape parameters in the spatial prioritization of protected areas (Bostrom et al. 2011).

This study has contributed quantitative ecological knowledge to the efforts of the Hā‘ena community to manage their own marine resources in a manner consistent with local cultural practices. Recent resurgence of ecosystem-based marine resource management and the integration of customary practices and local ecological knowledge into conventional management has the potential to effectively address declining resources (Berkes 1999, Johannes 2002, Cinner and Aswani 2007, Friedlander et al. 2013). This project lays the groundwork for similar studies to contribute to community-based management efforts across the main Hawaiian islands and in other regions of the world.

5.1 Juvenile fish-habitat associations

Several juvenile fish-habitat associations emerged as consistent across spatial scales and environmental data collection methods. Other inferred relationships varied in the strength of association or in the variable(s) driving the distribution of a species, emphasizing the importance of selecting the scale and methods that are appropriate for the objectives of a study or management action.

5.1.1 Influential variables

Depth was shown to be strongly correlated with juvenile fish distributions using both *in situ* as well as remote methods. The strong association with shallow habitats documented for juveniles *A. triostegus*, an endemic Hawaiian species, is consistent with local knowledge (Maly and Maly 2003), as well as with studies of habitat selection by juveniles of this species elsewhere in Hawai‘i (Sale 1968, 1969). In an interview with ethno-historian Kepa Maly, a local *kūpuna* (elder) fisherman indicated a shallow, nearshore portion of the reef in Hā‘ena as a known area for *piaea* (small *A. triostegus*, $< \sim 3$ cm). Few studies have specifically addressed the juvenile distributions of the other three depth-influenced species, but in a survey of small reef fishes in Kaneohe Bay, Oahu, Greenfield (2003) found *M. geoffroy* and *C. vanderbilti* to occur most abundantly in habitats of greater depths, and *C. venusta* in shallow spur and groove habitats and open patch reefs, results consistent with the depth preferences demonstrated in the CCA analyses in our study.

Macroalgal cover, commonly found to be strongly associated with juvenile fish distribution (Jones 1988, Carr 1989, Levin 1991, Carr 1994, Aburto-Oropeza et al. 2007), also emerged as a significant variable for *A. triostegus* and other species of juveniles in Hā‘ena. Since macroalgal habitats are close to shore (Fig. 4a), it is logical that proximity to shore also emerged as a highly influential variable for *A. triostegus* in the analyses using remotely sensed data (Fig. 9). However, these patterns differ from those found by Adams and Ebersole (2002), who found juvenile *Acanthurus* spp. in the U.S. Virgin Islands were rarely present in algal plains, but differentially located in patch-reef and rubble habitats, a discrepancy that may underline the importance of location-specific studies.

The association of the juvenile assemblage as a whole with macroalgae is important to consider in the context of climate change and increased nutrient input into coastal waters. Changing ocean conditions can directly or indirectly change the level or composition of algal cover impact (Harley et al. 2006, Diaz-Pulido et al. 2007, Hoegh-Guldberg et al. 2007), which in turn could affect fish populations, based on the associations detected in this study and others. Increases in macroalgal cover could potentially positively influence species such as *A. triostegus* that have an affinity for macroalgae. However, algal cover inhibits coral recruitment and survival therefore (Hoegh-Guldberg et al. 2007, Hughes et al. 2007), so fish species that are associated with coral habitat could be negatively affected by an increase in macroalgal cover. Future monitoring of changes in algal cover and the associated juvenile fish distributions in Hā'ena could provide information on the resistance of juvenile fish species to shifts in habitat characteristics, a pertinent topic in the consideration of impacts of climate change. There has been extensive evidence of thresholds (points on gradient at which sudden changes in response variable occur) of habitat coverage and complexity for fish assemblages (Pittman et al. 2004, see review by Bostrom et al. 2011), but information specific to Hawai'i and to juvenile fishes is lacking.

Structural complexity has shown to be an important factor in the distribution of adult fishes (Hixon and Beets 1993, Friedlander and Parrish 1998, Pittman et al. 2007a, Wedding et al. 2008, Pittman and Brown 2011), and *in situ* measures of rugosity provide evidence of similar importance of fine-scale complexity for juvenile assemblages in Hā'ena (Fig. 6). Predation is a driver of juvenile abundance (Hixon and Jones 2005, Almany and Webster 2006), and structurally complex habitats are likely to support higher abundances of fishes due to increased

survivorship, particularly for fishes of a size class that would benefit from the size of available refuge niches (Hixon and Beets 1993, Beukers and Jones 1998, Almany 2004).

Some habitats have an uneven spatial distribution of structural complexity. Scattered rock and coral habitats are areas characterized by flat pavement punctuated by rock and coral features, refuges of structural complexity. In the analysis of remotely sensed structural habitat data, scattered rock and coral habitats were highly influential on the juvenile assemblage, particularly on *S. rubroviolaceus* (Fig. 9, 10). This was the dominant structural habitat represented in the Makua back-reef area, the location of the proposed *pu'uhonua*. Based on the importance of that habitat type, especially for resource species, results from this study provide supporting evidence of appropriate spatial designation of the *pu'uhonua* in Hā'ena.

The importance of rugosity varies by species. Some species avoid predation in ways other than sheltering in the reef structure. *Mulloidichthys* spp. and *Caranx* spp. have been known to use nearshore surf zones, sandy beaches, and inshore or estuarine habitats as nurseries (Blaber et al. 1995, Smith and Parrish 2002, Lecchini and Galzin 2005, Friedlander et al. 2014), possibly using the shallow depths and turbid waters as refuges from evasion (Suda et al. 2002). While species of those two genera rarely occurred on transect surveys, field observations of *Mulloidichthys* spp. and *C. melampygius* in Hā'ena were consistent with the afore-mentioned juvenile habitat associations, observed primarily in areas of shallow depths (< 1 m), sandy seafloor, and close to shore (within 25 m). This pattern demonstrates the challenge of developing management that addresses the patterns of multiple species, and illustrates the considerations to be made when designing spatial closures, especially on a small scale.

The strength of influence of structural complexity was only moderate in analyses with remotely sensed methods. LiDAR-derived slope of slope has previously been shown to be a good predictor of fish distributions (Pittman et al. 2009, Pittman and Brown 2011), but no previous studies have explicitly used this metric for assessing juvenile distributions. The spatial scale at which slope of slope was derived for this study (20 m radius) may be too large to capture the fine-scale variation in structural complexity that would influence juvenile fish populations. This limitation should be taken into consideration in future applications of remote sensing data to investigate juvenile fish distributions. Additionally, the LiDAR-derived measures were limited by missing bathymetric data in the shallowest areas of the nearshore ecosystem. The omission of these shallow sites in analyses with remotely sensed data potentially resulted in compromised representation of the fish assemblage and associated habitats, although inclusion of all samples in analyses without the slope of slope variable did not result in substantially different fish-habitat relationships. For future studies, bathymetric information of higher spatial resolution and complete coverage should be used. If unavailable, it is recommended that fine-scale (*in situ*) measures of rugosity be used when possible.

5.1.2 *Variations between data collection methods*

Estimates of seascape parameters are sensitive to methods of investigation (Cullinan and Thomas 1992, Fortin 1999, Fortin et al. 2000), so it is important to identify the variables which can be accurately estimated by various methods and which will be informative in the description of juvenile fish distribution patterns. While we were able to infer juvenile habitat associations

based on remotely sensed data, we suggest a combined approach for future investigations of juvenile fish habitat relationships. Fine-scale *in situ* data captures the associations with benthic cover types at a spatial resolution most appropriate for juvenile fish assessments, while remote sensing methods allow for the inclusion of broad-scale variables, such as cross-shelf location on the reef (e.g., distance from shore), which showed to be influential. Juvenile fishes may be influenced by both micro-scale (Tolimieri 1998) and seascape characteristics (Drew and Eggleston 2008), so methods that incorporate both into assessments of associations will generate a more complete understanding of the ecological dynamics at play.

The habitat associations of *S. rubroviolaceus* demonstrated the variation that can occur between data collection methods. The CCA using *in situ* habitat data showed juvenile *S. rubroviolaceus* to have a strong association with coral cover (Fig. 6), a variable not present in the analyses using remotely sensed data due to minimal frequency of occurrence. This reveals a limitation of the use of the remote sensing methods for investigations of fish-habitat relationships. On the north shore of Kaua‘i, a region of high exposure to heavy winter swells, coral does not compose a high proportion of the total cover (Jokiel et al. 2004, Jokiel 2006). Remotely sensed imagery was delineated and classified by cover as could be identified from aerial imagery, and since coral cover was not a spatially-dominant cover class, it was largely undetected in remotely sensed imagery. This omission of this ecologically important habitat class (Bell and Galzin 1984, Friedlander and Parrish 1998, Jones et al. 2004) leads us to conclude that fine-scale *in situ* measures of benthic cover are better suited to quantify the influence of habitat classes such as coral that have low spatial cover but relatively high influence, particularly on food resource species.

Remotely sensed biological cover data indicated turf algae had the strongest correlation with *S. rubroviolaceus* (Fig. 8), a variable that did not show strong association with the juvenile fish assemblage as a whole in the *in situ* analysis. The latter observation is likely explained by the ubiquitous representation of turf in *in situ* benthic surveys. Turf algae was present in every sample in the analysis, with a mean percent cover of 56.3% (\pm 17.5%). It likely did not emerge as influential due to this universal presence. Remotely sensed habitat classes are delineated on a much broader scale, with a single classification describing an entire area. The classification scheme does not recognize the presence of anything other than the dominant cover, depicting a more uneven distribution of habitats than may be detected by *in situ* methods. Therefore, the universal distribution of turf algae is overlooked, perhaps magnifying the influence of the variable on the juvenile assemblage.

Remote methods did however provide for the inclusion of variables that influence juvenile fishes at a seascape scale that may not have otherwise been included in data from *in situ* surveys. In the analyses of biological cover and of geomorphological structure, juvenile fish distribution was strongly influenced by distance to shore, a finding consistent with local knowledge. In Hā'ena, schools of juveniles of certain species occur in the shallows right next to the shore, and some community members will not even walk along the shoreline of these areas, so as not to scare the juvenile fishes into deeper water where predators may be present (Mehana Vaughan, pers. comm). Some spatial metrics that may help explain distribution of juvenile fishes are not easily quantified using *in situ* techniques, demonstrating the value of remote sensing technology and geospatial studies to better understand ecological drivers of fish distribution patterns.

5.1.3 *Habitat generalists*

In addition to identifying variables that are highly influential for various species, these methods provide a means of identifying species which are *not* strongly influenced by measured seascape variables (i.e. habitat generalists; Brown 1984, Wilson et al. 2008), and thus may exhibit less of a response to management efforts that are based on the concept of specific habitat protection. It can be expected that if measures of habitat protection are not taken and influential habitats are disturbed or lost, there would be a disproportionate loss of habitat specialist species and fish communities would become dominated by habitat generalists (Munday 2004, Wilson et al. 2008). This study identified *T. duperrey*, *S. balteata*, and the endemic *S. marginatus* as habitat generalists. It is important to recognize which species may be habitat generalists, and in the case that the identified species are of particular interest for management, to assess the appropriate way to target conservation efforts. If a target species is a habitat generalist, conservation efforts would likely need to consider different approaches to managing for that species (e.g., bag limits, seasonal restrictions, etc.), as generalists are less likely to be site-attached (Adams et al. 2006) or governed by habitat availability (Brown 1984) and protection of specific habitats may not be the most effective approach.

The differences in habitat associations among species should also be noted in a discussion of the measured overall strength of relationships when the juvenile assemblage is analyzed as a whole. Reported results include a measure of the percent of variance in response data explained by the explanatory variables, ranging from 18.6 to 26.0% in these analyses. It is prudent to recognize that habitat generalists, which are poorly associated with particular habitat variables and which typically make up a large proportion of an assemblage impact (Brown 1984), affect

the overall measure of the strength of fish-habitat relationships. *S. marginatus*, *T. duperrey*, and *S. balteata* made up a cumulative 62.7% of the total abundance of juveniles observed on transect surveys. Removal of these generalist species in the analysis of *in situ* habitat data resulted in a nearly 20% increase in the percent variance explained by seascape variables (from 26.0 to 31.1%). Acknowledging that a large portion of the response data represent species that do not have strong relationships with habitat variables, it is apparent that some species included in the analyses are likely more strongly influenced by habitat variables than the overall measure suggests.

5.1.4 *Ontogenetic variation in habitat relationships*

Investigation and identification of nursery habitat is predicated on the condition that the species in question have at least some disjunction between juvenile and adult habitats (Beck et al. 2001). Fish have been shown to associate with the benthos in a manner scaled to their body size (Hixon and Beets 1989, 1993, Friedlander and Parrish 1998) and to shift habitat requirements with ontogeny (Sale 1998, Lindeman et al. 2000, Appeldoorn et al. 2003) so relationships between fish and habitat should be evaluated by distinct life stages.

Results here have demonstrated that habitat associations of *A. triostegus* shift with ontogeny, a pattern previously observed in Moorea, French Polynesia (Lecchini and Galzin 2005). Juveniles were highly correlated with unconsolidated substrate, macroalgae, and depth; adult abundance was most strongly affected by macroalgae and coral cover. Also apparent in this study was a generalizing of habitat use, where juveniles were found to be restricted to one zone

on the reef while adults were observed across geographic location on the reef (Fig. 11). Similarly, in an investigation of habitat associations by size groupings, Adams and Ebersole (2002) found that in contrast to small and medium *Acanthurus* spp. (*A. bahianus* and *A. chirurgus*), larger sizes (> 5 cm) of *Acanthurus* spp. exhibited no significant variation in habitat use. This emphasizes the value of life stage-specific evaluations of habitat associations. The results from this study add to the evidence that some species of juvenile fishes have habitat associations that vary from those of adults, and these life-stage-specific patterns should be recognized in management of nursery habitats.

5.1.5 *Value of a seascape approach*

This study has produced valuable knowledge on fish-habitat associations in a seascape context, addressing the influence of the combination and composition of nearby habitats. Previous studies have identified certain habitats or seascape characteristics as important drivers in fish distribution (Adams and Ebersole 2002, Friedlander et al. 2003b, Aburto-Oropeza et al. 2007, Friedlander et al. 2007a, Grol et al. 2014). However, fish are not influenced by single isolated variables but by multiple variables acting in concert (Kendall et al. 2003, Pittman et al. 2007a, Grober-Dunsmore et al. 2008, Nagelkerken 2009, Olds et al. 2012). The importance of co-occurrence and proximity of various suitable habitats as a determinant of adult fish distribution patterns has been well-documented in mangrove impact (Mumby et al. 2004b, Nagelkerken 2007) and seagrass habitats (Valentine et al. 2007, Nagelkerken et al. 2008b), as well as for sand and hard-bottom habitat mosaics (Kendall et al. 2003, Friedlander et al. 2007a).

Fish distributions have also been shown to be affected by cross-shelf location on a reef (Williams and Hatcher 1983, Lindeman et al. 1998, Christensen et al. 2003b, Pittman and Brown 2011). A better understanding of variables that affect fish distributions in a seascape context is appropriate and beneficial to conservation efforts that take an ecosystem approach in their management actions (Christensen et al. 2003a, Friedlander et al. 2003b), and the fish-seascape patterns detected in this project provide information specific to juvenile distributions in Hawaiian reef systems.

5.1.6 Spatial scale

The analysis of fish-habitat relationships at multiple spatial scales allowed for the examination of the effects of scale on interpreted associations. The concept is that the spatial scale showing the highest explained variation would be interpreted as the neighborhood size, or the most ecologically influential scale for the assessed combinations of variables (Holland et al. 2004, Kendall 2005). A number of studies have assessed the effects of spatial scale for studies on adults fishes (Kendall 2005, Grober-Dunsmore et al. 2007, Purkis et al. 2008, Kendall et al. 2011), but comparative evaluations of appropriate spatial scale for juvenile fishes is lacking. This study investigated appropriate spatial scale for juvenile reef fishes, which generally have a smaller home range and are expected to be influenced by habitats at a different scale than adults. At the spatial scales assessed in this study, strong differences in the strength of fish-habitat associations were not apparent among scales. Explained variation among analyses with remote biological cover data ranged from 18.6 to 20.6% and did not exhibit a pattern of reaching an

optimum spatial scale. Similarly, analyses with geomorphological structure data ranged from 21.5 to 24.7%. This is likely indicative of an omission of the appropriate spatial scale, i.e. all of the analyses were at too large a spatial scale to detect the strongest associations of juvenile fishes with nearby habitat. In the case that juvenile fishes are primarily influenced by their surroundings at a micro-habitat scale, the survey methods used (25×2 m transects) would need to be modified so as to detect micro-scale variations in habitat and the associated patchy distribution of juvenile fishes.

In situ observations suggest such a possibility. Juveniles were generally observed very close (< 0.2 m) to coral heads, rock piles, or similar forms of structural complexity. Such micro-scale variations and associations are not likely to be detected at analyses of larger spatial scales. For example, on a swim between survey locations, 500+ *A. triostegus* juveniles (2-3 cm) were observed at a pock-filled boulder which provided an oasis of structural complexity in an otherwise flat, shallow (< 0.5 m) seascape of rock bench habitat. In a heterogenous seascape, fish and habitat quantifications at a fine-scale resolution may provide the most accurate and strongest relationship interpretations. Fish-habitat associations can be further examined with data which classifies and measures the proximity of the habitat nearest to observed juvenile fishes (sensu DeMartini et al. 2010). Fish and seascape data collected on a micro-habitat scale would allow for analyses that are on a spatial scale more appropriate for examining ecological drivers of juvenile fish distribution.

The resolution of the delineated habitat map was perhaps restrictive to the assessment of juvenile distribution. The map created in this study had an MMU of 100 m^2 . This is a much higher mapping resolution than the previous NOAA benthic habitat mapping efforts, and

provides an enhanced tool for assessing adult fish distributions. However, it may still be too coarse of a resolution to detect the fine-scale patterns and patchy distribution of juvenile fish assemblages. Purkis et al. (2008) arrived at a similar conclusion with respect to fishes of small size classes, finding that distribution of fishes with maximum attainable sizes of <20 cm was poorly explained by remotely sensed habitat data, which the authors ascribed to insufficient resolution of benthic information. To resolve this issue, higher resolution imagery is necessary for the delineation of more detailed habitat maps. With the imagery used in the delineation of these habitat maps, the MMU of 100 m² was the smallest MMU that could confidently be used to classify distinct habitats. In the utilization of remote imagery for ecological investigations of juvenile fishes, higher-resolution imagery is an important aspect of improved ability to interpret associations and predict distributions.

Analyses comparing spatial scales were based on varying buffer sizes around transect locations. At increasing spatial scales, buffer rings around transects began to overlap one another, as will happen with sampling in any constrained geographical area (Pearman 2002). The small area of this study site presented the challenge of compromising sample size in order to avoid spatial overlap of samples. In exploration of the effects of spatial autocorrelation on interpreted fish-habitat relationships, one of every pair of overlapping samples was randomly removed in order to create subsets of the data that represented spatially independent samples, and analyses were compared between the full and reduced datasets. At the smallest spatial scales (20 m), reduction in sample size was minimal (4% of original dataset). This value increased dramatically at the next spatial scale (40 m), with a 44% reduction, but nevertheless, consistent

patterns between full and reduced datasets were still apparent. As spatial autocorrelation did not appear to strongly impact the interpretations, results for the full datasets were reported.

At larger scales, particularly 100 m, datasets resulting from removal of overlapping samples were drastically reduced ($n = 25$) and were not deemed to provide reliable interpretations of fish-habitat associations. For this reason, results from full datasets were reported. While it is not uncommon for landscape ecology studies to use datasets with spatial overlap (Lepczyk et al. 2008), or to lack measures of spatial autocorrelation (see review by Wedding et al. 2011), it is recognized that the invalidation of the assumption of independent samples can distort estimated parameter influences (Mellin et al. 2010). Thus it is suggested that future studies of fish-habitat relationships should avoid extensive overlap if the spatial area of the study site allows for a sufficient sample size of non-overlapping areas.

5.1.7 Limitation of temporal restriction: Only a snapshot

It should be recognized that this study provides only a snapshot of the juvenile fish assemblage. This is an important limitation to note, as juvenile fish assemblages can vary substantially both seasonally and among years in Hawai'i (Walsh 1987) and elsewhere (see review by Doherty and Williams 1988). With data from only two points in time, this is not an assessment of complete recruitment data. In a snapshot, not all species that may use the area in juvenile stages are described in the results. If juveniles did not recruit during the periods in which surveys were conducted, they were not observed and thus not represented in the data. Future investigations of juvenile fish habitat relationships should involve multiple survey periods

throughout the year, and across a span of years, capturing different recruitment pulses and creating a more comprehensive representation of the juvenile assemblage that uses the area.

The limitations that often restrict the ability of scientific or conservation agencies to carry out extensive studies highlight the value of recognizing the merit of local ecological knowledge. There is much value in the knowledge held by the people of a place (Berkes 1999, Ames 2003, Berkes and Berkes 2009, Jokiel et al. 2010). Local knowledge – that which is obtained through intimate connection with the ecosystem, or passed on from generation to generation (Berkes 1999, Johannes et al. 2000) – is rich in detail and precision, and as Johannes (1982) described, it is often superior to the information gathered by “imported consultants constrained by insufficient time and money.” Seasonal or nocturnal nature, lunar periodicity, and annual recruitment variations were traditionally observed through vigilant attention to local fish populations (Lowe 2004), and this difference in temporal resolution can lead to important variations in collected ecological information (Johannes et al. 2000). Scientists or consultants who gather data from only a few points in time may likely miss such temporal patterns as lunar or seasonal variations, or the ecological dynamics otherwise at play under particular conditions. The information gathered from visitors should be acknowledged as snap-shot data that can be used in conjunction with local knowledge.

5.2 Community-based ecosystem management

Traditional customs, practices, and transmission of knowledge in Native Hawaiian populations deteriorated in the late eighteenth and early nineteenth centuries as a result of

Western influence (Johannes 1978b, Friedlander et al. 2013). Contemporary resource management in Hawai‘i has been a centralized, top-down system, an approach to marine resource management in which decisions are made at the state governmental level without consideration of the resource needs or ecological dynamics of local communities and the ecosystems that support them (Jokiel et al. 2010, Friedlander et al. 2013), and one in which the resource users are not the managers (Berkes 1999). However, a recent resurgence of customary fisheries management gives hope for revitalized sustainability of marine resource practices (Johannes 2002, Cinner and Aswani 2007, Friedlander et al. 2013). The efficacy of customary management regimes in the conservation of marine resources has been documented (Friedlander et al. 2003a, McClanahan et al. 2006), and with declines in resources becoming increasingly apparent (Shomura 1987, Friedlander and DeMartini 2002, Friedlander 2004), the value of community-based and traditional approaches to management is reemerging in the context of conventional methods (Huntington 2000, Johannes 2002, Poepoe et al. 2003, Jokiel et al. 2010).

Local communities hold knowledge that is accumulated over generations and results from living in close contact with nature and the resources it provides (Berkes 1999, Berkes and Berkes 2009). Historically, this knowledge was applied towards the effective management of natural resources (Titcomb 1972, McClenahan and Kittinger 2013). By recognizing local knowledge such as protection of areas to allow resources to replenish (e.g., *pu ‘uhonua*) or fishing *kapu* (closure) periods based on community-based moon calendars that indicate species spawning times, customary and conventional management approaches can be effectively integrated (Friedlander et al. 2002, Poepoe et al. 2003, Aswani et al. 2007, Cinner and Aswani 2007, Jokiel et al. 2010, Friedlander et al. 2013).

5.2.1 *Contribution to CBSFA efforts in Hā‘ena*

The results from this study identified seascape variables of particular importance to the juvenile fish assemblage in the Hā‘ena nearshore ecosystem, and the project provided quantitative support for the spatial designation of the proposed *pu‘uhonua*. While the management plan was largely informed by ecological knowledge that already existed within the community, knowledge built from constant, extended, and close connection with the ecosystem (Berkes 1999), scientific studies played a key role in the legislative approval of the proposed plan. This has been a tangible demonstration of the power and value of the integration of multiple knowledge sources towards efforts to conserve natural marine resources.

In a discussion of ecosystem-based management in Hawai‘i, Tissot et al. (2009) commented that to achieve such management throughout the state would take a lot of time and resources, and that “the first challenge is to support existing community-based fishery management and research efforts throughout the state, learn from their experiences, and help them achieve financial sustainability” (pg. 271). With the contribution of this work, along with the persevering efforts of the Hā‘ena community, the Hawai‘i state Board of Land and Natural Resources approved the proposed CBSFA management plan on October 24, 2014, making Hā‘ena the first community in Hawai‘i to have state-sanction community-based marine resource management. The inclusion of quantitative studies that supported the area proposed for *pu‘uhonua* designation were instrumental in this historic decision, and the project serves as a prototype study for others that may contribute to similar management efforts elsewhere in the state.

As the first area in Hawai'i to have an approved CBSFA rules package, Hā'ena has set a ground-breaking precedent for other communities in the state who seek to achieve similar goals. Under Act 271, which created the infrastructure that allows communities to work with the state to create management strategies based on local knowledge and native Hawaiian values (Higuchi 2008), there are currently eighteen other communities that are at various stages of creating CBSFAs. As foreseen by Tissot et al. (2009), the successes achieved in Hā'ena provide a template for other efforts throughout the state, and an example from which communities can learn and adjust future efforts.

More generally, the identification of essential fish habitat can be applied to inform reserve design in regions around the globe (Lindeman et al. 2000, Rieser 2000, McLeod et al. 2009). Quantitative estimates of ecological linkages and associations are needed for management efforts (Leathwick et al. 2008, Palumbi et al. 2009) and an understanding of the relationships between fishes and the seascape is important for effective conservation (Doak and Mills 1994, Collinge 2001). Information on the ecological functions provided by different habitat types can help ensure that a proper suite of necessary habitats is protected and that spatial design of reserves incorporates the seascape components influential to fish distributions (Drew and Eggleston 2008, Bostrom et al. 2011).

5.2.2 Baseline studies

With the recent establishment of the Hā'ena management plan, as with any new implementation of management, it is important that information exists on the current resource

distributions and ecological relationships, collected prior to conservation actions. This is essential to environmental impact assessment and effective conservation programs (Johannes 1993, Edgar et al. 2004, Sandin et al. 2008), as natural resources under new management regimes can then be monitored and changes can be evaluated based on a known baseline. Without baseline data, changes due to management cannot be concluded and performance of the reserve cannot be evaluated (Botsford et al. 2003, Edgar et al. 2004, Aswani et al. 2007). This work has provided crucial baseline data on the nearshore reef ecosystems of Hā'ena, Kaua'i, information that will be vital in future assessments of the efficacy of newly established community-based resource management. Regular monitoring and evaluation provides a way for stakeholders to see changes that may result from management actions, and allows for conservation efforts to be adjusted and adapted in response to monitoring.

Here again, the value of local ecological knowledge should be recognized. While recent ecological surveys provide a baseline from which forthcoming management changes can be assessed, information drawn from LEK can be used to synthesize an antecedent baseline (Eddy et al. 2010), a reference point which would likely illustrate the existence of a shifting baseline syndrome as described by Pauly (1995). When evaluations of changes in the abundance of a resource or state of an ecosystem are based upon perspectives of limited temporal scope, the result is a “gradual accommodation of the disappearance of resource species” (Pauly 1995). Recognition of historical ecological statuses through traditional knowledge helps to put community-based management into context (Berkes 1999), illuminating that which motivates actions and illustrating a target for conservation that is not simply based on maintenance of current levels, but recovery of resources to a former baseline (Calamia 1999, Pitcher 2001).

5.2.3 *Future monitoring efforts*

The produced benthic habitat map, converted to a Google Earth file, can serve as a foundation for future community monitoring efforts. For example, the habitat map populated with georeferenced photos of the underwater habitat could be used as a training tool for habitat classification. Furthermore, while this study was an investigation of spatial rather than temporal differences, the produced map provides a tool to be used for future temporal studies. Vegetation maps over an extended period can be used to document change over time (Manson et al. 2003). Georeferenced photos could be used to evaluate changes in benthic habitat, which would help detect ecosystem shifts resulting from factors such as climate change, nutrient or sediment inputs, or changes in levels of herbivory. These shifts can impact fish distributions and nearshore ecological dynamics, indirectly affecting fishing operations (Sumaila et al. 2011). While landscape changes over time are commonly addressed in terrestrial studies (Schlosser 1991, Foster 1992, Foster et al. 1998, Compton and Boone 2000), there is much work to be done in marine science to document and assess seascape change over time. A monitoring tool that can be used and maintained by the community empowers local resource users to assess their own ecosystem and evaluate their management actions.

The ability to assess and evaluate management allows for improvement based on trial-and-error learning (Berkes et al. 2000). A monitoring tool to be used by the community would provide a feedback learning mechanism by which the community could see the effects that their management actions have on the ecosystem, which would facilitate adaptive management and provide an increased (or renewed) sense of stewardship over local resources (Berkes et al. 2000). A greater sense of stewardship over local resources is likely to improve compliance with fishing

regulations, level of self-policing, and an awareness of changes in resource levels that would facilitate adaptive responses and bring management back into the hands of the resource users (Johannes 1982, Poepoe et al. 2003, Aswani et al. 2007, Aswani 2010, Friedlander et al. 2013).

CHAPTER 6. CONCLUSION

This project has addressed the importance of integrating knowledge sources towards the preservation of nearshore marine resources, and has demonstrated effective application of ecological science to community-based fishery management efforts. The methods used in this study allowed for the investigation of species-specific habitat associations within juvenile fish assemblages. Identification of the drivers of spatial distribution of juvenile fishes in the nearshore marine ecosystems of Hā‘ena has helped to develop a more complete understanding of the ecological dynamics of the area, and has contributed valued knowledge to the process of passing management legislation. While remote sensing technology does not replace the importance of fine-scale *in situ* measurements, interpreted patterns of fish-habitat relationships were comparable between the methods, and remote sensing methods can have a valuable contribution to future investigations of fish-habitat relationships. This is particularly advantageous for large scale assessments where efficiency is often necessary. It is suggested that mixed-methods approaches are applied to similar studies in order to improve our understanding of how seascape affects fish distributions.

Cultural practices and traditional ecological knowledge in Hawai‘i have eroded over the past two centuries under the influence of Western contact however (Johannes 1978b, Friedlander et al. 2013), yet some communities across the state have retained much of their local knowledge and customs. It is critical to the preservation of Native Hawaiian culture and local marine resources that these communities continue subsistence fishing in a manner consistent with their customary practices (McGregor et al. 1998, McGregor 2007). Recent Hawai‘i state legislation that enables the establishment of CBSFAs is an example of integration of conventional and

customary management (Friedlander et al. 2013), and the community of Hā‘ena is the first in the state to successfully develop an approved rules package for management of their local marine resources. This project has contributed to community efforts knowledge drawn from quantitative ecological studies, and the patterns of juvenile distributions inferred from this study supported the spatial designation of the proposed *pu‘uhonua*. The presentation of this quantitative support to the State of Hawai‘i Department of Land and Natural Resources played an integral role in the approval of the management plan, and demonstrated the importance of multiple forms of knowledge towards the preservation of nearshore marine resources. The project provides a template for successful integration of knowledge systems towards resource conservation, to be applied to similar efforts throughout Hawai‘i and elsewhere in the world.

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Appendix 1. Benthic taxa observed on *in situ* surveys, pooled into cover types. Note: All listed taxa were observed in the surveys, but total percent cover for some taxa rounds down to 0.00%.

Type	Taxon	Total percent cover
CorAlg	Coralline algae	8.79
Coral	<i>Porites lobata</i>	4.31
	<i>Montipora flabellata</i>	2.35
	<i>Montipora patula</i>	2.24
	<i>Pocillopora meandrina</i>	1.48
	<i>Porites compressa</i>	1.14
	<i>Montipora capitata</i>	0.82
	<i>Pavona varians</i>	0.24
	<i>Pavona duerdeni</i>	0.03
	<i>Pocillopora ligulata</i>	0.00
	<i>Pocillopora damicornis</i>	0.00
Macro	<i>Dictyota</i> spp	4.67
	<i>Microdictyon</i> spp	2.71
	<i>Padina</i> spp	0.75
	<i>Galaxaura</i> spp	0.64
	<i>Amansia glomerata</i>	0.59
	<i>Dictyosphaeria vershuyisii</i>	0.26
	<i>Chryso cystis fragilis</i>	0.23
	<i>Liagora</i> spp	0.22
	<i>Asparagopsis taxiformis</i>	0.21
	<i>Derbesia</i> spp	0.15
	<i>Laurencia</i> spp	0.14
	<i>Ralfsia</i>	0.12
	<i>Lyngbya majuscula</i>	0.11
	<i>Sargassum</i> spp	0.11
	<i>Dictyosphaeria cavernosa</i>	0.09
	<i>Bryopsis hypnoides</i>	0.08
	<i>Acanthophora spicifera</i>	0.04
	<i>Gracilaria coronopifolia</i>	0.03
	<i>Cyanobacteria</i>	0.03
	<i>Turbinaria ornata</i>	0.02
<i>Halimeda discoidea</i>	0.02	
<i>Tolypocladia glomerulata</i>	0.02	

	<i>Sphacelaria</i> spp	0.01
	<i>Martensia flabelliformis</i>	0.01
	<i>Dasyopsis</i>	0.01
	<i>Leptolyngbya crosbyana</i>	0.00
	<i>Halichrysis coalescens</i>	0.00
	<i>Codium edule</i>	0.00
	<i>Cladophora</i> spp	0.00
	<i>Cryptonemia umbraticola</i>	0.00
Uncons	Sand	8.82
	Rubble	1.28
Turf	Turf algae	55.66

Appendix 2. Classification scheme adapted from Coyne et al. (2003) and Battista et al. (2007); description of habitats.

Class scheme	Habitat class	Description
Geomorphological structure	Aggregate reef	Coral-dominated formations with high relief and structural complexity, typically oriented parallel to the shore of shelf edge.
	Artificial	Man-made habitats such as submerged wrecks, large piers, and submerged portions of jetties. Includes active and remnant fish ponds walled off from the open ocean along the shoreline.
	Individual patch reef	Distinctive single coral formations that are isolated from other coral reef formations by sand or other habitats. Have no organized structural axis relative to the contours of the shore or shelf edge.
	Mud	Unconsolidated fine sediment often associated with river discharge and buildup of organic material in areas sheltered from high-energy waves / currents.
	Pavement	Flat, low-relief, solid carbonate rock, often colonized by macroalgae, turf algae, hard coral, and sessile invertebrates.
	Pavement with sand channels	Habitat having alternating sand and colonized pavement formations that are oriented perpendicular to the shore. Typically occurs in areas exposed to moderate wave surge.
	Rock and boulder	Exposed volcanic rock or large boulders.
	Rubble	Unconsolidated habitat characterized by broken rock, coral pieces. Grain size > sand; typically fist-sized.
	Sand	Coarse sediment typically found in areas exposed to currents or wave energy.
	Scattered rock and coral	Habitat (typically sand or pavement) scattered with rocks or small isolated coral heads that are too small to be delineated individually.
	Spur and groove	Habitat having alternating sand and coral formations that are oriented perpendicular to the shore. The coral formations (spurs) typically have high vertical relief relative to pavement with sand channels and are separated from each other by 1-5 meters of sand or bare hardbottom (grooves).

	Unknown	Habitat uninterpretable due to turbidity, cloud cover, water depth, breaking waves, or other interference.
Biological cover	Coral	An area characterized by hard, scleractinian corals, typically forming a habitat of structural complexity.
	Coralline algae	An area characterized by any combination of numerous species of encrusting or coralline algae.
	Emergent vegetation	Emergent habitat, typically mangrove and hao trees. Usually occurs along shorelines.
	Macroalgae	An area with coverage of any combination of numerous species of red, green, or brown macroalgae. Usually occurs in shallow back-reef and deeper waters on the bank / shelf zone.
	Turf algae	An area with coverage of small, filamentous algae, typically forming a fine fuzz or carpet-like cover. Finer than macroalgae.
	Uncolonized	Substrate (typically unconsolidated, i.e. sand or rubble) with little or no coverage of macroalgae, hard coral, turf algae, or sessile invertebrates.
	Unknown	Habitat uninterpretable due to turbidity, cloud cover, water depth, breaking waves, or other interference.

Appendix 3. Observed juvenile species; total abundance over 126 transects.

	Species	Common Name	Hawaiian Name⁵	n	% Total abund	Freq. of occur
1	<i>Stethojulis balteata</i>	Belted Wrasse	‘ōmaka	557	27.33	91
2	<i>Thalassoma duperrey</i>	Saddle Wrasse	hīnālea			
			lauwili	428	21.00	101
3	<i>Acanthurus triostegus</i>	Convict tang	manini	292	14.33	40
4	<i>Plectroglyphidodon imparipennis</i>	Brighteye Damsel fish		167	8.19	65
5	<i>Gomphosus varius</i>	Bird wrasse	hīnālea ‘i‘iwi	114	5.59	38
6	<i>Stegastes marginatus</i>	Pacific Gregory		89	4.37	49
7	<i>Macropharyngodon geoffroy</i>	Shortnose Wrasse		50	2.45	24
8	<i>Plectroglyphidodon johnstonianus</i>	Blue-eye Damsel fish		35	1.72	24
9	<i>Scarus rubroviolaceus</i>	Redlip Parrotfish	pālupaluka	35	1.72	22
10	<i>Mulloidichthys flavolineatus</i>	Yellowstripe Goatfish	weke‘ā	33	1.62	2
11	<i>Chromis vanderbilti</i>	Blackfin chromis		30	1.47	14
12	<i>Acanthurus leucopareius</i>	Whitebar Surgeonfish	māikoiko	27	1.32	18
13	<i>Coris venusta</i>	Elegant coris		23	1.13	14
14	<i>Chlorurus perspicillatus</i>	Spectacled parrotfish	uhu uliuli	21	1.03	9
15	<i>Dascyllus albisella</i>	HI dascyllus	‘alo‘ilo‘i	15	0.74	6
16	<i>Paracirrhites arcatus</i>	Arc-eye Hawkfish	piliko‘a	13	0.64	10
17	<i>Acanthurus nigrofuscus</i>	Brown Surgeonfish	mā‘i‘i‘i	12	0.59	10
18	<i>Canthigaster jactator</i>	HI Whitespotted toby		12	0.59	8
19	<i>Halichoeres ornatissimus</i>	Ornate Wrasse	lā‘ō	12	0.59	6
20	<i>Ctenochaetus strigosus</i>	Goldring surgeonfish	kole	8	0.39	7
21	<i>Coris gaimard</i>	Yellowtail coris	hīnālea ‘akilolo	5	0.25	4
22	<i>Cirrhitops fasciatus</i>	Redbar Hawkfish	piliko‘a	4	0.20	4
23	<i>Scarus psittacus</i>	Palenose Parrotfish	uhu	4	0.20	2
24	<i>Thalassoma purpurum</i>	Surge Wrasse	hou	4	0.20	2
25	<i>Anampses cuvier</i>	Pearl wrasse	‘opule	3	0.15	3

⁵ Randall, J. E. 2010. Shore fishes of Hawai‘i. Revised edition. University of Hawaii Press.

26	<i>Labroides phthirophagus</i>	HI Cleaner		3	0.15	3
27	<i>Oxycheilinus bimaculatus</i>	Twospot Wrasse		3	0.15	2
28	<i>Parupeneus insluaris</i>	Doublebar Goatfish	munu	3	0.15	3
29	<i>Parupeneus multifasciatus</i>	Manybar Goatfish	moano	3	0.15	3
30	<i>Rhinecanthus rectangulus</i>	Reef triggerfish	humuhumu nukunuku a pua'a	3	0.15	2
31	<i>Cantherhines sandwichiensis</i>	Squaretail filefish	'o'ili lepa	2	0.10	2
32	<i>Chlorurus spilurus</i>	Bullethead parrotfish	uhu	2	0.10	2
33	<i>Cirrhitus pinnulatus</i>	Stocky Hawkfish	po'opa'a	2	0.10	2
34	<i>Cirripectes vanderbilti</i>	Scarface Blenny		2	0.10	2
35	<i>Parupeneus porphyreus</i>	Whitesaddle Goatfish	kūmū	2	0.10	2
36	<i>Zebrasoma flavescens</i>	Yellow Tang	lau'īpala	2	0.10	2
37	<i>Abudefduf abdominalis</i>	Sergeant Major	mamo	1	0.05	1
38	<i>Acanthurus blochii</i>	Ringtail Surgeonfish	pualu	1	0.05	1
39	<i>Acanthurus nigroris</i>	Bluelined Surgeonfish	maiko	1	0.05	1
40	<i>Asterropteryx semipunctatus</i>	Halfspotted goby	'o'opu	1	0.05	1
41	<i>Bodianus alboteniatus</i>	Hawaiian Hogfish	'a'awa	1	0.05	1
42	<i>Cephalopholis argus</i>	Peacock Grouper	roi	1	0.05	1
43	<i>Chaetodon multicolor</i>	Multiband butterflyfish	kikākapu	1	0.05	1
44	<i>Exallias brevis</i>	Shortbodied Blenny	pāo'o kauila	1	0.05	1
45	<i>Naso unicornis</i>	Bluespine Unicornfish	kala	1	0.05	1
46	<i>Ostracion meleagris</i>	Spotted Boxfish	moa	1	0.05	1
47	<i>Parupeneus cyclostomus</i>	Blue Goatfish	moano hulu	1	0.05	1
48	<i>Paracirrhites forsteri</i>	Blackside Hawkfish	hilu piliko'a	1	0.05	1
49	<i>Parupeneus pleurostigma</i>	Sidespot Goatfish	malu	1	0.05	1
50	<i>Pseudocheilinus tetrataenia</i>	Fourline Wrasse		1	0.05	1
51	<i>Scarus dubius</i>	Regal Parrotfish	lauia	1	0.05	1
52	<i>Thalassoma ballieui</i>	Blacktail Wrasse	hīnālea lauhine	1	0.05	1
53	<i>Thalassoma trilobatum</i>	Christmas Wrasse	'āwela	1	0.05	1
54	<i>Zanclus cornutus</i>	Moorish Idol	kihikihi	1	0.05	1

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