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Publication Date

2014

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Modeling the Effects of Sea Level Rise and Introduced Species on Hawaiian Anchialine Pool Ecosystems

By

Elizabeth Case Marrack

A dissertation submitted in partial satisfaction of the

Requirements for the degree of

Doctor of Philosophy

in

Environmental Science, Policy, and Management

in the

Graduate Division

of the

University of California, Berkeley

Committee in charge:

Professor Patrick O'Grady, Chair
Professor Stephanie M. Carlson
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Professor Mary E. Power

Fall 2014

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Abstract

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Elizabeth Case Marrack

Doctor of Philosophy in Environmental Science, Policy, and Management

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Professor Patrick O'Grady, Chair

Global mean sea levels are expected to rise up to 1.9 m by 2100 and will change the distribution and community structure of low-lying coastal ecosystems due to flooding, erosion, and salt-water intrusion. Although habitats will be inundated, ecosystems have the potential to shift inland and endemic species may persist if conditions are favorable. Multiple-stressors including invasive species and destructive land-use practices have caused widespread coastal aquatic ecosystem degradation over the last century. Predictions of ecosystem migration due to sea level rise need to account for these stressors, which, even at low levels, may reduce the resilience of these ecosystems.

The goal of this dissertation was to predict potential consequences of future sea level rise on groundwater-fed anchialine pool ecosystems in Hawaii by comparing scenarios of inundation with current patterns of habitat, introduced species, and land use. First, high resolution sea level rise models that incorporate groundwater were developed for the west coast of the island of Hawaii. Ecological surveys were also conducted to identify habitat condition and the occurrence of native and non-native species at 398 pools located along 280 km of the coastal corridor. Statistical models were used to determine the current relationship between native and non-native species occurrence and various physical and biological parameters. Stable isotope analysis was used to examine food web relationships within pools. Geospatial analyses were used to predict future pool inundation, pool creation, and non-native species dispersal under various sea level rise scenarios. Results showed that sea level models incorporating groundwater levels were up to 37% better at detecting known anchialine pools than corresponding models without groundwater levels (Chapter 1). Pool surveys showed that two dominant endemic shrimp *Halocaridina rubra* and *Metabetaeus lohena* were located across the region in a wide range of habitats, but that introduced fishes (tilapia, poeciliids) were present in ~ 25 % of pools. Statistical models showed that introduced fishes had a strong negative effect on the occurrence of *H. rubra* and *M. lohena*, while benthic silt cover and adjacent development also had significant negative relationships with shrimp occurrence (Chapter 2). Geospatial models indicate that current habitats will be increasingly inundated by marine waters, but that new habitat will emerge in the landscape in low lying open space (Chapter 3). Because of high subsurface hydrologic connectivity, many endemic species are likely to populate these new habitats by moving through the coastal aquifer. However, in some areas, rising sea levels will provide surface connectivity between pools currently infested with introduced fishes (Chapter 3). Additionally, results suggest that tilapia are a bigger threat to endemic anchialine species and ecosystem health and should be targeted for

removal before poeciliids (Chapter 4). This study demonstrates an interdisciplinary approach to examining ecosystem risk due to sea level rise. Successful conservation of coastal aquatic biodiversity will continue to require current restoration efforts along with protection of potential habitat sites under future climate conditions.

Dedication

I dedicate this with all my love to my family who exposed me to the wonders of the natural world, taught me their intrinsic value, and supported me in my endeavors.

"Now I hear the sea sounds about me; the night high tide is rising, swirling with a confused rush of waters against the rocks below ..... Once this rocky coast beneath me was a plain of sand; then the sea rose and found a new shore line. And again in some shadowy future the surf will have ground these rocks to sand and will have returned the coast to its earlier state. And so in my mind's eye these coastal forms merge and blend in a shifting, kaleidoscopic pattern in which there is no finality, no ultimate and fixed reality – earth becoming fluid as the sea itself."

Rachel Carson,

The Edge of the Sea (1955, Houghton Mifflin)

"When we try to pick out anything by itself, we find it hitched to everything else in the Universe"

John Muir,

My First Summer in the Sierra (1911, Boston: Houghton Mifflin)

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Introduction

Anchialine Ecosystem Distribution, Ecology, and Threats with a Focus on Hawaiian Anchialine Pools

Global sea levels are expected to rise up to 1.9 m by 2100 (Vermeer and Rahmstorf 2009, Parris *et al.* 2012). Current coastal ecosystems are expected to significantly change due to flooding, erosion, saltwater intrusion, or a combination of these phenomena (IPCC 2013, Nicholls and Cazenave 2010, Williams 2013). However coastal ecosystems may shift inland and persist if open space is available and conditions are suitable (Woodroffe 1990, Kirwan and Magonigal 2013). Multiple-stressors including invasive species, elevated nutrient loads, and destructive land-use practices have caused widespread coastal aquatic ecosystem degradation over the last century (Vitousek *et al.* 1997, Paine *et al.* 1998, Foley *et al.* 2005, Halpern *et al.* 2008). Predictions of ecosystem shifts due to sea level rise need to account for these stressors which, even at low levels, may reduce the resilience of these ecosystems to withstand change (Folke *et al.* 2004). For example, sea level rise may create new habitat, but it may also provide introduced aquatic species with dispersal pathways into uninfected habitats. Continued rapid human population growth in coastal areas could lead to further fragmentation and disturbance of existing habitats, thus threatening biodiversity and habitat resilience during climate change (Scavia *et al.* 2002). Coastal aquatic systems that rely on freshwater inputs from groundwater or river flow will be impacted by changing precipitation regimes, human extraction of freshwater, and human contamination of freshwater supplies (Vitousek *et al.* 1997, IPCC 2013). My goal is to examine the potential response of coastal aquatic ecosystems to sea level rise in the context of current invasive predators and land-use practices using the brackish anchialine pool ecosystem in Hawaii as my study system. Ideally the results will be used for local conservation planning as well as provide insights for protecting other coastal systems.

Global Perspective on Anchialine Ecosystem Distribution, Biodiversity and Ecology

Anchialine ecosystems are brackish coastal water bodies that are tidally influenced but have no overland connection to the ocean (Holthuis 1973). They occur worldwide as caves or pools in highly porous bedrock such as lava or karstic limestone where marine and groundwater lenses mix (Figure 1; Holthuis 1973). Anchialine cave habitats exist within several kilometers from the shoreline and are partially or totally submerged with limited exposure to open air (Iliffe and Kornicker 2009). Anchialine caves existing in eroded karstic limestone are known in Eastern Europe (Zaksek *et al.* 2007), the Yucatan and Caribbean (Iliffe and Kornicker 2009), Australia (Humphreys 1999, Boulton *et al.* 2003), and the Sinai Peninsula (Por and Tsurnamal 1973). The "cenotes" of the Yucatan Peninsula, Mexico and "blue holes" in the Bahamas and Belize are examples of karstic anchialine cave ecosystems. Anchialine caves occurring in lava tubes and are known from the Canary Islands (Iliffe *et al.* 1984), Galapagos Islands (Alvarez *et al.* 2005), Hawaii, and Western Samoa (Holthuis 1973).
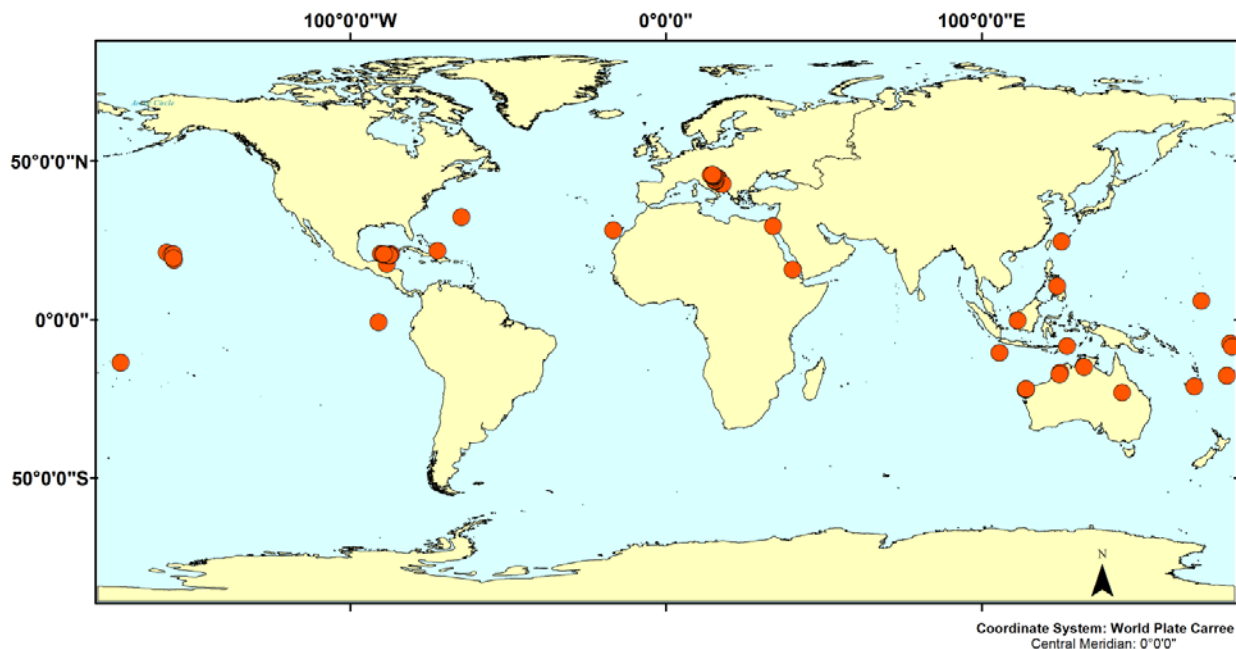
Figure 1: Global Distribution of Reported Anchialine Cave and Pool Systems. Locations are compiled from Holthuis (1963), Holthuis (1973), Por and Tsurnamal (1973), Wear and Holthius (1977), Humphreys (1999), Boulton et al. (2003), Kano and Kase (2004), Zaksek et al. (2007), Iliffe and Kornicker (2009), Becking et al. (2011), Weese et al. (2013).

Anchialine pools are distinguished from anchialine cave habitats in that they are totally exposed to open air (Holthuis 1973, Maciolek and Brock 1974). Pool habitats also exist in lava or karst and have been documented for the Sinai Peninsula (Por and Tsurnamal 1973), Dahlak Archipelago in the Red Sea (Holthuis 1963), the Philippines (Wear and Holthius 1977, Kano and Kase 2004), Indonesia (Becking *et al.* 2011), the Ryukyu Archipelago in Japan (Weese *et al.* 2013), Bermuda and the Bahamas (Iliffe and Kornicker 2009), as well as in the Hawaii, Fiji, Funafuti, Tuvalu (Ellice), Tokelau and Loyalty archipelagos (Holthuis 1963, Holthuis 1973, Wear and Holthius 1977). Although the literature distinguishes between anchialine pools and caves (Sket 1996, Iliffe and Kornicker 2009), this is somewhat of an artificial differentiation in terms of hydrology. In both cases, pools are surface expressions of a subterranean groundwater habitat of cracks and crevices in porous bedrock. In Hawaii and elsewhere, mobile anchialine pool fauna move between pools and subterranean habitats, sometimes on a daily basis (Maciolek 1983, Marrack, personal observation).

Anchialine pool fauna are dominated by crustaceans but include restricted numbers of fishes, sponges, turbellarian worms, gastropods, annelids, chaetognaths, and water mites (Holthius 1963, Maciolek and Brock 1974, Iliffe and Kornicker 2009). Crustaceans are the most abundant and diverse group and, in order of diversity, include amphipods, copepods, decapods, ostracods, isopods, mysids, and thermosbaenaceans (Iliffe and Kornicker 2009). The true biological diversity of these habitats has only recently been recognized as more than 450 new species of anchialine organisms have been discovered and described over the past 25 years (Iliffe and Kornicker 2009, Anker 2010, Weese 2012). For example, Remipedia is a class of Crustacea first described in 1981 by Yager from Bahamian caves. Currently 24 living remipede species are known from the marine dominated portion of anchialine caves within the Carribbean and

Yucatan with isolated species from Western Australia and the Canary Islands (Neiber *et al.* 2011). Anchialine species have high endemism and may be found on single islands or even within single cave systems (Iliffe and Kornicker 2009, Weise *et al.* 2012). Due to the difficulties in studying subterranean anchialine habitats, it is likely that more cave dwelling species (stygofauna) will be discovered in the future.

   A number of anchialine taxa are distributed across the worlds' oceans in highly disjunct locations (Maciolek 1983, Iliffe *et al.* 1984). For example the anchialine copepod genera *Speleophria* is found in Australia, the Mediterranean, and the Yucatan as well as Bermuda (Jaume and Boxshall 1996; Jaume *et al.* 2001). Similarly, anchialine shrimps from the family Aytidae and genus *Typhlata* are found in the Caribbean Sea, along the Mediterranean and Adriatic coasts, and on oceanic islands in the Atlantic and eastern Pacific oceans (Alvarez *et al.* 2005). These widespread but disjunct distributions are surprising given that anchialine taxa have limited dispersal abilities. One explanation is that they represent old phylogenetic lineages that have persisted in subterranean refugia for long periods of time (Zuzek *et al.* 2007, Humphreys and Danielpol 2006). Many of these taxa are thought to be derived from marine or freshwater ancestors of the Miocene period that were separated during the split of Gondwanaland and the Tethys Sea (Iliffe *et al* 1984, Kano and Kase 2004, Zuzek *et al.* 2007). Subsequent rising and receding sea levels would have led to successive, sometimes repeated, colonization and isolation of fauna in anchialine pool and cave habitats (Humphreys and Danielpol 2006, Zuzek *et al* 2007). Ultimately, isolation led to allopatric speciation. This vicariance model could explain why anchialine taxa with common ancestry have widespread but disjunct distributions with high endemism at the species level (Iliffe and Kornicker 2009).

   An alternate hypothesis for explaining distributions of anchialine taxa is the long range dispersal of anchialine species across oceans by currents during larval and/or post larval stages (Danielopol *et al.* 1994, Kano and Kase 2004). For example, long range dispersal events could explain the distribution of the anchialine aytid shrimp *Antecaridina lauensis* documented at limited locations on Mozambique, Dahlak islands in the Red Sea, Solomon Islands, Ryukyu Islands, and the remote Hawaii Archipelago (Maciolek 1983). The Ryukyu and Hawaiian Archipelagos as well as some islands in the Atlantic Ocean are volcanic in origin and geologically young therefore dispersal via oceanic currents is more likely than the Tethyan vicariance model (Maciolek 1983, Kano and Kase 2004, Botello *et al.* 2012). Organisms with broad ecological tolerances and marine larval phases capable of high dispersal rates would be particularly suited to long range dispersal (Danielopol *et al.* 1994, Kano and Kase 2004, Page and Hughes 2007, Weese *et al.* 2012). A number of shrimp species, such as *Halocaridina rubra*, *Metabateaus lohena* and *Procaris hawaiana* from the Hawaiian Islands (Maciolek 1983), are endemic to single islands or archipelagos in the Pacific indicating that the open ocean is a strong barrier to dispersal (Craft *et al.* 2008, Weese *et al.* 2012). Population genetic analysis of the Hawaiian aytid shrimp *H. rubra* demonstrates that populations of endemic anchialine organisms may exhibit significant levels of genetic structure and restricted levels of gene flow at fine spatial scales of 20 km (Craft *et al.* 2008). Successful colonization of new habitat requires that species arrive, survive, and reproduce. This becomes less and less likely in highly remote areas such as the Hawaiian Islands which are approximately 2000 miles from the closest land mass. However numerous organisms have successfully colonized marine and freshwater habitats and evolved into endemic species in Hawaii making this process seem less rare than one might imagine (Kay and Palumbi 1987, Hourigan and Reese 1987, Jokiel 1987, McDowall 2003, Bowen *et al.* 2013).

In an ecological context, anchialine fauna live at the boundaries of marine and fresh water as well as surface and subterranean habitats. Within this matrix, salinity, oxygen, and light levels range from high to low with some portions of cave systems completely dark and anoxic (Sket 1996, Humphreys 1999). Some anchialine cave dwelling organisms have evolved features to survive in dark, low oxygen environments including reduced eyes, enhanced chemo-mechanical sensors, and reduced oxygen consumption (Iliffe and Kornicker 2009). While there have been few studies examining species specific tolerances, field observations indicate that while some taxa may have wide tolerance ranges others may be more restricted. In the Caribbean, anchialine caves typically possess a highly stratified water column, with surface layers of freshwater or brackish water underlain by marine waters (Iliffe and Kornicker 2009). In these caves, remipedes inhabit the underlying marine component (Neiber *et al.* 2011) while caridean shrimp and amphipods may exist in fresher waters above the halocline (Debrot *et al.* 2003, De Grave *et al.* 2008). The halocline is also associated with sharp changes in oxygen, water chemistry and hydrogen sulfide that is associated with chemoautotrophic bacteria (Humphreys 1999). In Caribbean caves and Pacific pools, some atyid shrimp species are found in wide salinity ranges from near freshwater (< 1 parts per thousand, ppt) to marine (> 35 ppt) (Maciolek 1983; Alvarez *et al.* 2005). In the laboratory, *H. rubra* tolerated salinities of ~0–56‰, (Holthuis 1973) acting as both a hyper- and hypo-osmoregulator (Haviland *et al.* 2014). Furthermore, some anchialine species, such as the aytid shrimp *H. rubra* and *M. lohena* as well as the gastropod *Neritilia*, live in brackish conditions as adults but have marine adapted larvae (Couret and Wong 1978, Kano and Kase 2004).

Studies on the trophic ecology of anchialine communities show that anchialine fauna may utilize several sources of energy. In pools and cave mouths, diatoms and macroalgae as well as terrestrial plant litter are available to gastropod and crustacean consumers (Maciolek 1983, Bailey-Brock and Brock 1993). However in caves, anchialine species exist in the dark and photosynthetic energy sources are not always available. Using stable isotope data, Pohlman *et al.* (1997) showed that at least three sources of organic nutrients support anchialine food webs in Yucatan caves including: soil from the overlying forest, freshwater algae from the adjoining open water pools, and chemoautotrophic bacteria in the cave. In some Australian caves, rootmats from surface vegetation may provide energy for anchialine organisms (Eberhard 2004, Humphreys 2006). Stable isotope data suggests that cave dwelling aytid shrimp utilize sulphide-oxidising chemoautotrophic bacteria in Australia (Humphreys 1999) and in the Yucatan (Pohlman *et al.* 1997). These bacteria are common in anoxic portions of anchialine cave systems, thus making these systems at least partially independent from the surface much like deep-sea vent communities (Engel 2007). Upper trophic levels consist of amphipods, remipedes, cave fish, and shrimp which may scavenge or consume other arthropods (Pohlman *et al.* 1997, Iliffe and Kornicker 2009). In general, cave systems are characterized by low amounts of potential food and faunal densities are typically low (Iliffe and Kornicker 2009). By contrast, anchialine pools may harbor high densities of shrimp (hundreds of individuals per square meter) presumably because of greater food availability through primary productivity (Maciolek 1983, Marrack personal observation). In some locations such as Hawaii, limited human access to subterranean portions of the anchialine system make it difficult to examine the possibility that organisms below the ground surface are utilizing chemoautotrophic energy pathways similar to anchialine fauna elsewhere.

Threats to Anchialine Ecosystems

Although anchialine ecosystems are high in biodiversity and harbor unique, little understood species, they are threatened worldwide by infilling, groundwater contamination, groundwater withdrawal, introduced species and sea level rise. Mining, quarrying, and coastal development have caused habitats to collapse and/or be filled in with rock or sediment (Iliffe 1979, Maciolek and Brock 1997, Boulton *et al.* 2003, Humphreys 2006). In many areas where anchialine ecosystems are formed, highly porous substrate means that groundwater can easily be contaminated by polluted surface waters (Boulton *et al.* 2003, Thornberry-Ehrlich 2011). For example groundwater pollution threatens anchialine pool biodiversity on the island of Bermuda where sewage and other wastewater enters cesspits or is pumped down boreholes contaminating the groundwater with nitrates, detergents, toxic metals, and pharmaceutical (Iliffe and Kornicker 2009). Groundwater withdrawal in arid regions such as Australia can lower the water table thus jeopardizing isolated endemic anchialine fauna (Boulton *et al.* 2003). Groundwater quantity and quality are a great and growing issue for human populations around the world (Giordano 2009), especially because many areas where water is scarcest may become even drier with climate change (IPCC 2013). Plentiful, uncontaminated groundwater supplies will be important for humans as well as anchialine fauna in the future.

Loss of endemic biodiversity due to introduced species has been well documented in ecosystems worldwide (Vitousek *et al.* 1997, Simberloff 2010, Lockwood *et al.* 2013). Published research on introduced species effects on anchialine biota has focused on introduced fishes in Hawaiian anchialine pools. Poeciliids (*Gambusia affinis* and *Poecilia reticulata*) were introduced to Hawaii as early 1905 for mosquito control (USGS 2014). Tilapia were introduced in the 1950s for aquatic weed control, bait and food (Randall 1987). Coastal surveys of the Island of Hawaii from the 1970's showed that out of 318 anchialine habitats visited, approximately 7% had introduced poeciliids and 7% had Tilapia (Maciolek and Brock 1974). Since then the number of pools with introduced fishes has greatly increased (Brock and Kam 1997). However, regional analysis of the true percent of pools containing introduced fishes is lacking.

In Hawaiian anchialine pools, invasive fishes prey on the candidate endangered damselfly *Megalagrion xanthomelas* (Englund 1999), the dominant herbivorous aytid shrimp *H. rubra* (Brock and Kam 1997, Capps *et al.* 2012), and probably other rare shrimp species. In response to the presence of the mosquitofish *Gambusia affinis*, *H. rubra* change their behavior and begin hiding in the lava substrate during the day, only grazing in pools at night when fish are inactive (Capps *et al.* 2009, Carey *et al.* 2012, Sakihara 2012, Havird *et al.* 2013). Havird *et al.* (2013) examined the gut contents of invasive poeciliids (*Gambusia affinis* and *Poecilia reticulata*) from four anchialine sites. Predation on endemic *H. rubra* was only documented for one site and in low numbers indicating that the diel shift in behavior adopted by *H. rubra* in the presence of introduced fishes is a successful strategy for avoiding predation. Gut contents showed that poeciliids utilized terrestrial invertebrates such as amphipods, ants, mites and other winged insects more than *H. rubra*. Stable isotope data indicates *G. affinis* may also utilize algae as a food source (Capps *et al.* 2009).

Elimination and reduction of grazing by *H. rubra* has been suggested as the primary mechanism for ecosystem phase shifts resulting in rapid macroalgal accumulation, eutrophication, and pool senescence (Brock 1987, Brock and Kam 1997). Manipulative studies by Dalton *et al.* (2013) showed that pools with invasive fish had higher epilithon biomass, productivity and nutrient content compared to pools without fish. However, while some pools with introduced fishes appear to have degraded water quality, many do not show evidence of

macroalgal growth or eutrophication (Marrack, personal observation). Determining the specific affect of introduced fishes on anchialine ecosystems would be helpful for management.

Evidence strongly suggests that groundwater pollution could compound loss of grazing and lead to anchialine pool degradation. Eutrophication caused by excessive inputs of nutrients (nitrogen, phosphorus) is one of the most common causes of impairment of surface waters in the United States (Carpenter et al 1998, US EPA 2004). Elevated nutrients, especially when combined with loss of grazer capacity, often results in increased primary producer biomass (Gruner *et al.* 2008) and major shifts in ecosystem structure and function (Folke *et al.* 2004). Sewage enriched irrigation water, storm water runoff, fertilizers, and septic/cesspool effluent can leach through porous basalt or karst substrate into groundwater and flow into anchialine pools. Although anchialine pool nutrient levels in Hawaii may vary naturally, monitoring has shown that pools in proximity to developments have had significant increases in nutrients after project build out (Jackson and Rosenlieb 1989, Brock and Kam 1997, Weigner *et al*. 2006). The long-term effects of elevated nutrients on anchialine pools, especially when combined with introduced predators, are presently unknown. Determining the role of introduced predators and groundwater pollution on anchialine ecosystem degradation is extremely important for managers so that they can target resources for successful outcomes.

Sea level fluctuations have been a naturally occurring process over geologic time with sea levels as much as 100 to 200 meters higher 80 million years ago (Miller *et al.* 2011) with the last sea-level low stand at 120 m below present levels during the Last Glacial Maxima 18,000 years ago (Miller *et al.* 2005). With marine transgressions, flooding of habitats allows organisms to disperse into new areas, sometimes connecting formerly separated habitats and taxa (Humphreys 2006, Zaksek *et al.* 2007). Conversely, marine regression or relative sea level drop, may fragment or isolate habitats and species (Moritsch *et al.* 2013). Coastal ecosystems have been modified by successive marine transgressions and regressions throughout geological time (Miller *et al.* 2011). Currently sea levels are expected to rise up to 1.9m by 2100 (Vermeer and Rahmstorf 2009, Parris *et al.* 2012). Coastal ecosystems are expected to persist under sea level rise if they are allowed to shift inland (Woodroffe 1990, Kirwan and Magonigal 2013). However, human structures such as sea walls, levees, pavement and urban landscapes will prevent the natural processes of ecosystem shifts inland (Mawdsley *et al.* 2009, Stralberg *et al.* 2011). Accurate models of sea level rise inundation are lacking along most coastlines and have only just begun to become available within the last five years for the planning community (Marrack and O'Grady 2014). High resolution geospatial models are necessary for planners and managers intending to protect coastal ecosystems and biodiversity.

Hawaiian Anchialine Pools

Hawaiian anchialine pools are the only known anchialine ecosystems in the United States other than the anchialine caves within the territory of Puerto Rico. Other aquatic karst cave habitats do exist in the lower 48 but these are neither brackish nor do they have subterranean connection to the ocean (Culver *et al.* 2000). Hawaiian anchialine systems support seven candidate endangered invertebrate species including decapods shrimp and an endemic damselfly (US FWS 2011). In Hawaii, pools and caves exist primarily on the younger islands of Hawaii and Maui, especially in geologically young lava flows (< 100,000 years before present) that usually have little to no soil development (Maciolek and Brock 1974). Presumably, as soils develop and plants colonize, sedimentation increases in pools eventually filling in pools and blocking passageways for anchialine fauna to move (Maciolek and Brock 1974). Several pool

complexes exist on Oahu (Craft *et al.* 2008) but none are described on Kauai or Niihau, the oldest high islands in the archipelago. Interestingly, Oahu does have large areas of karst caves (Halliday 1998). These are described as heavily impacted by construction as well as containing poor water quality and introduced fishes. There is no mention in the literature whether Hawaiian anchialine pool shrimp, characteristic of most Hawaiian anchialine pools and caves (Maciolek and Brock 1974), have ever been observed in these urban karst habitats. However, the U.S. Fish and Wildlife Service recently restored pool habitat in karst platforms near the Honolulu Airport on Oahu and, after seven months, endemic anchialine shrimp populated pools (Lorena Wada US FWS, personal communication). It is quite possible that endemic shrimp live in subterranean karst and lava habitat that has not yet been explored.

Since the initial island-wide survey of anchialine pools was completed in the 1970's (Maciolek and Brock 1974), a great deal of development has modified Hawaii's coastal environment, invasive species have dispersed to many pools, and an un-quantified number of pools are presently in a degraded state (Brock and Kam 1997). Furthermore, when this project was initiated in 2010, state and county planning had not yet begun to incorporate sea level rise projections into coastal land-use planning. Coastal development permits allowed approximately five meter buffers between pool edge to hardened structures with less buffer required between golf course turf or landscaped vegetation. The goal of this dissertation was to document the status of anchialine pool habitats along the western and southern coastlines of the Island of Hawaii and to provide data and tools to assist managers and planners with protection of this unique ecosystem and the organisms that depend on it. In Chapter 1, I describe methods for creating sea level models that incorporate groundwater heights and assess the accuracy of various models based on their ability to detect known anchialine pools under current water level conditions. Groundwater has rarely been incorporated in sea level rise models but is shown to be much more realistic for current conditions than simple inundation models. Chapter 2 summarizes results from habitat assessments of over 400 anchialine pools. Univariate and generalized additive models were used to determine the relative effects of pool characteristics, invasive species, water properties, and land-use on endemic shrimp occurrence. In Chapter 3, I determine the extent of anchialine pool inundation and the probable number, location, and size of future pool complexes within different land use types under various sea level rise scenarios. I also examine the extent to which elevated water levels will aid in the dispersal of introduced fishes from current locations to future pool habitats under various sea level rise scenarios. In Chapter 4, I look at the effects of introduced fishes on anchialine pool habitats using survey data and stable isotope data. Finally, I summarize results and management implications in the Conclusion Chapter.

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Acknowledgements

CHAPTER 1

Incorporating Groundwater Levels into Sea Level Detection Models for Hawaiian Anchialine Pool Ecosystems

Abstract

As sea levels rise, the distribution and community structure of coastal ecosystems are expected to change. In many coastal aquifers, fresher groundwater floats on top of denser saltwater and will rise with sea level. Under these conditions, ecosystems dependent on groundwater may shift inland as a result of inundation, changes in salinity, or both. Groundwater-fed anchialine pool habitats existing in porous coastal substrates around the world have not been assessed for sea level rise impacts. As a first step toward examining ecosystem response to rising water levels, geospatial models were developed to detect anchialine pools on the island of Hawai'i at current water levels and models were validated with known pool locations. Specifically the objectives were to determine whether accounting for groundwater levels in the model improved pool detection, to identify the model that most accurately detected known pools, and to identify which pool features make some pools more likely to be detected than others. Six water level models were validated with the test data set of actual pool locations to determine how well they detected known anchialine pools. Water surface models that included groundwater levels were up to 37% better at detecting anchialine pools than corresponding models without groundwater levels. The model that included groundwater levels at mean higher high water was applied to 42 km of coastline where it correctly detected 62% of known pools. A generalized linear model showed that pools with surface areas greater than 5 m^2 and pools without canopy were the most likely to be detected. Future predictive modeling of anchialine pool response to sea level rise should include groundwater levels. Furthermore, geospatial models aimed at predicting ecosystem shifts due to sea level rise may be improved by including groundwater as a factor and should be validated using current ecosystem conditions.

Additional Index Words: Sea level rise; light detection and ranging (LiDAR); Model validation; tidal efficiency; accuracy assessment

Introduction

Global mean sea levels (MSLs) are expected to rise between 0.75 and 1.9 m by 2100 depending on various climate change scenarios (Vermeer and Rahmstorf, 2009). Sea level rise and changes in storm run-up during large surf events will affect coastal habitats and resources worldwide (IPCC, 2007; Nicholls and Cazenave, 2010; Williams, 2013). Ecosystem community structure and distribution are expected to change due to inundation, erosion, saltwater intrusion or a combination of these (IPCC, 2007). Many ecosystems may migrate inland if open space is available and conditions are suitable (Stralberg *et al.*, 2011; Woodroffe, 1990). Conservation of coastal ecosystems can be enhanced if accurate predictions of temporal and spatial change are available.

Geospatial predictions of coastal ecosystem change under sea level rise typically include elevation data and eustatic sea level scenarios (Dasgupta *et al.,* 2009; Gesch, 2009), but may also incorporate local subsidence, tidal variation, wave dynamics and shoreline erosion models (*e.g.* Jaffe *et al.*, 2011; March and Smith, 2012; Reynolds *et al.* 2012; Stralberg *et al.*, 2011). Predictive models including some or all of these factors have been applied to wetlands (Geselbracht *et al.*, 2011; Rogers, Saintilan, and Copeland*,* 2012; Stralberg *et al.*, 2011, Trail *et al.*, 2011), mangrove forests (Doyle *et al.*, 2010; Woodroffe, 1990), dune systems (Young *et al.*, 2011), and tidal freshwater forests (Doyle *et al.*, 2010). Some studies have modeled the effects of saltwater intrusion on groundwater salinity (Sherif and Singh, 1999; Werner and Simmons, 2009). Only a few have incorporated groundwater levels into models of ecosystem response to changing sea levels (Rotzoll and Fletcher, 2013).

Groundwater

In coastal regions, groundwater can play an important role in the location and community composition of ecosystems, especially those located slightly inland from shore. For example, tidal freshwater forests found along the U.S. Gulf and Atlantic coasts are at the upper elevation of the tidal exchange and are reliant on freshwater flow through the substrate (Doyle *et al.*, 2010). Field observations and models show that rising sea levels and coastal subsidence lead to saltwater intrusion and increased flooding resulting in a shift from the tidal forest biota to more salt-tolerant mangrove or wetland vegetation (Doyle *et al.*, 2010). In unconfined coastal aquifers, the groundwater table is elevated above MSL sloping up and away from the shoreline and typically moves in response to changes in ocean level (Bjerklie *et al.*, 2012; Oki, 1999). As a result, groundwater may exacerbate inundation as sea levels rise (Bjerklie *et al.*, 2012). Rotzoll and Fletcher (2013) modeled flooding in urban Honolulu, Hawaiʻi due to sea level rise and found that when groundwater levels were included in the model, the flooded area was more than twice as large as it would be without groundwater levels. Because coastal ecosystems may be sensitive to changes in groundwater levels or salinity, groundwater should be included in models predicting ecosystem shifts under sea level rise.

Anchialine Pools

Anchialine pools are brackish coastal ecosystems without surface connection to the ocean, where groundwater mixes with saltwater derived from the ocean (Holthuis, 1973). Pools are common in neotropical coastal areas, such as the Yucatan (Sanchez *et al.*, 2002) and the Indo-Pacific (Holthuis, 1973; Webb*,* Grimes, and Lewis*,* 2010) where porous substrates, such as karst or lava, provide good hydrologic connectivity between groundwater and ocean. In Hawaiʻi, groundwater flows through pools and out to wetlands and coral reefs making pools indicators of broad-scale groundwater recharge and contamination (Knee *et al*., 2008). Hawaiian anchialine pools are tidally influenced, range from less than 1 to about 3000 m^2, and support diverse endemic biota (Maciolek and Brock, 1974), including seven species listed as Candidate Threatened or Endangered Species (USFWS, 2011). Pool endemic shrimp are typically found in salinities ranging from 2 to more than 25 parts per thousand (ppt; Maciolek, 1983; Maciolek and Brock, 1974) however, it is unclear whether the apparent wide salinity tolerance pertains to all life stages. There is some evidence for intolerance of low salinities for some species (Sakihara, 2012). Anchialine pool shrimp and mollusk species disperse across oceans as larvae and through

groundwater as larvae or adults (Craft *et al.*, 2008). Endemic species are known to rapidly colonize newly excavated pools. For example, pools on Oʻahu that had been filled in decades earlier were excavated and restored by the US Fish and Wildlife Service (USFWS). Within 2 months, the dominant grazing shrimp *Halocaridina rubra* colonized the restored areas even though the closest pools are more than 20 miles away (Lorena Wada - USFWS, personal communication). Due to their ability for widespread dispersal and their wide tolerance of salinity, there is potential for endemic species to populate new pools created by sea level rise.

Conservation actions are needed to protect the anchialine pool ecosystem in Hawaiʻi. On the west coast of the island of Hawaiʻi, rapid coastal development has caused approximately 10% of pools to be filled in since the 1970s (Brock, 1987). An unknown number of remaining pools are affected by nutrient loading (Weigner *et al.*, 2006) and the introduction of nonnative fishes that prey on native grazers (Capps *et al.*, 2009; Chai, 1989). Intact systems still exist, but many are expected to be inundated as sea levels rise, merging them with nearby wetlands or rocky marine systems. In some areas, sea level rise may also provide invasive fishes potential pathways of dispersal into uninfected pools. Because anchialine pool ecosystems have good potential for inland migration as sea levels rise, fine-scale geospatial models predicting future pool locations would be useful for conservation planning efforts.

To date, no published studies examine the effects of sea level rise on anchialine pool ecosystems. As a precursor to predicting the ecosystem response to sea level rise, the goals of this study were to develop fine-scaled geospatial models to detect anchialine pools along the west coast of the island of Hawaiʻi at current water levels and to validate the models with actual pool locations. Specifically the objectives were to (1) determine whether accounting for groundwater levels in the model improved pool detection and identify the model that most accurately detected known pools, (2) quantify model error with values of pool omission and commission (false positive), and (3) determine which pool features make some pools more likely to be detected than others. Multiple water level models were validated with a test data set of actual pool locations to determine how well they detected known anchialine pools. Models incorporated Light Detection and Ranging (LiDAR)- derived Digital Elevation Models (DEMs), sea level, and groundwater levels. The best models and the error analysis will be incorporated into future work predicting effects of sea level rise on anchialine ecosystems.

Study Site

This study occurred on the arid west coast of the island of Hawaiʻi at two spatial scales (Figure 1). Annual rainfall in the study areas ranges from 250 to 500 mm/y (Giambelluca *et al.*, 2011). The first study unit, the Kaloko-Honokōhau National Historical Park (KAHO) site, includes anchialine pools along 3.5 km of coastline within KAHO and state lands just south of the park (Figure 1c). The second area includes pools along 42 km of shoreline from south of Kawaihae to the pools south of KAHO (Figure 1b). These areas fall within a coastal corridor that encompasses one of the highest concentrations of anchialine pools in the world (Brock and Kam, 1997). Pools within these sites have salinities ranging from less than 2 to more than 25 ppt and naturally occur up to 430 m inland (Maciolek and Brock, 1974). The pools are considered subaerial expressions of groundwater, and along with groundwater in wells, are tidally influenced (Holthuis, 1973; Maciolek and Brock, 1974; Thornberry-Ehrlich, 2011). Some shallow pools do become dry at low tide but are populated with endemic shrimp when the groundwater surface rises at higher tides.

Groundwater in west Hawai'i is found in two main forms: (1) a lens-shaped body of freshwater or brackish water floating on denser saltwater within permeable lava flows near the coast and (2) freshwater that is impounded at high levels within the inland part of the aquifer (Bauer, 2003; Oki, 1999). The elevated water levels are thought to be impounded by low-permeability subsurface rocks such as faults, dikes, low-permeability lava flows, or weathered ash layers and is where most drinking water is extracted (Oki, 1999). The low-elevation coastal groundwater ranges from fresh to brackish and slopes inland at a gradient between 0.2 and 0.6 m/km (Bauer, 2003). Long-term measurements by the U.S. Geological Survey (USGS) have shown that mean groundwater levels are as high as 0.3 m above MSL at 0.1 km from the shoreline. Flow direction is from upslope recharge areas to the coastline where groundwater naturally discharges offshore onto coral reefs (Grossman *et al.*, 2010; Johnson *et al.*, 2008; Oki, 1999). Salinity typically increases with depth and decreases with distance from the ocean (Bauer, 2003), a pattern also seen in anchialine pools (Bienfang, DeFelice, and Laws, 2011). The low slope of the groundwater surface away from the shoreline and the clear influence of tidal variation suggest a permeable, unconfined coastal aquifer with high hydraulic conductivity (Bauer, 2003; Oki, 1999).

Generally, subsurface lava composition and flow structure determine aquifer permeability in this region. Thin-bedded permeable basaltic pahoehoe (smooth) and a'a (rough) lava flows from Mauna Loa and Hualalai shield volcanoes form much of west Hawai'i. In some areas low-permeability trachyte lavas have been documented (Cousens, Clague, and Sharp, 2003) and are assumed to locally impede groundwater flow. Measurements of hydraulic conductivity using tidal response of groundwater levels in the Kona coast areas of west Hawai'i range from 100 to 10,000 m/d (Oki, 1999). Surface lavas in the study area are less than 10,000 years old with the most recent flow from AD 1801 (Wolfe and Morris, 1996). Well bore data indicate that in some areas subsurface basalts are 92,000 to 107,000 years old (Cousens *et al*., 2003). The young rock is relatively unweathered compared to wetter, older areas on the Island of Hawai'i or on other islands, and this contributes to the relatively high permeability of the rock.

Because of the excellent subterranean hydrologic connectivity between the coastal areas and the ocean, semidiurnal tidal oscillations are observed in anchialine pools (USGS, 2012) and coastal groundwater wells (Oki, 1999; USGS, 2012). USGS records from wells in the KAHO area for 2009-10 show that 0.2 km from shore, groundwater had a 0.74-m maximum annual tidal range which was 70% of the ocean tide range. At 3.6 km inland, the maximum tidal range was 0.27 m or 25% of the ocean tide range. On the west coast of the island of Hawai'i mean higher high water (MHHW) is 0.374 m above MSL (Kawaihae Tidal Benchmark 1617433B, Figure 1a). The highest observed tide level at the Kawaihae tide gauge was in 1993, when it was at 0.743 m above MSL (NOAA, 2012). Tide height varies seasonally with the highest tides in August and the lowest in March and April (Figure 2). This seasonal pattern of tides has also been measured in wells and anchialine pools with in situ continuous loggers by the USGS. Local sea level rise has been recorded at island of Hawai'i tide gauges at a rate of 3.5 mm/y which reflects regional eustatic sea level rise combined with island subsidence (Vitousek *et al*., 2010). As sea levels rise, groundwater in porous unconfined aquifers is also expected to rise eventually causing increased salinities in existing wells and pools. Surface depressions that are low enough in elevation will fill at high tides and become new pool habitats. Due to the connection between ocean and aquifers in porous coastal areas, inundation by groundwater is an unavoidable consequence of rising sea levels and should be incorporated into sea level rise predictions.

Methods

To model current anchialine pool locations, sea surface and groundwater levels above MSL were combined into raster surfaces in Environmental Systems Research Institute's (ESRI's) ArcGIS 10.0. These water surfaces were then compared to topographic surfaces (DEMs) to determine where anchialine pools would be expected to occur. Areas where the water surface was higher than the topographic surface were classified as water bodies. These models were validated with actual pool locations obtained with a high-resolution Global Positioning System (GPS). The best model was selected based on the highest number of correctly identified pools, the relatively low numbers of falsely classified pools, and observed coastal inundation. To determine which features make some pools less likely to be detected than others, the best model was then applied to a larger area of the coastline. Generalized linear models (GLMs) were used to examine the relationship between pool detection and pool characteristics (size, canopy, and pool morphology).

Model Input Data

Digital Elevation Models

Topographic data were derived from Federal Emergency Management Agency (FEMA) – LiDAR data collected in 2006 for the Hawaiian Islands (Dewberry and Davis Corp., 2007). The LiDAR data were collected as discrete returns with scanning airborne laser altimeters and extend from the waterline to the 15-m elevation contour. The LiDAR was not water penetrating therefore points over water bodies represent water surface elevations at the time of data collection. Coverage includes the western and southern coastlines of the island of Hawai'i with an average point distance of 0.9 m for bare earth returns. Data were horizontally referenced to the North American Datum 1983 and were reported as horizontally accurate to 0.3 m with 68.2% of laser returns. The North American Vertical Datum 1988 is specific to the Continental United States and does not exist for Hawai'I; therefore, the vertical datum was referenced to a Local Tidal Datum established by the National Geodetic Survey (NGS) with 0 m as MSL.

Digital elevation models were created from the LiDAR bare earth returns using ESRI's ArcGIS. First, Triangular Irregular Networks (TINs) were created from LiDAR point files. The TINs were then converted to a raster format (1-m grid) using linear natural neighbor interpolation. This interpolation technique constructs DEMs that retain original peak and valley elevation values which is useful for finding small isolated pits that exist in the lava surfaces (Longley *et al.*, 2005; Maune, 2007).

DEM validation and correction

Initial analysis of FEMA- LiDAR data over ocean surfaces indicated that either LiDAR data were collected at high tides or that some vertical correction was necessary. In the 1-km area around the Kawaihae tidal benchmark, the mean elevation of LiDAR points over the ocean surface was 0.3 m above MSL. For most of the west coast corridor including the KAHO study area, ocean surfaces captured by LiDAR data were elevated by 0.5 m or more over MSL. These elevations could be explained by high tides. The MHHW at the Kawaihae tidal benchmark is 0.374 m, and the highest tides measured in August 2006 when the LiDAR was collected were 0.61 m above MSL. Because the LiDAR metadata do not indicate tidal stage or date and time of

collection, the tide height during LiDAR collection could not be confirmed. Due to uncertainty in LiDAR accuracy and concern that LiDAR errors would propagate directly to the DEMs used in this study, the LiDA-derived DEMs were examined for vertical offset prior to pool detection analysis.

To assess DEM elevation accuracy, DEM elevations were compared to NGS benchmark elevations using the methods described by Cooper *et al.* (2012). Benchmarks in the accuracy assessment included the Kawaihae tidal benchmark -1617433B (NGS, 2012) along with five NGS benchmarks surveyed in the KAHO area in 2009. Other NGS benchmark location data available in the study region were not of high enough resolution to include in the accuracy assessment. The orthometric elevations for the benchmarks were derived using the NGS GEOID12A model for the Kawaihae tidal benchmark and GEOID03 for the 2009 benchmarks. All benchmark orthometric elevations are relative to the Local Tidal Datum of MSL defined by the 1983-2001 Tidal Epoch. The LiDAR elevation data were derived using the NGS GEOID03 model and were referenced to an adjusted Local Tidal Datum. Original LiDAR data processing by Airborne One, the company that collected the data, included vertical adjustments of + 0.16 m to account for offset detected during accuracy assessment surveys and - 0.031 m to account for sea level rise (McGee Surveying Consulting, 2007). Therefore, although NGS benchmark and LiDAR elevations are both relative to MSL, elevation differences due to data processing needed to be assessed.

As described in Cooper et al. (2012), LiDAR DEM elevations were compared to associated benchmark elevations. The average difference between the LiDAR DEM elevations and NGS benchmark elevations was 0.25 m (Table 1). The Root Mean Square Error (RMSE) was 0.19 m. At the time of collection FEMA-LiDAR data were assessed for accuracy using independent checkpoints by Dewberry and Davis Corp. (2007) which reported that for bare earth surfaces the mean vertical error of LiDAR points was 0.03 m (RMSE = 0.08m). The mean error for all terrain types was reported as 0.05 m (RMSE = 0.11 m). Because the mean difference between the LiDAR DEM elevations and the NGS benchmark orthometric heights was an order of magnitude higher than the reported vertical error, the LiDAR DEM elevations were corrected by -0.25 m for subsequent analysis.

Water Surface Models

Water surface models were created to represent a range of sea levels combined with groundwater levels (Table 2). Sea levels included here were 0 m, 0.374, and 0.74 above MSL. The 0.374-m value represents the MHHW datum at the Kawaihae tidal benchmark. The 0.74-m value represents the highest tide observed at the Kawaihae tide gauge between 2001-11 (NOAA, 2012). Three models were created to represent each sea level height with no groundwater component, while three additional models were created to represent each sea level height including groundwater.

<u>Groundwater Surface Models</u>

Groundwater surface models were created by combining measured groundwater levels above MSL and tidal influence on groundwater with distance from shore. Groundwater level data for coastal wells along the western and southern shorelines of the island of Hawai'i were obtained from the USGS (2012). Like the LiDAR data, these groundwater level data are referenced to the Local Tidal Datum. A subset of nine sites (six wells and three anchialine pools)

clustered within and around KAHO was selected to create the groundwater models because they are the only records within the study areas with recent long-term continuous measurements located near anchialine pools (Figure 1c). Data were recorded every 10 minutes from these sites from March 2009 to September 2010. Sites had the most complete records between June 18, 2009 and August 17, 2010 therefore, this time frame was used for summary statistics on groundwater levels. For each site, mean groundwater levels, as well as daily, monthly and mean tidal ranges, were calculated.

Observed mean groundwater levels were used to create a groundwater surface model for the KAHO site. Using the equation of Glover (1959), groundwater levels in an unconfined, homogenous aquifer are expected to be a function of the square root of distance from the shoreline:

$$h = \sqrt{\frac{2(\rho_s - \rho_f)qx}{\rho_s K}} \tag{1}$$

Where:
h = groundwater level above MSL (in m).
ρ_s = saltwater density (in kilograms per cubic meter) .
ρ_f = freshwater density (in kilograms per cubic meter).
x = distance to the coastal boundary (in meters).
q = freshwater flow per unit length of shoreline (in square meters per day)
K = hydraulic-conductivity (in meters per day)

By letting all components of the equation but the groundwater level h and the square root of the distance from the shoreline x become a constant, h can be predicted using x. Linear regression analysis was used to determine the relationship between the observed mean groundwater levels h and the square root of the distance from the shoreline x. The resulting relationship was used to predict a simplified two-dimensional groundwater surface in the KAHO site assuming a homogenous, steady-state aquifer (Rotzoll and Fletcher, 2013). First a Euclidean distance raster with respect to the shoreline (2 m^2 resolution) was created. Next a groundwater level raster was calculated by applying equation (1) to each pixel within the distance raster. Each pixel within the resulting groundwater surface raster represented mean groundwater level above MSL at that location when the ocean surface is at MSL.

To incorporate tidal effects on groundwater levels, a tidal efficiency raster was also created for the KAHO site. Tidal effects decay with distance inland from shore and can be represented by the tidal efficiency, which is the ratio of mean daily groundwater tidal range at a site to mean daily ocean tidal range at the tide gauge. Tidal efficiency is 1 at the shoreline, decreasing to 0 inland where no tidal effect exists (Ferris, 1951; Jacob, 1950). For the period between June 18, 2009, and August 17, 2010, tidal efficiency was calculated for the same nine pool and well sites used to create the groundwater surface raster, along with a 10th site representing the ocean surface where tidal efficiency equals 1 (Figure 1c). Ocean tidal ranges used in tidal efficiency calculations were collected from the Kawaihae tide gauge (NOAA, 2012). The natural logarithm of tidal efficiency is linearly related to the distance from the shoreline within a homogeneous, semi-infinite aquifer (Todd, 1980). Although the aquifer in the

study area is neither semi-infinite nor homogeneous, this model represents the general observed behavior of the tidal response in the aquifer. Once a log-linear equation was determined from the observed data, a tidal efficiency raster surface for the KAHO site was calculated by applying the equation to each pixel within the Euclidean distance raster. The three water models that incorporate groundwater were created by multiplying the tidal efficiency raster by each sea level height (0, 0.374, and 0.74 m) and adding this tidal component to the mean groundwater level above MSL raster. Depending on the interaction of individual tidal constituents during extreme tides, the estimated average tidal efficiencies may not necessarily reflect actual tidal efficiencies; however, for simplicity, the average tidal efficiencies were assumed to be reasonably representative of the aquifer tidal response during extreme high tides.

Current Anchialine Pool Locations

Current anchialine pool location data were used to validate water surface models. Point feature data were created by the National Park Service for 215 pools located within and adjacent to KAHO along 3.5 km of coastline (Figure 1c). The point data were collected at the edge of each pool with a Trimble GeoXT GPS for 2007-09 and were differentially corrected. All pools sit within the area bounded by the groundwater level measurements collected by the USGS for 2009-10 and were therefore used to validate and select the best water level model.

During July and August 2012, location and feature data were collected along the coastal corridor for an additional 141 pools (Figure 1b). Pool perimeters were obtained with a Trimble GeoXH using real-time and postprocessed differential corrections using local continuously operating reference stations for highest accuracy. Pool surface area at high tide, canopy cover, and morphology data were collected at all pools. The most accurate water level model for the KAHO site was applied to the larger anchialine pool data set along a 42-km section of coastline (Figure 1b). Detection results were then used to examine which pool types are most likely to be detected with groundwater models.

Pool Detection: Model Testing and Validation

To compare the accuracy of water surface models, each model was first used to predict pool locations within the KAHO site using ArcGIS Spatial Analyst tools (ESRI, 2011). The water surface model was compared with the DEM. Where the topography was lower or equal to the level of the water surface, that area would be categorized as a water body. The resulting raster was converted to polygons of water surface.

Because the DEMs cover coastal areas, the ocean surface, tide pools, and large fishpond embayments were also categorized as water surface. To ensure that only anchialine pool type habitats were included in the analysis, water surface polygons were visually examined over Quickbird true color imagery (Digital Globe, 2006) and all features including ocean surfaces, shoreline features, and fishpond embayments were deleted. This process was duplicated for each water level model included in the analysis resulting in different predicted pool locations for each model.

Once pool locations were predicted using each water surface model, these were compared to actual pool locations. Because pools within the KAHO site were mapped as point locations, a 3-m buffer around each point was used as the pool location. The buffer accounted for horizontal errors in LiDAR or GPS data acquisition as well as variation in pool surface areas. Known pools were scored as correctly detected if predicted pools overlapped with any part of the 3-m buffer.

If models showed no water surface within the buffer, pools were scored as not detected. False detection of pools (commission) was also measured. Water surface polygons that appeared in models but were outside pool buffers were summarized with total counts and surface area statistics. Among the models with the most accurate shorelines, the model with the best detectability score and a relatively low false detection rate was considered the most realistic and was applied to the larger coastal area for the subsequent analysis.

Pool Detectability Analysis

To determine the factors that make some pools easier to detect than others, GLMs were used to examine the relationship between detection and pool characteristics. To incorporate more pools into this analysis, the best water surface model was applied to 42 km of coastline. Groundwater level data within this larger area are limited to measurements collected prior to 2002 at inland wells (Bauer, 2003; Figure 1b). Therefore, a modeled groundwater level raster surface with a 2-m resolution was calculated with the same methods used for the smaller KAHO area. The aquifer within the 42-km site was assumed to be homogeneous with properties similar to the KAHO site. The groundwater surface model was then used to predict pool locations. Predicted pool locations were compared against known pool locations and ranked as correctly or incorrectly detected. The methods were identical to those used for the smaller KAHO site except that a 0.5-m buffer was used for pools outside of KAHO because they were mapped as polygons instead of points.

Using logistic regression analysis, pool detection (success *vs.* failure) was modeled against three predictor variables: morphology, pool surface area, and canopy. Morphology indicated whether pools were open, in lava fissures, or in collapsed lava tubes underneath overhanging rock. Pool surface area (in square meters) was estimated at high tide from field measurements of length and width or from GPS polygon files. Canopy cover was recorded in the field as an estimation of percent cover. To use a continuous variable in a logistic regression, the effect of the explanatory variable must be linear to the response variable on the log odds scale which is calculated as the natural logarithm of the probability of successful detection divided by the probability of failed detection (Quinn and Keough, 2009). The pool surface area and canopy cover data did not fulfill this assumption and were therefore converted to binary variables for the analysis. Interactions between area and canopy cover were included in regression models; larger pools may have less canopy cover because tree branches have a limit to how far they can reach over a pool. The full model is:

$$g(x) = \beta_0 + \beta_1(\text{Morph}) + \beta_2(\text{Can50\_100}) + \beta_3(\text{Area5\_20}) + \beta_4(\text{Areaovr\_20}) + \beta_5(\text{Hicanxarea}) +$$

$$\beta_6(\text{Hicanxhiarea}) \tag{2}$$

where *g(x)* is the natural log of the odds of successful detection of pools within the 42-km site and β indicates parameters to be estimated. β_0 is a constant (intercept) and $\beta_{(1-6)}$ are the regression coefficients (slopes), which measure the change in the *x* per unit change in the predictor variable (Table 3). Restricted models were compared against the full model using the likelihood ratio test and Wald test. To calculate relative risk values, which are useful for looking at the relative importance of variables, the same variables were used in a GLM with a binomial distribution, a maximum likelihood estimation, and a log link function. Because this model

would not converge, a GLM with a Poisson distribution, a log link function, and robust standard error was used instead (Zou, 2004).

Results

Water Surface Models

Linear regression analyses yielded expected relationships between groundwater levels and distance from the shoreline and were used to create the water surface models incorporated into pool detection analyses. There was a strong positive relationship between mean groundwater level and square root of distance from the shoreline for anchialine pools and wells within the KAHO study site (Figure 3b). Measured mean groundwater levels were 0.12 m above MSL at 0.33 km from shore and 0.76 m above MSL at 3.5 km from shore. Groundwater level data collected prior to 2003 within the larger study area (Figure 1b; Bauer, 2003) show that average groundwater levels at a particular distance from shore may more variable than those observed in 2009-10 at the KAHO site (Figure 3b), but that the trend found at KAHO generally applies to a broader spatial and temporal scale in west Hawai'i. As expected, tidal efficiencies (natural logarithm) at the KAHO sites decreased with increasing distances from shore (Figure 3a). Tidal efficiencies were 95% at 0.33 km from shore and 25% at 3.5 km inland. Therefore, a 0.5-m tidal oscillation in the ocean would add 0.13 m to the mean groundwater levels 3.5 km inland. Mean tide height at the Kawaihae tide gauge was 0.0008 m above the MSL datum during the period of data collection used to calculate groundwater levels and tidal efficiencies thus satisfying the assumption that groundwater models were relative to MSL.

Pool Detection: Model Testing and Validation

Detection success and false detection of pools were assessed for six water surface models at the KAHO study site (Table 4). Out of 215 known anchialine pools in the study area, 20 are known to be in narrow fissures (< 0.5 m) or in collapsed lava tube caves that the LiDAR did not detect and these were excluded from analyses. Water surface models that included groundwater levels were up to 37% better at detecting anchialine pools than corresponding models without groundwater levels. The model representing MSL without groundwater sloping up away from the coast was the least successful, detecting no pools (Table 4, Figure 4 & 5). The groundwater at MSL model detected only 4 of 195 pools. The model representing sea level at MHHW without groundwater detected 18% of pools correctly. Adding in mean groundwater levels at a MHHW resulted in the successful detection of 107 pools, increasing detection by 37%. The model representing sea level at an extreme tide correctly detected 73% of pools and was improved by 7% when groundwater was included in the model.

As success of pool detection increased, false detection or commission increased in both number of features and total area of features (Table 4, Figure 5). These "false pools" were visually examined over Quickbird imagery. For both MHHW models, more than 85% of false pools were located within large areas known to be covered in marsh vegetation such as *Batis maritima* (pickleweed) and *Paspalum vaginatum* (seashore paspalum). Previous work in these locations does confirms that at least some of these areas are wet at higher tides and are marsh type habitat (Figure 6). Removing commission errors within known marsh habitat greatly reduced false detection for MHHW models (Table 4). The groundwater at extreme tide model

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had the highest number of commission items with 61% not explained by marsh type habitat (Table 4). In the groundwater at extreme tide model, low-elevation areas that were detected as isolated pools in other models merged with ocean and fishpond surfaces; therefore, the total surface area calculated for falsely detected pools decreased (Figures 5c and f).

Visual observation of all model results over Quickbird imagery showed that the MHHW models represented the current shoreline best (Figure 5). The MSL models failed to detect the ocean surface completely because ocean surfaces were elevated above 0 m in the DEMs (Figures 5a and d). Both extreme tide models inundated coastal features that are not submerged at most high tides. In most parts of the coast, the shorelines represented by the extreme tide models were 1 to 5 m inland of the MHHW model shorelines, but in a few locations the extreme tide shoreline was up to 24 m farther inland than the MHHW shoreline. The groundwater at MHHW model was selected for the larger regional analysis because it had a relatively high pool detection rate (55%), was associated with a low false detection rate, and was the most representative of the current shoreline.

Pool Detectability Analysis

To determine which pool characteristics affect detection, the groundwater at MHHW model was applied to 42 km of coastal area containing a total of 356 pools. This included the 215 pools from the KAHO site along with 141 additional pools mapped in this larger section of coastline. The model did not detect any of the 42 pools found in deep narrow fissures or in caves, therefore these pools and the `Morph` variable were removed from the GLMs. An additional 3 pools without surface area data were also excluded, resulting in 311 pools that were included in the GLMs. Of these 311 pools, 62% were successfully detected by the model. Pool surface areas ranged from 0.2 to 3208 m^2 and were 79.6 m^2 on average. Canopy cover ranged from 0% to 100% with an average of 15.4%.

Using a significance criterion of $p = 0.1$, the full logistic regression model results showed that both interaction variables Hicanxarea and Hicanxhiarea were not significant, meaning that in this data set, pool size did not affect canopy cover. Therefore, a restricted model without these variables was tested. In the restricted model Can50_100, Area5_20, and Areaovr_20 all appeared to have significant effects on pool detection ($p < 0.01$; Table 5). Comparing the full *vs.* the restricted model with a Wald Test ($X^2 = 4.4$, df $= 2$, $\alpha = 0.05$, $p = 0.11$) and a likelihood ratio test ($G^2 = 4.29$, df $= 2$, $\alpha = 0.05$, $p = 0.12$) indicated that there was no difference between the full and the restricted models; therefore, the restricted model was used. Finally, the Hosmer-Lemeshow Goodness of Fit test, used to test the adequacy of a regression model (Quinn and Keough, 2009), indicated that there was no difference between the observed and the modeled results ($C = 4.69$, df $= 2$, $\alpha = 0.05$, $p = 0.1$).

To obtain relative risks, a GLM with binomial distribution and a log link function was run. This model did not converge, but the GLM with Poisson distribution, a log link function, and robust standard errors was successful (Zou, 2004; Table 5). The relative risk results indicate that when all other variables are held constant, pools with tree canopy greater than 50% are 0.7 times less likely to be detected than pools with 50% canopy cover or less. Also, larger pools are more likely to be detected than small pools. Pools of 5 to 20 m^2 are 1.7 times more likely to be detected and pools of more than 20 m^2 are 2.2 times more likely to be detected relative to pools of less than 5 m^2.

Examination of pool detection success by surface area and canopy categories supports the GLM results. Using the groundwater at MHHW model, 91% of pools larger than 20 m^2 were

correctly identified, but only 41% of pools smaller than 5m^2 were correctly identified (Table 6). Pools with less than 50% canopy cover were 64% correctly identified, whereas pools with greater than 50% canopy were correctly detected 47% of the time. Therefore, smaller pools and pools with high canopy were not detected as well by the geospatial model.

Discussion

Efforts to conserve coastal systems under changing climates have begun to include geospatial predictions of future habitat so that these land areas can be protected (Mawdsley, O'Malley, and Ojima, 2009). As sea levels rise, low-elevation coastal ecosystems will become inundated more frequently through the tidal cycle until they are eventually underwater 100% of the time. For coastal ecosystems that depend on groundwater, changes to groundwater levels and salinities may also drive shifts in community structure. Ecosystems may gradually migrate inland if conditions are appropriate and open space is available (Doyle *et al.*, 2010; Stralberg *et al.*, 2011). Decisions about which lands to protect can be helped by using models that predict future ecosystem location under climate change (Mawdsley, O'Malley, and Ojima, 2009). Predictive models will be most useful if they incorporate factors that are appropriate for the system of interest and can be validated using current or past data so that error and bias can be quantified.

In this study, groundwater levels were incorporated into anchialine pool detection models. The model that most realistically represented sea level and groundwater level was 37% better at detecting anchialine pools than the corresponding model that did not include groundwater. Therefore, groundwater levels should be incorporated into geospatial models intended to predict future pool location under sea level rise. False detection did occur but for models that incorporated realistic sea levels, commission was primarily in low-lying areas that contain *B. maritima* and other marsh vegetation or in areas of thick mesquite forest that have not been previously field checked for pool presence. These "false pool" sites may hold surface waters at some tide states.

Even the best model (groundwater at MHHW) failed to detect 45% of known anchialine pools within the KAHO site (Table 4) and 38% of pools within the 42-km section of coastline. One reason for the low success could be that the LiDAR data used to create the DEMs were not water penetrating. As a result, DEMs represented bare earth topography in dry areas and water surfaces over water bodies. Therefore, if the tide levels used in the water level models were lower than the tidal states during LiDAR collection, pools may have missed detection. Field surveys confirm that all pools used in the analysis, even pools that go dry at low tides, have water in them at high tide daily. Therefore, the water surface model incorporating the MHHW (0.374 m) level would be expected to correctly identify a large number of pools. The exact times and tidal stages during LiDAR collection could not be confirmed. During August 2006 when the LiDAR data were collected, the monthly mean of higher high tides was 0.36 m; however, some tides were higher, with a maximum tide of 0.61 m above MSL (NOAA, 2012). A water level model incorporating groundwater and a tide stage of 0.61 m would improve pool detection at the KAHO site (Figure 4) but would still fail to detect 14.5% of pools. Pool elevations derived from the DEMs have a wide distribution and do not indicate a "best" tide state to incorporate into the groundwater level model. Fortunately, this issue becomes less important for predicting habitat distribution under sea level rise scenarios, because future pools will emerge in low-lying dry areas where LiDAR captured bare earth elevations.

Pool size and, to a minor extent, canopy cover were additional factors that limited pool detection. Within the larger site, pools that were smaller than 5m^2 were the least likely to be detected (Table 6). This bias is likely due to the point spacing of the LiDAR data with an average sampling distance of 0.91 m. Close examination of the LiDAR points and pools smaller than 5 m^2 shows that LiDAR point data are sometimes spaced farther apart than pool area, effectively missing these pools. In such cases, the DEM surface at the pool location would have a higher elevation than the actual lava surface and may therefore be elevated above the water surface model. More accurate pool detection could be achieved by finer-scale LiDAR data. Predictions of future habitat locations using this LiDAR data set would probably underestimate the number of new pools created, especially pools smaller than 5m^2. Despite this, areas with a high density of pools are still detected as pool complexes, and small pools are detected within these complexes.

In an unconfined aquifer, the tidal efficiency should be 1 at the shoreline decreasing to zero inland where 0 tidal effect exists (Ferris, 1951, Jacob, 1950). However, in the linear regression model (Figure 1a), the tidal efficiency at 0 m from shore (*y* intercept) was 0.72 (natural logarithm of -0.27) not 1 (natural logarithm of 0). The lower-than-expected tidal efficiency at the shoreline is an indication that lower-permeability sediments may overly nearshore basalts (Li *et al.,* 2007; Rotzoll, El_Kadi, and Gingerich, 2008; Rotzoll *et al.*, 2013). In the KAHO area, thin beach deposits and reef development may be the cause for the reduced tidal efficiency close to the shoreline. Because most anchialine pools are located slightly inland 30 to 250 m from shore, where the predicted tidal efficiency values closely match observed values (Figure 3a), the lower-than-expected tidal efficiency at the shoreline should not affect the pool detection analysis or results.

Theoretically, in a homogeneous unconfined coastal aquifer with constant recharge from an inland source, the groundwater level should be a function of the square root of distance from the coast (Glover, 1959). Groundwater data from the 3.5 km of coastline at the KAHO site (USGS, 2012) supports this theoretical relationship with some error (Figure 3b). Although the application of the KAHO relationship across 42-km of coast improved pool detection, the model did not incorporate site-specific, short-term, or seasonal variation in groundwater surfaces. Well data collected prior to 2003 along the 42 km section of coastline (Bauer, 2003) diverges from the model created with the 2009-10 KAHO data (Figure 3b), illustrating that temporal, spatial, or both types of variation exist. Localized variation in groundwater levels is bound to exist due to differences in rock permeability among lava flows, recharge rates, and groundwater withdrawal (Bauer, 2003; Oki, 1999). Furthermore, seasonal and decadal variation in precipitation and recharge affects groundwater levels.

Future human use of groundwater and changes in precipitation due to climate change will also affect groundwater levels and salinity. In the area near KAHO, model simulations indicate that groundwater withdrawals at capacity rates could cause water levels to decline by about a foot and groundwater discharge to the ocean to decrease by about 50% (Oki, 1999). In west Hawai'i, future urban growth will result in increasing groundwater withdrawal (Thornberry-Ehrlich, 2011). Evidence also indicates that annual rainfall on the island of Hawai'i has decreased in the past century and may continue to do so with climate change (Giambelluca *et al.*, 2011). Reduced recharge and increased withdrawal could lead to lower groundwater levels and elevated salinities. Temporal and spatial variations in groundwater levels will affect anchialine pool location and inundation. Long-term monitoring of groundwater levels and salinity with better spatial coverage would help track ecosystem changes and allow models to be refined.

Application to Sea Level Rise Modeling

Geospatial predictions of coastal change typically include coastal elevation data and local sea level rise scenarios, but may also incorporate wave dynamics and erosion models (Hoeke *et al.*, 2013; Reynolds *et al.*, 2012). Erosion, wave run-up, and wave setup may be important factors to include in sea level rise predictions for some ecosystems, but these were not included in anchialine pool detection models because of their relative unimportance to long-term pool inundation. In wetlands, the balance between sediment accretion and erosion determines marsh areas that will remain above rising sea levels *vs.* those that will become inundated (Stralberg *et al.*, 2011). Erosion can also move the shoreline inland. At KAHO, for example, the dominant shoreline change is erosional with maximum rates estimated at 0.7 m/y on unconsolidated beach sediments (Hapke, Gmirkin, and Richmond, 2005). However, erosion impacts are minimal on solid lava bedrock which becomes submerged as sea levels rise and shorelines subside (Vitousek *et al.*, 2010). Anchialine pools may have unconsolidated substrate but are typically found in bedrock depressions (Maciolek and Brock, 1974) and therefore are more affected by inundation than by erosional processes as sea levels rise. Ocean waves may temporarily inundate coastal habitat and groundwater levels may be affected by wave set-up (Rotzoll and El-Kadi, 2008) and run-up (Cartwright *et al.*, 2006; Hegge and Masselink, 1991). However, these episodic drivers do not usually have a long-lasting effect on anchialine ecosystems. Anchialine pools closest to the coast may be filled with sediment and ocean water during extreme wave events, but this is usually a temporary impact because groundwater rapidly flushes the system. In 2010, a powerful tsunami from Japan caused considerable erosion to beaches, seawalls, and homes on the island of Hawaiʻi, but only one anchialine pool in the study area was permanently affected when it was filled with sand. Because anchialine pools are in bedrock and usually more than 15 m inland, erosion and wave dynamics are relatively unimportant for modeling sea level rise impacts to this ecosystem.

As sea levels rise, current pools become increasingly saline until they are inundated. Simultaneously, high subsurface hydrologic connectivity causes future pools to emerge in the rugose lava terrain. Endemic anchialine shrimp and mollusks will be able to populate new pools because adults and larvae move in brackish coastal groundwater through subterranean cracks (Craft *et al.*, 2008). Pool endemic shrimp are typically found in salinities ranging from 2 to more than 25 ppt (Maciolek, 1983; Maciolek and Brock, 1974), but there is some evidence for tolerance threshholds for some species (Sakihara, 2012). Therefore increases in groundwater salinities due to sea level rise, inland groundwater withdrawal, and reduced rainfall may affect pool community structure.

Conclusions

Protection of anchialine pool habitats requires the most accurate modeling possible so that land managers and planners can avoid building on future pool complexes. Validation of anchialine pool detection models with current pool locations confirms that groundwater levels are important to include in sea level rise models. Furthermore, testing models with current pool locations has identified the relative success of various models and provided measures of error for these models. The methods developed within this project will be used to predict future locations of anchialine pools along the coastal corridor in west Hawaiʻi with the goal of protecting anchialine pool ecosystems as sea levels rise.

Acknowledgements

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Table 1: Elevation differences in meters between NGS benchmarks and DEMs created from FEMA LiDAR. The NGS benchmarks include the Kawaihae tidal benchmark (1617433B) and 5 benchmarks recorded in 2009 proximal to the KAHO study site. Z_{DEM} is the DEM elevation. Z_{BM} is the benchmark orthogonal elevation. Z_{DEM}- Z_{BM} is the elevation difference between the DEM and the benchmark in meters. RMSE is the root mean square error.

Benchmarks	Date	Z_{DEM}	Z_{BM}	Z_{DEM}- Z_{BM}
1617433 B	2010	2.28	2.05	0.23
KAHO Bound	2009	5.45	5.23	0.22
McKaskill	2009	11.57	11.32	0.25
KAHO Visitor Center	2009	12.90	12.57	0.33
Honokōhau Harbor	2009	2.45	2.11	0.34
Well-MW	2009	21.90	21.75	0.15
Mean				**0.25**
RMSE				**0.19**

Table 2: Water surface models used for anchialine pool detection within the KAHO site.

MSL	Mean Sea Level (0 m)
MHHW	Mean Higher High Water (0.374 m above MSL)
Extreme tide	Extreme annual tide (0.74 m above MSL)
GW at MSL	Mean groundwater levels above MSL
GW at MHHW	Mean groundwater levels above MSL at a MHHW tide
GW at Extreme tide	Mean groundwater levels above MSL at an Extreme annual tide (0.74m)

Table 3: Variables included in the full Generalized Linear Model.

Variable name	Type	Description
Pool_detect	Binary	1 = correct detection with GW + MHHW
Morph	Binary	1 = open
Can50_100	Binary	1 = canopy cover of 51 -100%
Area5_20	Binary	1 = surface area between 5 and 20 m^2
Areaovr_20	Binary	1 = surface area > 20 m^2
Hicanxarea	Interaction	Interaction between Can50_100 and Area5_20
Hicanxhiarea	Interaction	Interaction between Can50_100 and Areaovr_20

Table 4: Comparison of models used to detect anchialine pools (n=195) within the KAHO site. Commission is a "false positive" error in which pools are detected that do not actually exist. Items (non-marsh) and Total Area (non-marsh) are the commission items and total area that exist outside of marsh-like habitat containing *Batis maritima* and other wetland plants.

	Correctly Detected	Not Detected	Commission					
			# Items	Total area (m^2)	Mean area (m^2)	Stdev	# Items (non marsh)	Total Area m^2 (non marsh)
MSL	0	195	1	-	-	-	-	-
MHHW	35	160	27	86	3	4	3	8
Extreme tide	143	52	275	10724	39	178	129	1495
GW at MSL	4	191	1	1	1	-	0	0
GW at MHHW	107	88	292	7725	27	106	42	190
GW at Extreme	157	38	354	5202	15	47	215	2935

Table 5: Restricted logistic regression model results. The Odds Ratios are the β coefficients for the Logistic regression restricted model. The Relative Risk ratios are the β coefficients for the GLM with Poisson distribution, a log link function, and robust standard errors run with the same variables. Sample size = 311 pools. 95% Confidence Intervals (CI) are included.

	Odds Ratio	P - value	95% CI
Can50_100	0.36	0.012	0.16 - 0.80
Area5_20	3.34	0.000	1.91 - 5.86
Areaovr_20	15.4	0.000	6.49 - 36.57

	Relative Risk	P - value	95% CI
Can50_100	0.70	0.044	0.50 - 0.99
Area5_20	1.68	0.000	1.32 – 2.14
Areaovr_20	2.21	0.000	1.79 - 2.74

Table 6: Anchialine pool detection outcome for the GW at MHHW model subdivided into surface area and canopy categories. Total counts and percentage of pools detected or not detected within each category are shown.

Area (m2)	Not Detected, n (%)	Detected, n (%)
0 to 5	81 (59%)	57 (41%)
6 to 20	31 (32%)	66 (68%)
0ver 20	7 (9%)	69 (91%)
% Canopy		
0 to 50	100 (36%)	175 (64%)
51 to 100	19 (53%)	17 (47%)

Figure 1: Distribution of anchialine pools, groundwater sites (wells and pools), and NGS benchmarks included in this study: a) Island of Hawai'i with the Kawaihae tide gauge; b) The larger study area used to test the best-performing model. The KAHO site is shown bounded as inset c; c) Smaller study area (KAHO site) used for multiple model testing. This includes pools within Kaloko-Honokōhau National Historical Park boundaries and south of Honokōhau Harbor. Wells shown in (c) were used to create groundwater models.
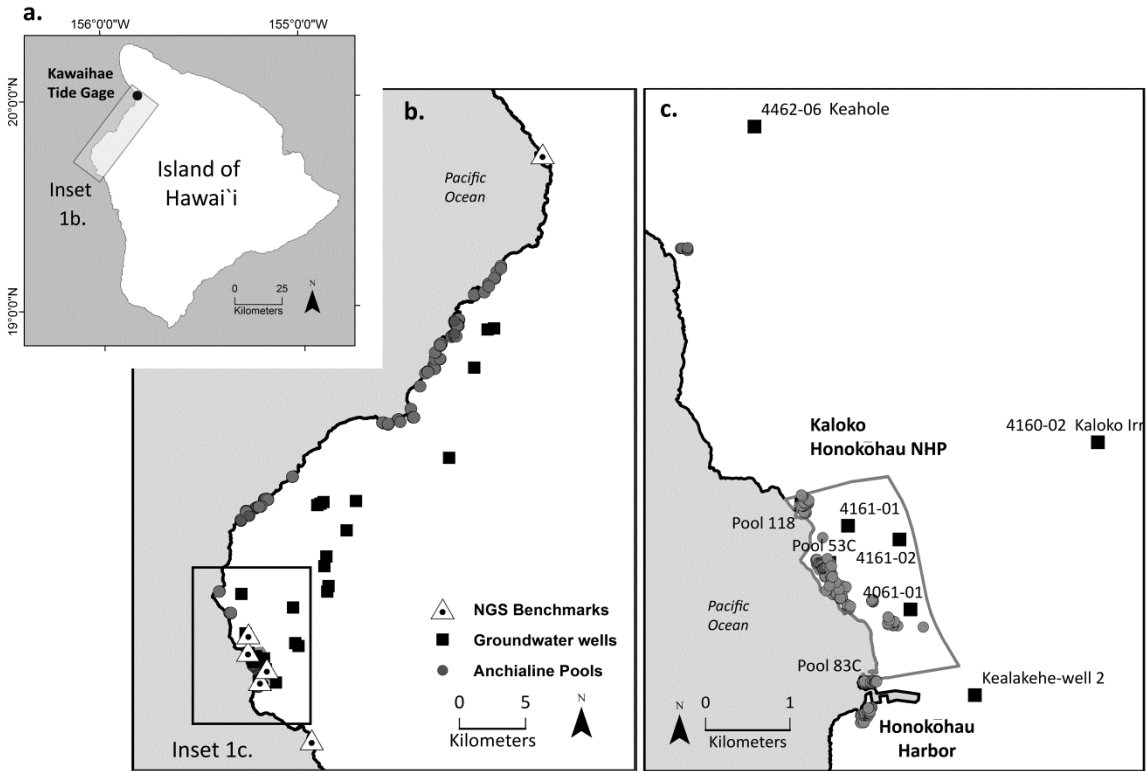
Figure 2: Monthly mean ocean levels at Kawaihae tide gauge (NOAA 2012) and monthly mean groundwater levels observed in the KAHO study site (USGS 2012) on the west coast of the island of Hawai'i from April 2009 to August 2010 (1=January and 12=December).
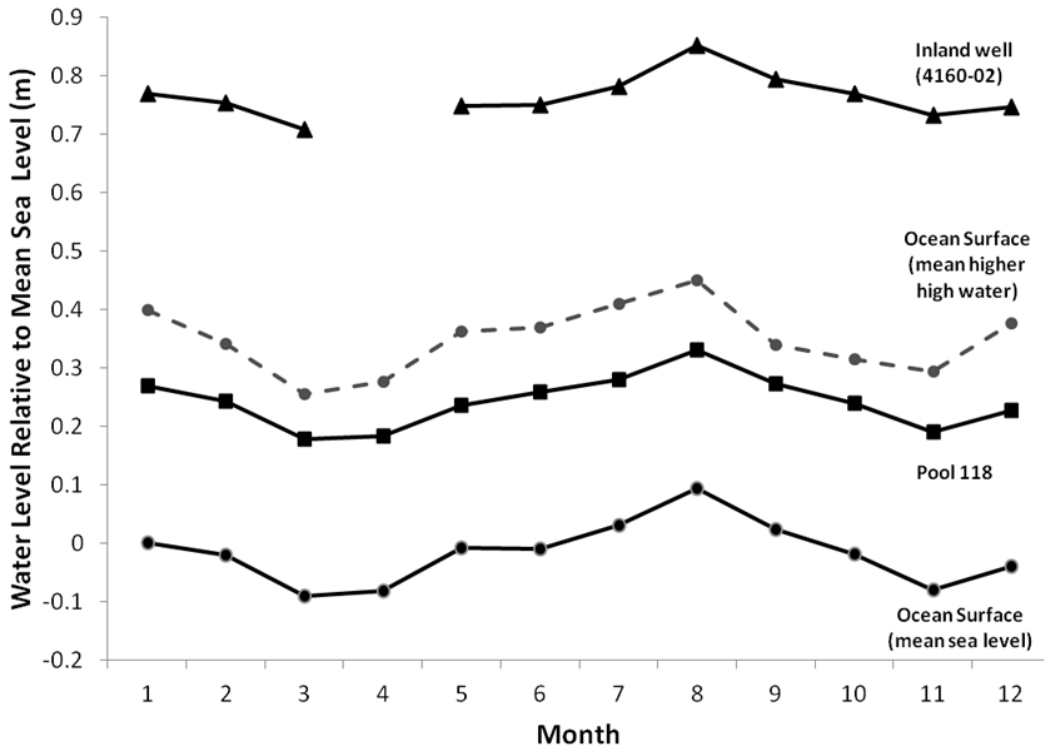
Figure 3: Linear regressions used to create groundwater surface models for the west coast of the island of Hawaiʻi based on groundwater level data for 2009-10 (USGS, 2012): a) Tidal efficiency (natural logarithmic) as a function of well distance from the shoreline; b) Groundwater levels as a function of well distance from the shoreline. Well data from the larger study site (Bauer, 2003) are included for comparison but were not used in the regression analysis. R is the Pearson correlation coefficient.

a.

$\ln(y) = -0.00034x - 0.26646$
$R = -0.92$

b.

$y = 0.00989\ x^{1/2} + 0.16734$
$R = 0.93$
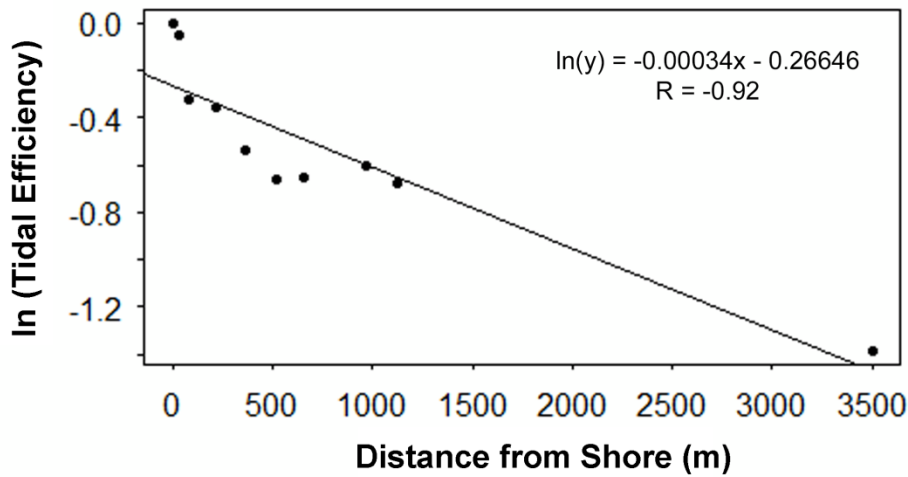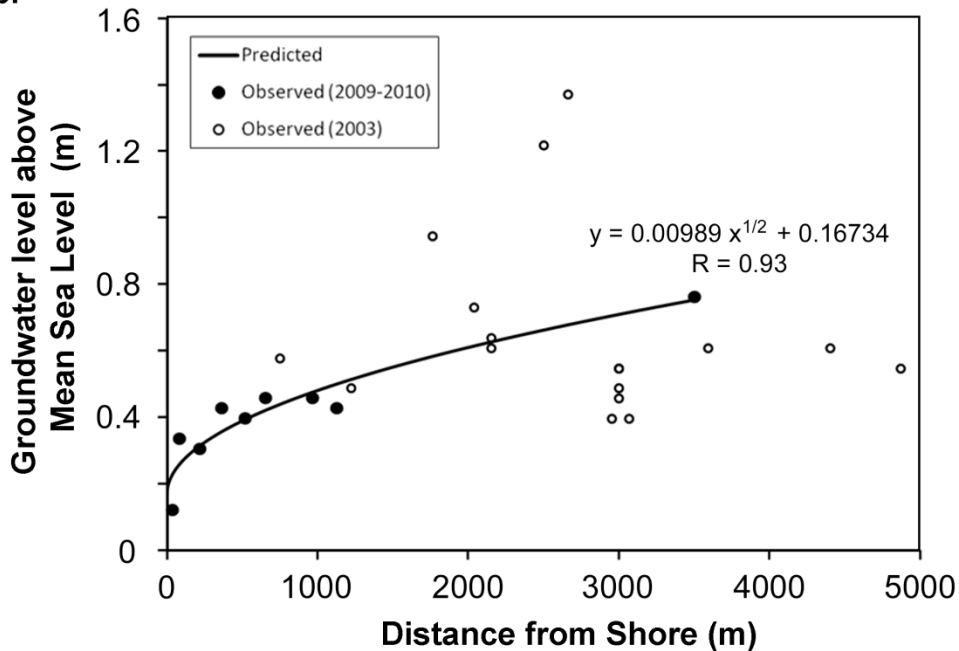
Figure 4: Water level model cross-sections and anchialine pool elevations relative to distance from shoreline at the KAHO site. Five water level scenarios are illustrated: (1) MHHW (0.374 m sea level) without groundwater, (2) GW at MSL, (3) GW at MHHW, (4) GW at a 0.61m-tide stage, (5) GW at an extreme 0.74 m-tide stage. The groundwater surface models are derived from observed groundwater level data (USGS, 2012).
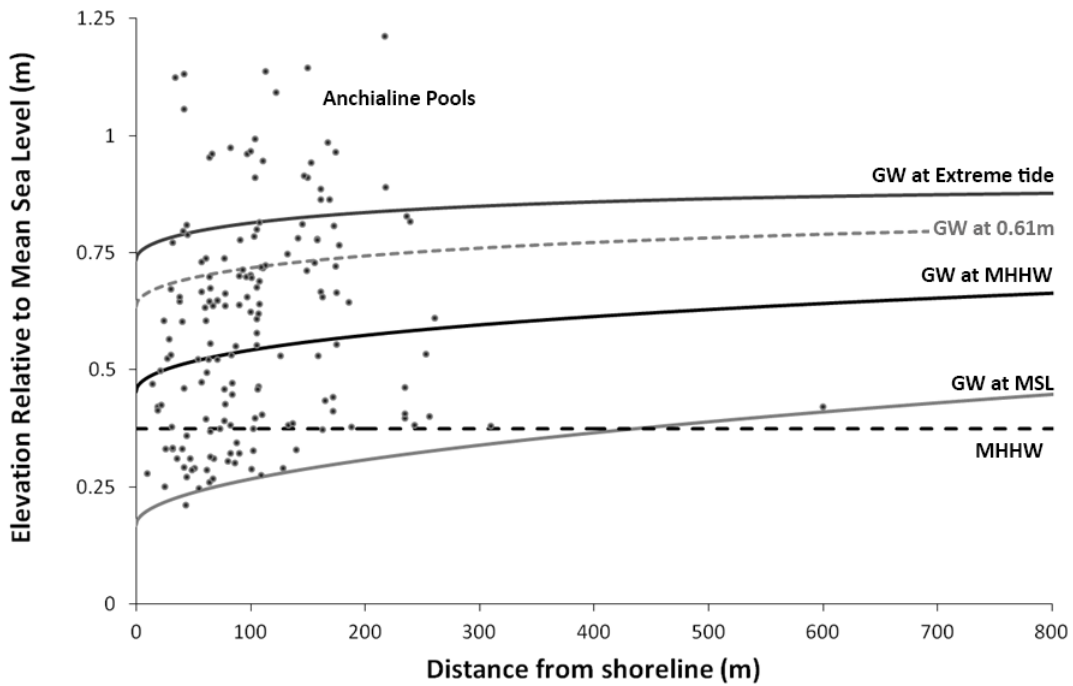
Figure 5: Known anchialine pool locations within a 3-m buffer relative to predicted pool locations from six water surface models in part of the KAHO site. Models represent a range of sea level and groundwater (GW) surfaces relative to MSL: (a) sea level at MSL with no GW, (b) Sea level at Mean Higher High Water (MHHW = 0.374 m) with no GW, (c) Sea level at an extreme tide of 0.74 m with no GW, (d) GW at MSL, (e) GW at MHHW, and (f) GW at an Extreme tide. Most of the pools indicated by black lines are in deep fissures and were excluded from the analysis.
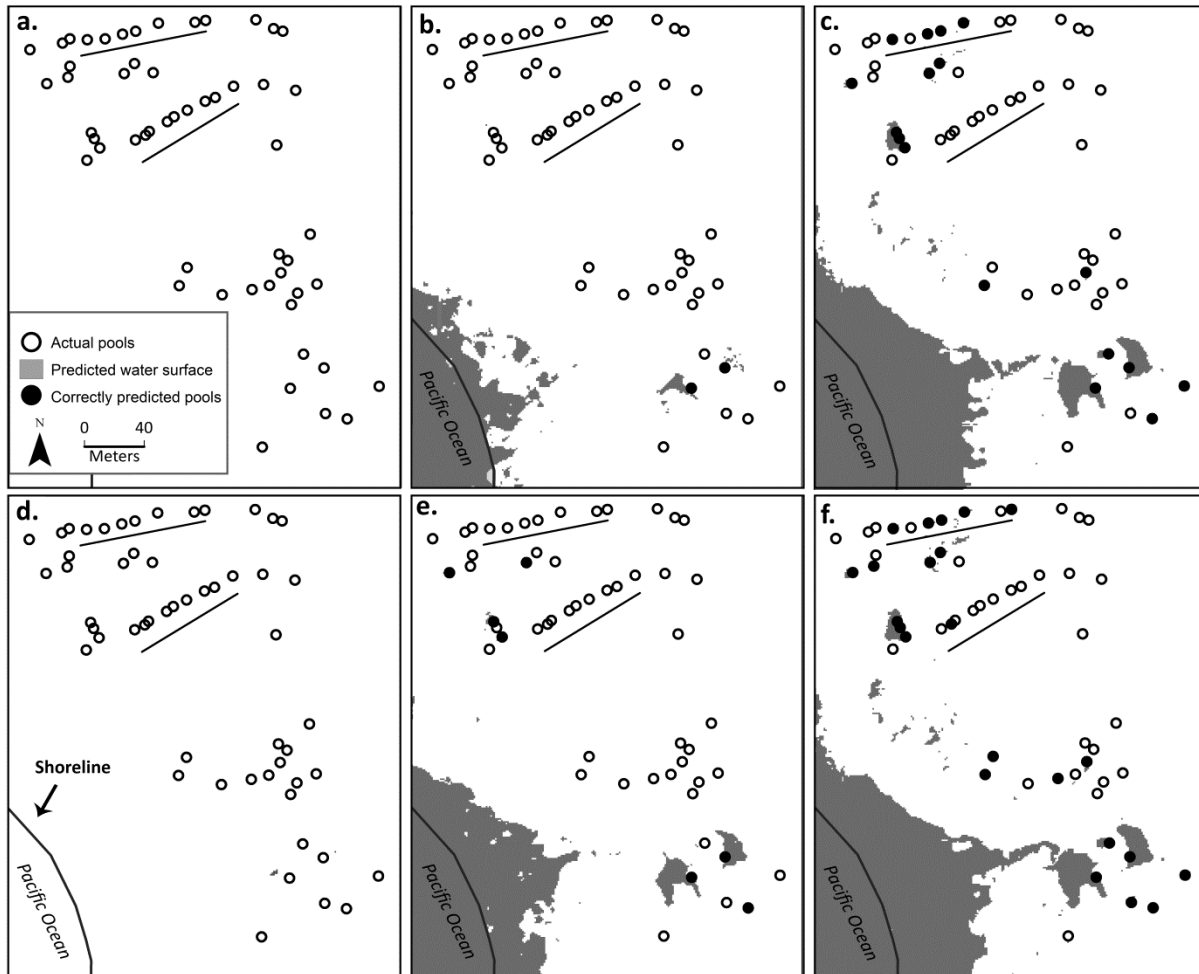
Figure 6: Distribution of marsh habitat: (a) in the KAHO site and (b) around 'Aimakapa fishpond in relation to the GW at Mean Higher High Water model. The model correctly detected known anchialine pools as well as marsh habitat covered in wetland vegetation. Areas without anchialine pools or wetland vegetation were considered detection or commission errors.
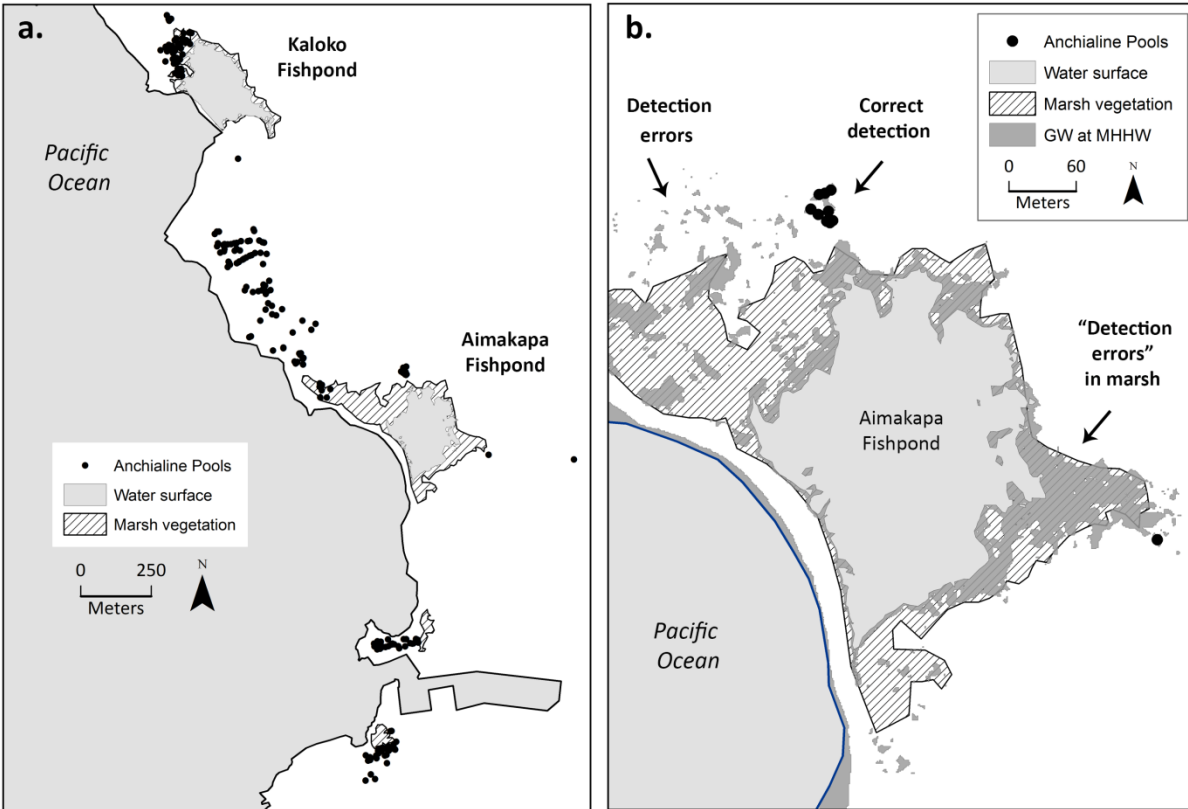
CHAPTER 2

The Relative Importance of Introduced Fishes, Habitat Characteristics, and Land use on Brackish Anchialine Pool Ecosystems

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Abstract

Actions to protect coastal ecosystems and native biodiversity need to account for current stressors which, even at low levels, may reduce the resilience of ecosystems to withstand changing climate conditions. Groundwater-fed, brackish anchialine ecosystems are an example of unique coastal ecosystems which contain high percentages of endemic fauna that are at risk from changes in climate, but for which there is a paucity of information on current stressors that might limit benefits of conservation efforts. Daytime surveys of 398 anchialine pools on the island of Hawaii documented that the two dominant endemic shrimp *Halocaridina rubra* and *Metabetaeus lohena* were located across the region in a wide range of habitats, but that introduced fishes (tilapia, poeciliids) were present in ~ 25 % of pools. Statistical models determined the relationship between shrimp occurrence and pool characteristics, invasive species, water properties, and land use. Introduced fishes had a strong negative effect on the occurrence of *H. rubra* and *M. lohena*. High benthic silt cover and adjacent development also had significant negative relationships with shrimp occurrence. Conservation efforts aimed at reducing introduced fish, minimizing groundwater contamination, and protecting low lying coastal areas from development may enable the unique Hawaiian anchialine pool ecosystems to persist.

Keywords: Groundwater ecosystem, Generalized additive model, Island conservation, Aytid shrimp, Tilapia, Poeciliids

Introduction

Over the last century, multiple human caused stressors including invasive species, elevated nutrient loads, and destructive land use practices have caused widespread coastal aquatic ecosystem degradation and native biodiversity loss (Foley et al., 2005; Halpern et al., 2008; Paine et al., 1998; Vitousek et al., 1997). Understanding the mechanisms by which coastal ecosystems are resilient to these and other stressors, such as climate change, is key for successful conservation efforts (Jackson and Hobbs, 2009). However, determining the specific effects of these perturbations on ecosystem community structure may be difficult due to natural variability and ecosystem complexity (Paine et al., 1998), as well as synergistic effects (Crain et al., 2008, Ormerod et al., 2010, Piggot et al., 2012). This study examined, a wide range of physical and biological characteristics to identify their relationship and relative importance to the occurrence of endemic species within Hawaiian anchialine pools, a rare brackish water coastal ecosystem.

Anchialine pool habitats are unique, tidally influenced coastal water bodies without surface connection to the ocean that are brackish due to subterranean mixing of groundwater and

marine waters (Holthuis, 1973). These ecosystems include caves and open pools and are common in tropical coastal areas, such as the Indo-Pacific (Holthuis, 1973; Maciolek, 1983; Webb et al., 2010) and the Yucatan (Sanchez et al., 2002) where porous substrates, such as karst or lava, provide good hydrologic connectivity between the groundwater and ocean. The true biological diversity of these habitats has only recently been recognized as more than 450 new species of anchialine organisms have been discovered and described over the past 25 years (Anker, 2010; Iliffe & Kornicker, 2009; Weese, 2012). The only anchialine ecosystems in the United States exist in Hawaii, and these are concentrated on the younger islands of Maui and Hawaii (Brock & Kam, 1997).

Hawaiian anchialine habitats are dominated by open pools and lava caves and support diverse endemic biota, including seven species listed as Candidate Threatened or Endangered Species (US Fish and Wildlife, 2013). Anchialine pools are typically devoid of macroalgae, have clear water, contain endemic species, and may include a unique microbial mat that covers the lava substrate (Bailey-Brock, 1993). The 2 - 4 mm long endemic red shrimp *Halocaridina rubra* is a dominant species within this ecosystem with densities ranging between tens to hundreds of shrimp per m^2. *H. rubra* graze on algae and diatoms and are thought to keep macroalgae in check (Brock & Kam, 1997). *Metabetaeus lohena* is a larger candidate endangered shrimp (~ 5 mm long) that preys on *H. rubra* and other invertebrates (Holthuis, 1973). Other endemic anchialine shrimp as well as gastropods are occasionally seen in pools with some rare species found in highly localized distributions (Chai et al., 1989; Maciolek & Brock, 1974; Sakihara, 2012). The larvae of *H. rubra* and other shrimp species may disperse as oceanic plankton, while all life stages may move through subterranean groundwater (Craft et al., 2008). Interestingly, Santos (2007) found highly structured populations of *H. rubra* on the west coast of the Big Island. In contrast, *M lohena* populations show very little genetic structure (Russ et al., 2010). Anchialine gastropods are thought to have the same mechanisms of dispersal (Kano & Kase, 2004).

In Hawaii, pools are considered subaerial expressions of groundwater, are tidally influenced, and salinities may range from 0.5 to 30 parts per thousand (ppt; Maciolek & Brock, 1974). Pools may occur in bare lava substrate with no associated vegetation or on older lava flows surrounded by trees or wetland vegetation (NPS, 2012). Eventually pools may become filled in with new lava flows or older sediments which would explain their sparse distribution or absence on older Hawaiian islands (Maciolek & Brock, 1974). Since the initial island-wide survey of anchialine pools was completed in 1973 (Maciolek & Brock, 1974), a great deal of development has modified Hawaii's coastal environment and non-native species have invaded many pools (Brock & Kam, 1997), suggesting the need for more current assessments anchialine pool habitats and communities.

Introduced species and land use practices appear to be severely degrading anchialine habitats and threatening rare species within them (Brock et al., 1987; Brock & Kam, 1997; Iliffe & Kornicker, 2009). The negative effects of introduced fish species on native biodiversity and habitat have been well documented in aquatic ecosystems (Cucherousset & Olden, 2011; Gozlan et al., 2010). Tilapia (Canonico et al., 2005), *Gambusia affinis* (Global Invasive Species Database, 2010) and *Poecilia reticulata* (Deacon et al., 2011) are strongly associated with ecosystem declines across the globe. Introduced predatory fishes such as tilapia (*Oreochromis mossambicus* and other species) and poeciliids (*Poecilia reticulata, Gambusia affinis*), along with the invasive prawn, *Macrobrachium lar,* are thought to be a primary cause of pool degradation in Hawaii where these taxa prey on the herbivorous *H. rubra* (Capps et al. 2009; Carey et al., 2010; Chai et al., 1989). Reduction of grazing by *H. rubra* has been suggested as the

primary mechanism for ecosystem phase shifts resulting in rapid macroalgal accumulation and pool senescence (Brock & Kam, 1997). Groundwater nutrient loading may also be a compounding factor leading to anchialine pool degradation. Elevated nutrients (nitrogen, phosphorus), especially when combined with loss of grazer capacity, often results in increased primary producer biomass (Gruner et al., 2008) and major shifts in aquatic ecosystem structure and function (Carpenter et al., 1998; Jackson et al., 2001; Folke et al., 2004; U.S. EPA, 2004). Rapid development on the west coast of Hawaii Island has occurred in coastal and upslope areas over the past thirty years, with substantial urbanization planned for the future (County of Hawaii, 2011). Nutrient enriched irrigation water, storm water runoff, fertilizers, and septic/cesspool effluent can leach through porous basalt substrate into groundwater and flow into anchialine pools (Knee et al. 2008). Although pool nutrient levels may vary naturally, monitoring has shown that pools in proximity to developments have had significant increases in nutrients after project build out (Brock & Kam, 1997; Weigner et al., 2006). The long-term effects of elevated nutrients on anchialine pools, especially when combined with introduced predators, are presently unknown.

The primary goal of this study was to quantify the effects of a wide variety of biotic and abiotic factors on the distribution of the dominant endemic shrimp species within anchialine pools on the Island of Hawaii. Specifically, the objectives were to determine: 1) the habitat characteristics associated with endemic anchialine pool biota across the region; and 2) the effects of pool characteristics, invasive species, water properties, and land use on endemic shrimp *H. rubra* and *M. lohena* occurrence. Biotic and abiotic characteristics were examined at over 400 pools across the western and southern coastlines of the Island of Hawaii. Results examining the relationships between pool characteristics and the occurrence of endemic anchialine shrimp species are essential for successful restoration efforts and to prioritize conservation of this unique habitat. This approach would be useful for researchers interested in prioritizing conservation actions in other regions or habitats.

Materials and Methods

Study area

This study occurred along the Ala Kahakai National Historic Trail (ALKA) corridor on the arid western and southern coastlines of the Island of Hawaii (Figure 1a). Annual rainfall in the study area ranges from 25 to 50 cm per year (Giambelluca et al., 2011). Ala Kahakai National Historic Trail passes through Kaloko-Honokohau National Historical Park, Puʻukohola Heiau National Historical Site, Puʻuhonua O Honaunau National Historical Park, and Hawaiʻi Volcanoes National Park, as well as numerous state and county parks and private lands (Figure 1a). These areas encompass one of the highest concentrations of anchialine pools in the world (Brock & Kam, 1997). Previous anchialine pool habitat assessment studies along the ALKA corridor include localized baseline inventories on state conservation and national park lands (Brock & Kam, 1997; Chai et al., 1989; NPS, 2012; Sakihara, 2012) as well as state mandated water quality monitoring near resort developments (Weigner et al., 2006). The most spatially extensive survey occurred in 1972-1973 (Maciolek & Brock, 1974; Figure 1b).

Anchialine Pool Surveys

Data describing the habitat and faunal characteristics of 330 anchialine pools were collected during daylight hours on single site visits from July 12 to August 10, 2012 and July 2 to July 15, 2013. Some of the pools had not been surveyed since the 1970s (Maciolek & Brock, 1974) or had never been formally documented. Data for an additional 102 pools were added from previous surveys conducted by the National Park Service (NPS) between 2007-2009 (Jones et al., 2011; NPS, 2012). Pools were located within private, state conservation, and national park boundaries and were in proximity to a range of land uses including undeveloped, residential, resort, and urban. The objective was to visit as many pools as possible along the ALKA trail, therefore we used maps, reports, and interviews with locals to identify sites. Due to difficult or restricted access, we were not able to sample all known pools along the southern and western coastlines (Figure 1b). Data collected for each pool included physical attributes, water properties, the presence of plants and animals, and land use are described in more detail below.

Physical attributes

Physical attributes included location, surface area, maximum depth, substrate, and distance from the shoreline. Pool surface area was determined within ESRI's ArcGIS 10.0 using a polygon of the pool perimeter collected in the field with a Trimble GeoXH Global Positioning System (GPS). Surface area for small pools or those with high canopy cover was calculated as pool length x width measured with a transect tape at the high water line. Maximum depth was recorded at each pool at the time of the survey. Substrate was categorized as percent cover of rock, sand, and silt using visual estimates. Distance from coastal shoreline was calculated in ArcGIS as the Euclidian distance between the shoreline and the closest edge of each pool.

Water properties

Salinity, pH, temperature, dissolved oxygen (DO), turbidity, and Chlorophyll *a* (Chl *a*) were collected at pools with a portable sonde (YSI 6500 or Hydrolab Quanta). High turbidity and Chl *a* can be indicators of nutrient enriched systems (Clesceri et al. 1998).

Water measurements were collected at the surface of each pool to standardize for possible changes of salinity with depth (Jones et al. 2011). Recognizing that our water measurements represent a one-time snapshot, we assessed inter annual and daily variability in surface water salinities within a subset of pools. Previous work has indicated that although pools may exhibit variability in water properties with depth, the surface of each pool remains relatively constant on annual and daily timescales (NPS, 2012; Bienfang et al. 2011).

Plant and animal species

Endemic pool species as well as introduced fishes and the prawn *M. lar* were recorded as present or absent based on visual surveys during daylight hours. *Poecilia reticulata, Poecilia mexicana,* and *Gambusia affinis* were present in pools but were not always distinguishable in the field so were combined as poeciliids for statistical analysis. Tilapia species were also grouped together for this study. *Oreochromis mossambicus* probably makes up the majority of tilapia found on the Island of Hawaii, but this is not certain since other tilapia species exist on Oahu and Kauai, and they are difficult to identify as juveniles (Mackenzie & Bruland, 2012). *Kuhlia*

sandvicensis was the most common reef fish found in anchialine pools and was included in the analysis because it may prey on shrimp. Other reef fish were seen in less than 10 pools and were not included in the study.

Most pools were small and shallow enough that it was possible to visually examine the entire water body from the pool edges. Larger pools, where the center and bottom were not visible from the surface, were examined using mask and snorkel. Macro-algae was recorded as present or absent. Terrestrial vegetation associated with pools was documented including percent canopy cover by species, percent cover of emerging vegetation by species, and percent cover of plants within 0.5 meters of pool periphery by species.

Imperfect detection of organisms may cause biased results in habitat models, therefore multiple surveys per season are recommended for the most precise detection models (MacKenzie & Royle, 2005). Multiple visits per season, though, were not feasible for many of the remote and privately managed sites within this study. Nevertheless, we found that repeated visits to a subset of pools show that introduced fishes, *M. lar,* and the endemic anchialine shrimp *H. rubra* and *M. lohena* occurred consistently within pools. For example, within 58 pools visited repeatedly (2 or more times) between December 2007 and October 2008, *H. rubra* were consistently present (NPS, 2012). During 2013 surveys, *H. rubra* reoccurred in all but two of these same pools. Other pools visited multiple times between 2012 and 2013 throughout the entire study area showed consistent *H. rubra* presence unless shallow pools were visited at low tide when they appeared dry.

Land use

Land use was described using two categorical variables. One likely condition is that in more populated areas, nutrient and contaminant inputs to groundwater would be elevated due to septic tanks, irrigation with treated sewage water, golf courses, storm drains, or other activities (Dalton et al., 2013; Weigner et al., 2006). Because these contaminants often arrive in pulses to groundwater and may flow through the system quickly, they are difficult and expensive to measure across large areas. Land use categories were used as a proxy for potential groundwater effects on pools due to development. Rather than create separate categories for all possible land use types, we created two binary factors that describe the proximity of pools to development. LU_PROXIMAL scores pools situated in the middle of resort or residential developments with a 1 and assigns all other pools a 0. LU_UPSLOPE assigns all pools with development within 1 km upslope a 1 and all other pools to 0. While this is a very coarse measure of the potential impacts of development on groundwater flowing through anchialine pools, it is starting point for examining regional patterns of endemic shrimp distribution.

Analyses

To determine the importance of invasive species, pool characteristics, water properties and land use on endemic shrimp occurrence, each explanatory variable was first tested individually to determine if it related to a significant difference between shrimp occurrence categories (*H. rubra* present, both *H. rubra* and *M. lohena* present, and pools with neither shrimp present). Continuous and percentage variables were examined with a non-parametric Kruskal-Wallace one-way analysis of variance. The null hypothesis that all occurrence categories were the same was rejected when $P \leq 0.05$. Categorical explanatory variables such as introduced fish presence or absence were tested for effects on the occurrence of different shrimp species using

the Pearson chi-squared test with Yates correction (χ^2) and a significance level of $P \leq 0.05$. In some cases the counts were too low in one category (i.e. count of 1 or 0) for the chi-squared test to be calculated successfully.

We developed generalized additive models (GAMs) (Knapp, 2005; Miro & Ventura, 2013) to explore data relationships and determine the relative importance of factors on endemic shrimp occurrence. GAMs do not require constant variance or normally distributed errors, and therefore are useful when dependant variables are binary (ie. presence/absence data). GAMs relax the assumption that the relationship between the dependent variable (on the logit scale) and the explanatory variables are linear. Nonparametric loess smoothing functions are used in GAMs to describe the relationships between the dependent and continuous explanatory variables (Hastie & Tibshirani, 1991). Appendix 1 describes our approach in more detail.

The dependent variables in the GAMs were the presence or absence of *H. rubra* or *M. lohena*. The explanatory variables that were examined for potential use in exploratory GAM models represented water properties, pool characteristics, land use, and co-occurring endemic and introduced species. Spatial autocorrelation was accounted for with a loess smoothed term that combined the latitude and longitude of each pool (Knapp et al., 2003, Dormann et al., 2007). Chlorophyll *a* (n=201), turbidity (n=230), salinity (n=323) and temperature measurements (n=314) were not available for all of the pools included in the dataset so were examined in separate GAM models using a subset of pools. None of the water property variables were a significant term for explaining *H. rubra* or *M. lohena* occurrence, and therefore, were dropped from the full analysis.

Plots were created to depict the relationship between significant explanatory variables and the probability of species occurrence. For continuous variables the response curve shows the relative influence of the explanatory variable on the probability of species occurrence. The response curves are based on partial residuals, are plotted on a log-scale, and are standardized to have an average value of 0.

Results

Pools represented a wide range of physical and biological characteristics (Table 1). Pools ranged in size from $<1 \text{ m}^2$ to 952 m^2 and were located 11-600 m from the shoreline. A majority of pools were in lava bedrock and were exposed to open sky, but some were cave-like existing within collapsed lava tubes. Most pools (92%) were less than 1 m in depth with a mean depth of $0.38 \pm$ S.D. 0.7 m at the time of measurement, although in one large cave the water was at least 10 m deep. Some shallow pools that became dry at low tide were populated with *H. rubra* when the groundwater surface rose at higher tides.

In terms of water characteristics, salinity values ranged from 1.3 to 26.6 ppt but had narrower ranges within specific areas relating to distinct aquifers (Figure 2). During the study period, a subset of pools were sampled multiple times to examine variability in surface salinity across annual and daily time scales. In 18 pools located across the study area, the mean difference in surface salinity for an individual pool between 2012 and 2013 sampling periods was 0.02 ppt and was not significant (Two sampled T-test, $T_{(2\text{-tailed})}=0.01$, df = 34, $P = 0.99$). In 11 individual pools, the mean difference in surface salinity between morning and night was also 0.02 ppt and was not significant (Two sample T-test, $T_{(2\text{-tailed})}=0.05$, df = 20, $P = 0.96$). Although many of the pools in this study were sampled once for water properties, the above comparisons increase our confidence that they represent relatively stable water conditions useful for

comparison with other pools within the same time period. Throughout the study area, most pools had low turbidity (0.39 ± 2.5 S.D. NTUs) and Chl *a* (1.12 ± 5.5 S.D. mg/L) values.

Visible macroalgae and microbial crust was absent from a majority of pools, even in those with rocky substrate. Approximately 50% of the pools observed had substrates dominated by rocky substrate (≥ 70% rock) and contained no visible benthic algal or microbial crust growth. Macroalgae was visibly present within 10% of pools and was dominated by the genera *Ulva*, *Cladophora* and *Vaucheria*. Of the pools with visible macroalgae, 63% (n = 25) contained *H. rubra* and 18% (n = 8) contained *M. lohena*.

Terrestrial vegetation occurred at 33% of pools and included endemic wetland and shoreline plants as well as introduced pickleweed (*Batis maritim*a) and the introduced mesquite tree (*Prosopis pallida*). Percent silt cover was positively correlated with percent terrestrial vegetation cover including emergent vegetation (Pearson Correlation Coefficient (r) = 0.48, p<0.0001), perimeter vegetation (r = 0.72, p<0.0001), and canopy (r = 0.16, p<0.002).

The daytime surveys showed that *H. rubra* and *M. lohena* occurred over the entire study area (Figure 3). Both shrimp occupied pools representing the entire measured range of salinities (1.83 to 26.6 ppt), vegetation cover (0-100%), and substrate type (0-100%) (Figure 4). Turbidity and Chl *a* were higher in more pools without shrimp than with shrimp, and although this was statistically significant, the measured differences were minor except for a few outliers (Figure 4). There were significant differences in substrate type and percent vegetation cover (canopy, perimeter, and emergent) between pool categories (Figure 4). Compared to pools without shrimp, a majority of pools with *H. rubra* or both shrimp present had a higher percentage of rocky substrate. Compared to pools with no shrimp or *H. rubra* alone, pools with both *H. rubra* and *M. lohena* were associated with a higher percentage of canopy cover. Although *H. rubra* are usually a deep red color, a distinct white color morph occurred in pools with high amounts of terrestrial or aquatic vegetation throughout the study area (n=18 pools). This white color morph was absent in pools without associated vegetation.

Tilapia occurred in 3.5% (n=14), poeciliids in 23.9% (n=95), and *M. lar* in 3.8% (n=15) of the 398 pools surveyed (Figure 3). All three species were found at sites on the western and southern coastlines in a variety of land use areas including undeveloped, residential, resort and near urban areas. They were located in private lands, National Parks, and Hawaii state conservation lands. They also occurred in pools with substrates ranging from 100% rock to 100% sediment.

Other native species observed in anchialine pools during surveys included gastropods (*Nerita picea, Neritina vespertina, Theodoxus cariosus ,* and *Thiaridae* species), the endemic prawn *Macrobrachium grandimanus,* the glass shrimp *Palaemon debilis* and the candidate endangered damselfly *Megalagrion xanthomelas*. During our surveys at Manuka National Area Reserve we did observe *Antecaridina lauensis* and *Periclimenes pholeter* but did not see these rarely observed shrimp in any other locations visited along the ALKA trail corridor.

Factors related to shrimp occurrence

  Halocaridina rubra

H. rubra were detected at 230 of the 398 pools (45%) and were distributed throughout the daylight survey area (Figure 3). Univariate analysis indicated no significant difference in the probability of occurrence for *H. rubra* between sites at which non-native *M.lar* were present versus absent or between sites located within 1 km down slope from human development (Table

2). *H. rubra* occurrence was significantly less probable in pools that were immediately next to coastal development and in pools with tilapia, poeciliids, and *K. sandvicensis* (Table 2).

Non-native tilapia and poeciliids along with the native reef fish *K. sandvicensis* were negatively associated with the probability of occurrence for *H. rubra,* after accounting for the influence of other explanatory variables (Table 3). Two of the eight additional explanatory variables (silt substrate, location) were significantly correlated with *H. rubra* occurrence. The response curve describing the estimated effect of silt substrate on the probability of shrimp occurrence indicates a negative association with higher probabilities of shrimp presence at low silt levels and lower probabilities above 80% silt cover (Figure 5). Although the percent of perimeter vegetation was not a significant predictor variable in the GAM, it did have a high percent deviance (12%) indicating it might have some negative effect on the probability of *H. rubra* occurrence.

Metabateaus lohena

M. lohena occurred in 13% of pools surveyed during daylight hours and co-occurred with *H. rubra* in all but one pool. Univariate analysis indicated no significant difference in the probability of occurrence of *M. lohena* between sites located within 1 km down slope from human development or outside that distance (Table 2). However, this analysis indicated significant differences in the probability of *M. lohena* occurrence between pools with and without *H. rubra* and poeciliids. *M.lohena* occurred in none of the pools containing tilapia or the native reef fish *K. sandvicensis*, in one pool with *M. lar*, and in 3 pools located within coastal developments. Despite low numbers of *M. lohena* in pools with these characteristics, the chi-square tests were inconclusive due to low counts in some categories (Table 2).

GAM results also suggested that *H. rubra* occurrence was positively associated with the probability of occurrence for *M. lohena,* after accounting for the influence of other explanatory variables (Table 3; Figure 6). Canopy was the only other explanatory variable significantly correlated with the probability of *M. lohena* occurrence (Table 3). The response curve describing the estimated effect of canopy cover on the probability of *M. lohena* occurrence indicates a positive association between shrimp and canopy cover (Figure 6). Location was less important in the model used to explain *M. lohena* occurrence versus the *H. rubra* model.

Discussion

This study offers the first regional perspective on anchialine pool habitat characteristics along the western and southern coastlines of the Island of Hawaii since the 1970's. Our data show that while the endemic anchialine shrimp *H. rubra* and *M. lohena* are located across the study area, introduced fishes are present in > 25 % of pools and have a strong negative relationship with shrimp occurrence. Based on their habitat associations, these endemic shrimp have wide tolerances for a number of physical and biological characteristics of anchialine pools including salinity and temperature. However, there is a negative association between endemic *H. rubra* occurrence and human land use. This association was not as clear for *M. lohena* possibly because of the low number of pools observed with this species.

How do introduced species influence native anchialine pool biota?

Introduced fishes (tilapia, poeciliids) were the most important variables explaining the lower probability of *H. rubra* occurrence in anchialine pools during daytime surveys (explaining 21% of the deviance in GAMs; Table 3). The occurrence of the native reef fish *K. sandvicensis*, which may wash into pools during storms or may be placed in pools by people, explained an additional 3.5% of model deviance. Although fish effects on *M. lohena* occurrence were not significant in GAMs (Table 3), contingency table results indicated a significant negative relationship between poeciliids and *M. lohena* (Table 2). Furthermore, *M. lohena* were not found in any pools with tilapia or *K. sandvicensis*. These results support previous studies which have suggested that introduced fishes are a primary reason native fauna are absent from some Hawaiian anchialine pools (Brock and Kam, 1997; Chai et al., 1989). Our results also suggest that *K. sandvicensis* is likely to play a similar role in reducing native shrimp in anchialine pools.

Specific introduced species appear to have different affects on anchialine pool biota. During our daytime surveys, *H. rubra* occurred in 33% of pools with poeciliids (31 pools) but only 7% of tilapia pools (1 pool). One explanation for higher shrimp occurrence in pools with poeciliids is that poeciliids are gape limited in regards to larger *H. rubra*. Field observations support this hypothesis (Dalton et al., 2013). In pools with poeciliids, *H. rubra* were predominantly of a larger size class (~ 2mm wide carapace and 4mm long), whereas pools without fish in the same location contained *H. rubra* with a range of sizes (0.5 - 2 mm wide carapace and 2-4 mm long). Tilapia are larger fish and would not be gape limited in relation to *H. rubra* or *M. lohena* , which might explain the complete absence of shrimp in pools with tilapia.

Although the introduced prawn *M. lar* also preys on *H. rubra* and *M. lohena*, *M. lar* occurrence was not an important variable explaining the occurrence of either shrimp during daytime surveys. One explanation may be that *H. rubra* and *M. lohena* have evolved to co-occur with the native prawn *M. grandimanus,* which is similar in size and morphology to *M. lar*. Alternatively, unlike the introduced fishes, there is some evidence that *M. lar* actively hunts at night perhaps causing a reverse diel behavior in prey so that *H. rubra* and *M. lohena might* become most active in pools during the day (Carey et al., 2010). This kind of response in *H. rubra* and *M. lohena* diel behavior due to *M. lar* would not have been detected by our daytime surveys.

Empirical data on the effects of fish predation in anchialine pool systems is limited. However, stable isotope analysis indicates that mosquitofish (*G. affinis*) do eat *H. rubra* in anchialine pools (Capps et al., 2009). Additionally, Capps et al. (2009) showed that in the presence of mosquitofish, *H. rubra* did not disappear completely from pools, but avoided predators during daylight hours by hiding in the lava substrate and became active only at night when fish were inactive. Dalton et al. (2013) surveyed 20 pools and also found significantly fewer *H. rubra* during the day when poeciliids were present. Furthermore, pools containing poeciliids had significantly higher epilithon biomass and nutrient content than pools without fish. Algal consumption by fish and snails (Capps et al., 2009) may compensate for reduced *H. rubra* grazing and partially explain our observation that out of 237 pools with fish, only 17% contained visible macroalgae. By reducing *H. rubra* abundances and changing *H. rubra* behavior, introduced fishes are affecting food web dynamics and primary producer standing stocks within anchialine pools.

What role does the physical habitat play in structuring anchialine pool communities?

The second most important group of variables explaining shrimp occurrence included specific pool characteristics. For *H. rubra* the percent of silt substrate explained 9.9% of the model deviance. Due to the porous lava substrate that creates anchialine pools, anchialine shrimp are able to move freely between pool water and subterranean groundwater. Throughout the study area, this behavior was clearly seen in pools that appeared dry at low tide. When groundwater levels dropped below the elevation of the pool substrate, shrimp appeared absent. However, as groundwater levels rose with higher tides, shrimp moved into pools and were observed actively grazing on the substrate. High silt cover, especially if it is thick, may block access to subterranean passages and restrict movement of shrimp between the subterranean groundwater and open pools. It may also reduce grazing surfaces for *H. rubra*. Higher silt pools were often at the edges of wetland habitat and had higher amounts of associated terrestrial vegetation.

As pools age and soils develop in surrounding substrate, terrestrial vegetation can encroach and may provide additional sources of nutrients for anchialine food webs (Dudley et al., 2013). Canopy cover explained 24.2% of the model deviance for *M. lohena*, with higher canopy cover associated with a higher probability of *M. lohena* occurrence. Terrestrial subsidies may provide nutrient support for an additional trophic level above the grazing *H.rubra*. Stable isotope analysis shows that *H. rubra* do utilize terrestrial plant litter as a source of nutrients if it is available (Marrack, unpublished). The highest observed density of *M. lohena* during the survey (>100 per m^2) was in a pool that also had the highest density of *H. rubr*a (~1000 per m^2). This pool had 100% vegetation around the perimeter and 30% tree canopy. *M. lohena* occurrence is also strongly explained by *H. rubra* presence (14.3% of model deviance). In pools with and without terrestrial vegetation, *H. rubra* are often the only apparent prey item available for *M. lohena*. These results suggest that *M. lohena* is dependent on *H. rubra* for occurrence and that terrestrial subsidies support higher populations of both shrimp.

A potentially negative aspect of terrestrial vegetation for endemic shrimp is that as plant litter accumulates and decomposes, biogenic sediment may also accumulate. This may create a positive feedback whereby sediment continues to infill pools providing more substrate for marsh plants until pools eventually become filled in completely. This natural process may be accelerated by the presence of rapidly growing introduced plant species such as *Batis maritima*. Currently there are no published studies examining the role that introduced plants play in driving anchialine pool senescence.

Salinity and Temperature Tolerances

Based on their habitat associations, these endemic shrimp have wide tolerances for a number of physical and biological characteristics of anchialine pools including salinity and temperature. However, there are important distinctions to be made between an organism's habitat associations and optimum niche requirements (Hutchinson, 1957; Sax et al., 2013). First, surface water measurements do not capture the range of spatial or temporal variability that may exist within the full extent of an anchialine shrimp's above ground and subterranean habitat. Second, it is not clear if *H. rubra* and *M. lohena* are able to complete their entire life cycle within the full range of observed salinities and temperatures. Lab experiments show that the larvae of the candidate endangered damselfly *Megalagrion xanthomelas,* which are found within the study area, are sensitive to increased salinities with a threshold response above 15 ppt (Tango, 2010). Data on tolerance levels are important for the long term protection of anchialine pool endemic

communities because pool salinities are projected to increase due to increases in anthropogenic groundwater withdrawal (Oki, 1999; Thornberry-Ehrlich, 2011), sea level rise (Marrack, 2013) and decreases in precipitation (Giambelluca et al., 2011).

What is the role of land use on anchialine pool ecosystems?

Proximal development was the only land use category that showed significant effects on the probability of shrimp occurrences. Both land use variables, used as a proxy for potential groundwater effects or other influences on pools due to development, were very broad and do not account for specific factors affecting individual sites. Furthermore, the variables used represent land use at this particular time and do not represent effects of past actions. Past construction has filled in at least 10% of anchialine pools along the western coastline of the Island of Hawaii (Brock et al., 1987). Upslope and surrounding development has also led to increases in contamination of groundwater due to nutrient enriched irrigation water, storm water runoff, and septic/cesspool effluent (Weigner et al., 2006). In a comparison of twenty anchialine pools located within and outside of resort complexes, pools with human development on their immediate periphery had significantly higher concentrations of ammonium, dissolved inorganic nitrogen, and soluble phosphorus (Dalton et al., 2013). Groundwater contaminants flowing into anchialine pools will be expected to increase with increased urbanization. Because groundwater flows through pools and out to wetland and coral reef ecosystems (Knee et al., 2008), broad-scale groundwater contamination is also expected to affect other ecosystems. Finally, encroaching urbanization may cause new and current introduced species to spread into pools that are currently uninfected. These potential land use effects have serious implications for the integrity of anchialine pool ecosystems, therefore they need to be monitored and addressed in more detail.

Conclusion

While the anchialine shrimp *H. rubra* and *M. lohena* are located across the region, introduced fishes are present in > 25 % of pools and have a strong negative impact on shrimp occurrence. The fact that *H. rubra* and *M. lohena* move within subterranean groundwater and emerge in pools at night when fish are inactive, suggests that fish removal efforts should result in rapid recovery of shrimp in pool habitats during daylight hours. Fish removal efforts are resource intensive (Britton et al., 2011), therefore targeting the worst offender may be the most cost effective strategy. Evidence indicates that tilapia may have the largest effect on shrimp occurrence and sediment accumulation, and therefore may be a priority for removal efforts.

High sedimentation was negatively associated with shrimp occurrence, while canopy cover had a positive effect on the presence of the candidate endangered shrimp *M. lohena*. Current anchialine pool restoration efforts often involve the removal of fine benthic sediments and clearing of surrounding terrestrial vegetation. Our results indicate that removal of sediments may increase the probability that shrimp will occur in pools. However, removal of terrestrial vegetation may have a mixed effect on pools. While vegetation may increase the rate of pool infilling, *M. lohena* is positively associated with canopy cover. Adult *Megalagrion xanthomelas*, the candidate endangered damselfly, are also known to associate with canopy cover around anchialine pools (Tango et al., 2012).

As sea levels rise and current pools become inundated, high subsurface hydrologic connectivity will cause future pools to emerge in the rugose lava terrain (Marrack, 2013). Endemic anchialine shrimp and mollusks will be able to populate new pools, because adults and larvae move in brackish coastal groundwater through subterranean cracks (Craft et al., 2008). Low lying coastal areas that will become future anchialine habitat should be protected from development. Conservation efforts aimed at reducing introduced fish, minimizing groundwater contamination, and protecting low lying coastal area from development will ultimately allow the unique Hawaiian anchialine pool ecosystem to persist.

Acknowledgements

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Table 1: Summary statistics for all anchialine pool survey results included in the study including mean, standard deviation, median, minimum value and maximum value. Vegetation and substrate variables represent percent cover data.

Pool Characteristic	Pools sampled	Mean	Stdev	Median	Min	Max
Turbidity (NTU)	230	0.39	2.5	0	0.0	32.3
Chlorophyll *a* (ug/L)	201	1.12	5.5	0.1	0.0	66.3
Temp (Celsius)	314	23.3	2.4	23.1	19.3	29.6
Salinity (ppt)	323	10.9	5.8	11.7	1.3	26.6
Area (m^2)	398	38.8	104.8	8.0	0.5	951.5
Distance to Shore (m)	398	107.4	74.62	91.0	11	600
Maximum Depth (m)	398	0.38	0.7	0.25	0	10
Tree Canopy (%)	398	12.1	25	0	0	100
Emergent Vegetation (%)	398	8.1	23.2	0	0	100
Perimeter Vegetation (%)	398	28.7	38	5	0	100
Rocky Substrate (%)	398	71	40.8	100	0	100
Silt Substrate (%)	398	22.6	38.4	0	0	100
Sand Substrate (%)	398	5.1	17.7	0	0	100

Table 2: Contingency table analysis comparing *H. rubra* and *M. lohena* presence/ absence with categorical variables. "# of pools" is the number of pools within the category, for example 14 pools had Tilapia. These pools are grouped into "without shrimp" and "with shrimp" as % of pools and total number of pools in the species category. The χ^2 value is the Pearson's chi-squared test with Yates correction. In some cases the counts were too low in one category for the analysis. Significance level is P≤ 0.05. A total of 398 pools were surveyed.

Species						
H. rubra (present in 230 pools)	Factor	# of pools	Without shrimp % (total)	With shrimp % (total)	x^2	P-value
	Tilapia presence	14	99.6%(13)	0.4% (1)	13.2	**0.0003**
	Poeciliids presence	95	86.5%(64)	13.5%(31)	31.0	**< 0.0001**
	K. sandv. presence	14	98.3%(10)	1.7%(4)	3.9	**0.048**
	M.lar presence	15	97.8%(10)	2.2%(5)	2.9	0.09
	Proximity to development	24	96.5%(16)	3.5%(8)	5.2	**0.02**
	Land use upslope	222	44.3%(94)	55.7%(128)	0.0	ns
M. lohena (present in 53 pools)						
	H.rubra presence	230	1.9%(178)	98.1%(52)	38.9	**< 0.0001**
	Tilapia presence	14	100%(14)	0.0%(0)	1.2	-
	Poeciliids presence	95	90.6%(90)	9.4%(5)	6.1	**0.01**
	K. sandv. presence	14	100%(14)	0.0%(0)	1.2	-
	M.lar presence	15	98.1%(14)	1.9%(1)	0.2	-
	Proximity to development	24	94.3%(21)	5.7%(3)	0.0	-
	Land use upslope	222	49.1%(195)	50.9%(27)	0.4	ns

- counts too low for reliable chi-sq calculation.

Table 3. Results of generalized additive models developed for two endemic shrimp species in anchialine pools. Deviance increase means the increase in deviance resulting from dropping the selected variable from the model. The percentage increase was calculated as (deviance increase / (null deviance-model deviance)) x 100 (Knapp 2005). Non-significant p-values (ns) are > 0.01, but all P values < 0.1 are included for reference.

Parameter	Species					
	H. rubra			*M. lohena*		
Null deviance	542			312		
Degrees of freedom (null model)	397			397		
Model deviance[a]	328			152		
Degrees of freedom (full model)	362			367		
Explained deviance (% of total)	39.5			51.5		
Full model less:	Deviance increase	% deviance increase	*P* value	Deviance increase	% deviance increase	*P* value
H.rubra presence/absence	-	-	-	22.8	14.3%	**<0.001**
Location (UTME, UTMN)	45	21.0%	**< 0.001**	8.8	5.5%	ns(0.03)
Perimeter cover	25.6	12.0%	ns (0.08)	6.1	3.8%	ns
Tilapia presence/absence	21.8	10.2%	**0.002**	0.4	0.3%	ns
Poeciliids presence/absence	21.2	9.9%	**< 0.0001**	0.02	0.0%	ns
Silt Substrate	21.1	9.9%	**< 0.001**	24.8	15.5%	ns
K. sanv. presence/absence	7.3	3.4%	**< 0.01**	1.2	0.8%	ns
M.lar presence/absence	1.4	0.7%	ns	0.7	0.0%	ns
Surface area	1.3	0.6%	ns	2.9	1.8%	ns
Proximity to development	0.7	0.3%	ns	2.3	1.4%	ns
Canopy cover	0.4	0.2%	ns (0.08)	38.7	24.2%	**<0.001**
Landuse upslope	0.2	0.1%	ns	1.4	0.9%	ns

[a] Also referred to as ''residual'' deviance.

Figure 1: Maps showing the (a) island of Hawaii with locations of the five National Parks and Manuka Natural Area Reserve (State of Hawaii) shown, and (b) the distribution of anchialine pools within the Ala Kahakai National Historic Trail. The pools included in this study include the 2009-2013 surveys. Pools indicated as 1972 were documented by Maciolek and Brock in 1972 but were not visited for this study.
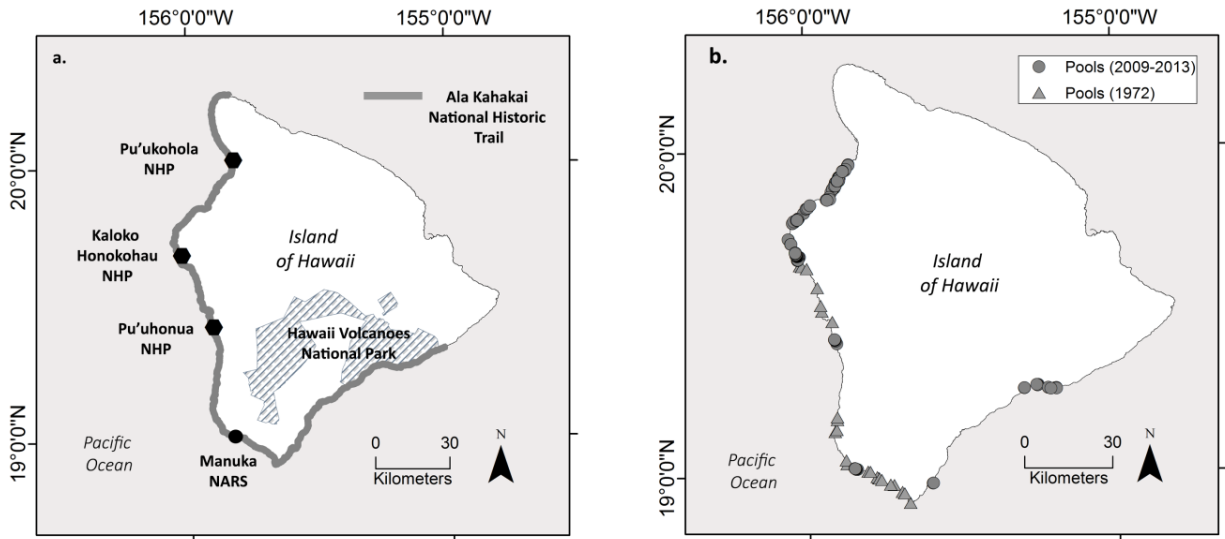
Figure 2: Salinity variation among anchialine pools and aquifers along the western and southern coastline of the island of Hawaii. Each histogram shows the frequency of pool salinities within a geographic cluster.
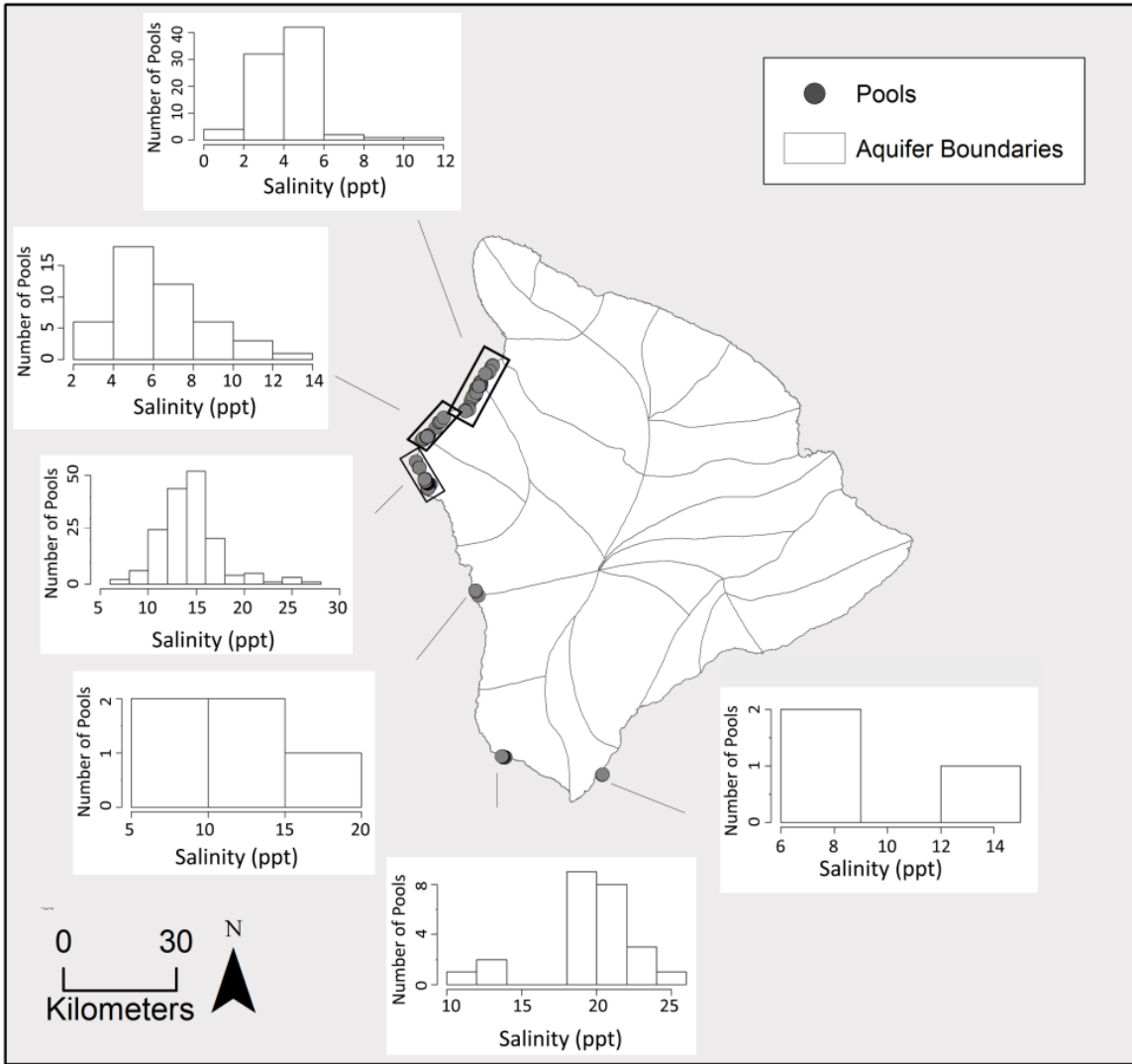
Figure 3: Maps showing distribution and percentage of pools with: (a) vegetation, (b,c) endemic anchialine shrimp species, and (d,e,f) introduced species known to prey on endemic shrimp. Pools where the biota was not observed during the time of the survey are indicated with white circles.
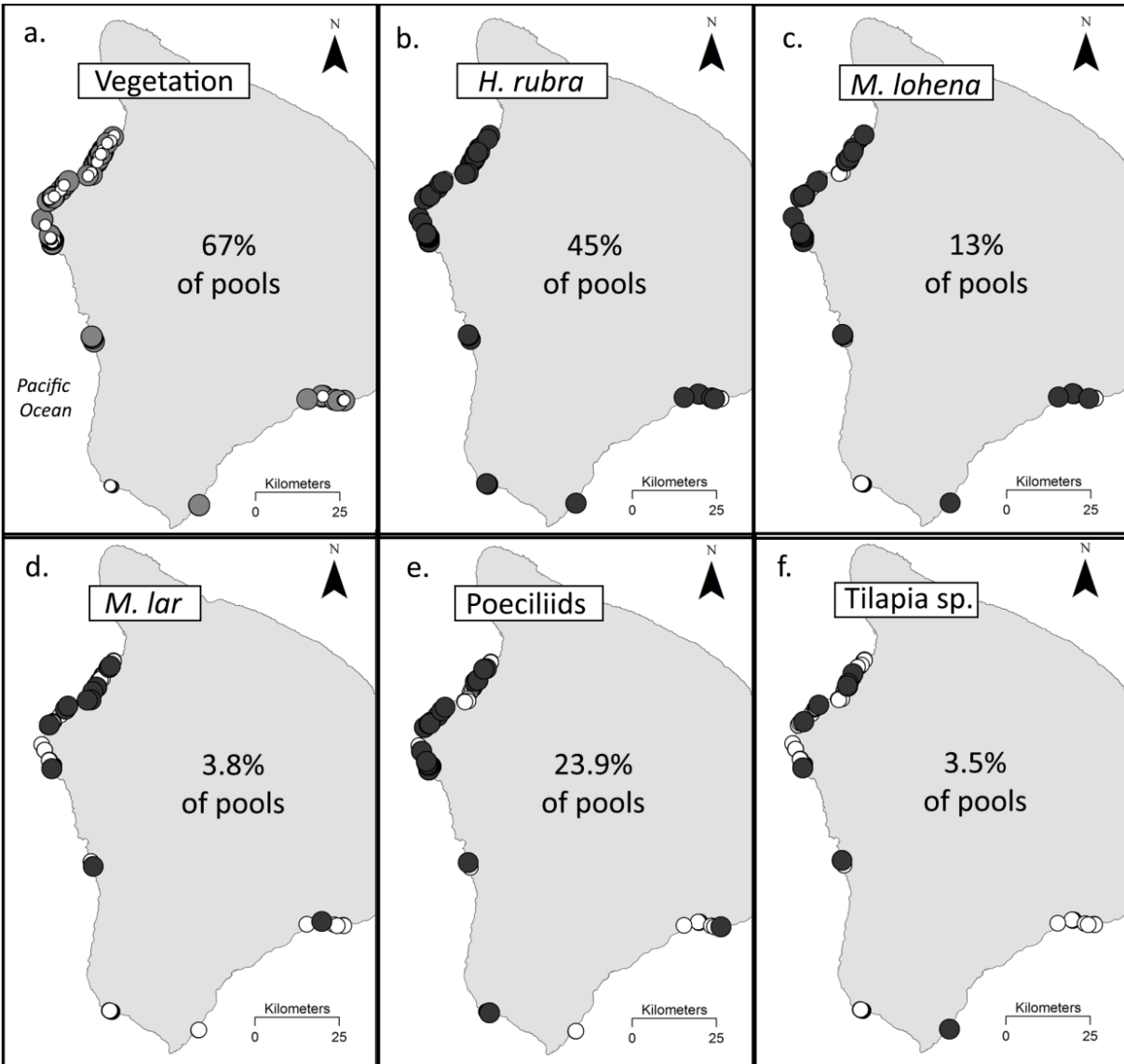
Figure 4: Boxplots comparing pool characteristics for pools with no shrimp observed (none), *Halocaridina rubra* present (hrub), and both *H. rubra* and *Metabateaus lohena* present (mloh) during daytime surveys. Kruskal – Wallis test p-values are at the top right of each plot. If p > 0.05 there is no significant difference (NS) between groups.

Figure 5: Estimated effect of each of the highly significant (p≤ 0.01) predictor variables on the probability of *Halocaridina rubra*, as determined from the generalized additive model. Note that perimeter vegetation has a p-value of 0.08 but has a high deviance value so is included. Response curves are based on partial residuals and are standardized to have an average probability of zero. For continuous variables, the dashed lines represent the approximate 95% confidence intervals, and hatchmarks along the x-axis describe the frequency of data points along the gradient of the continuous variable. For categorical (binary) variables the width of the horizontal lines in the boxplots are proportional to the frequency of data within each category not observed and present. Numbers in parenthesis are the percentage of explained deviance of each variable.
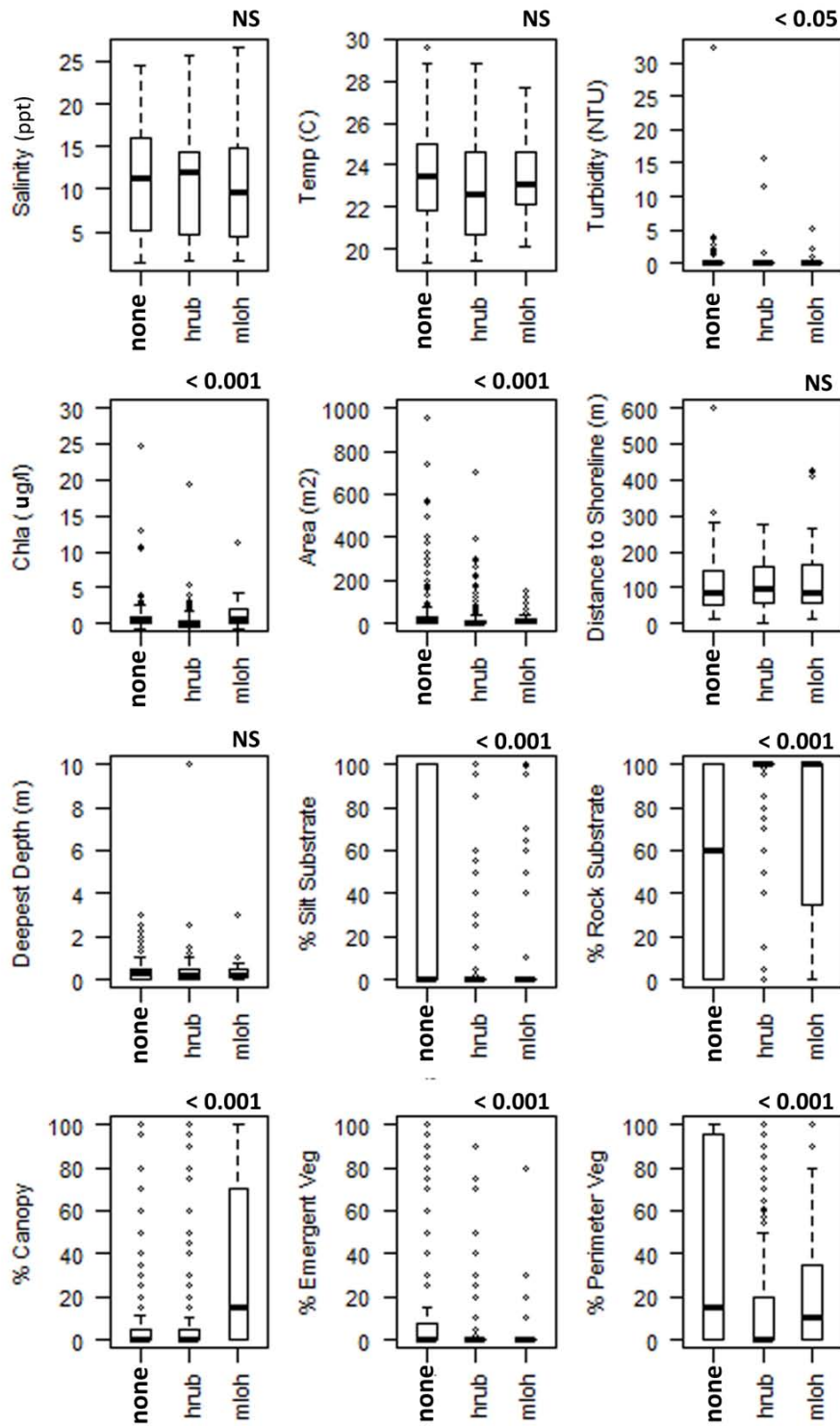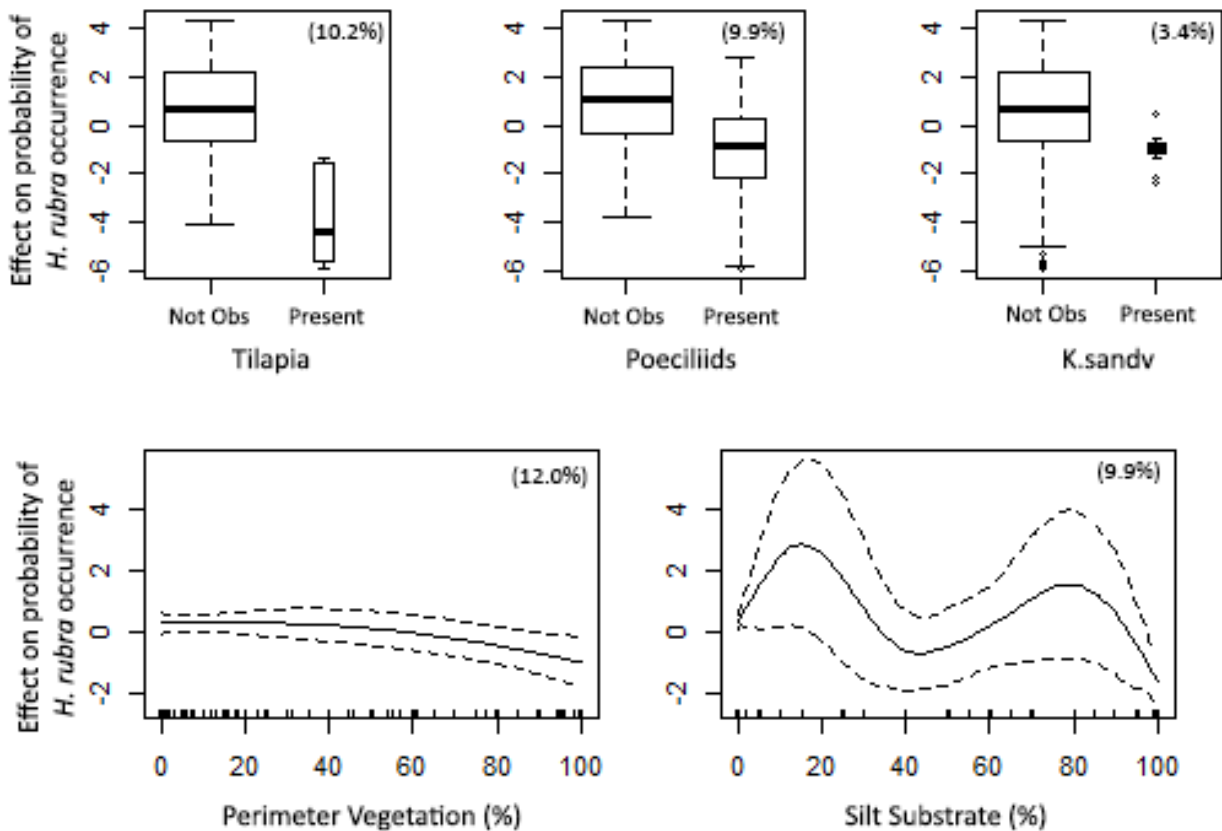
Figure 6: Estimated effect of each of the highly significant (p ≤ 0.01) predictor variables on the probability of *Metabateaus lohena*, as determined from the generalized additive model. Response curves are based on partial residuals and are standardized to have an average probability of zero. For continuous variables, the dashed lines represent the approximate 95% confidence intervals, and hatchmarks along the x-axis describe the frequency of data points along the gradient of the continuous variable. For categorical (binary) variables the width of the horizontal lines in the boxplots are proportional to the frequency of data within each category not observed and present. Numbers in parenthesis are the percentage of explained deviance of each variable.
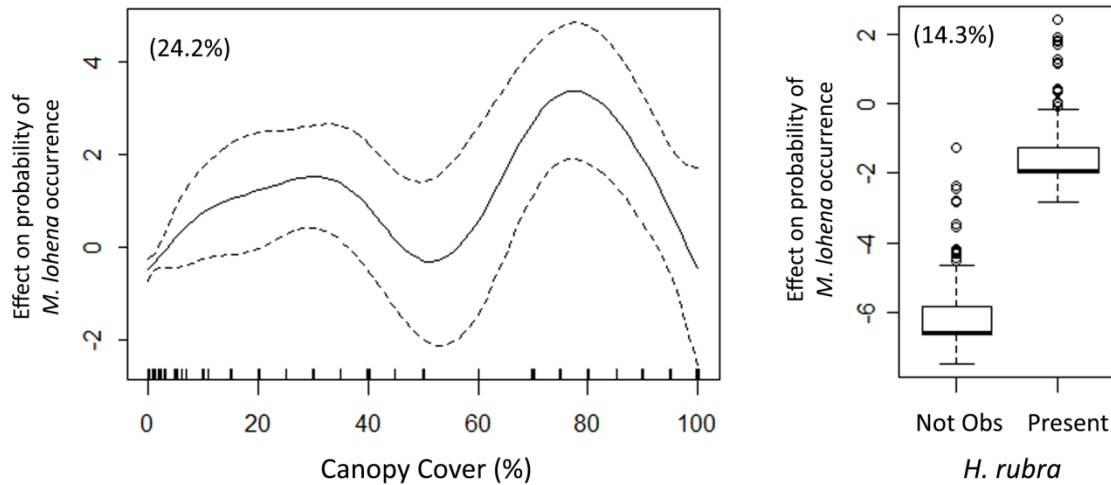
Appendix 1: Methods for Generalized Additive Modeling Approach

We developed generalized additive models (GAMs) (Knapp, 2005; Miro and Ventura, 2013) to explore data relationships and determine the relative importance of factors on endemic shrimp occurrence. GAMs do not require constant variance or normally distributed errors, and therefore are useful when dependant variables are binary (ie. presence/absence data). GAMs relax the assumption that the relationship between the dependent variable (on the logit scale) and the explanatory variables are linear. Nonparametric loess smoothing functions are used in GAMs to describe the relationships between the dependent and continuous predictor variables (Hastie and Tibshirani, 1991).

The dependent variables in the GAMs were the presence or absence of *H. rubra* or *M. lohena*. The predictive variables that were examined for potential use in exploratory GAM models represented water properties, pool characteristics, land use, and co-occurring endemic and introduced species (Table A1). Chlorophyll *a* (n=201), turbidity (n=230), salinity (n=323) and temperature measurements (n=314) were not available for all of the pools included in the dataset so were examined in separate GAM models using a subset of pools. None of the water variables were a significant term for explaining *H. rubra* or *M. lohena* occurrence, and therefore, were dropped from the full analysis.

Determining the relative importance of factors controlling distributions of a plant or animal can be confounded by spatial autocorrelation because sites that are closer to each other may be more similar than those at greater distances (Koenig 1999, Legendre 1993). Spatial autocorrelation is problematic for statistical tests which require independence between variables. Incorporating a spatial autocorrelation term into regression models is recommended otherwise environmental variables may appear to influence distributions when they are actually not statistically significant (Legendre, 1993). In the GAM models, spatial autocorrelation was accounted for with a loess smoothed term that combined the latitude and longitude of each pool (Knapp et al., 2003, Dormann et al., 2007).

Collinearity between predictor variables in multiple regressions, may confound their independent effects (Quinn and Keough, 2002). Prior to regression analyses, Pearson correlation matrices were calculated for all pairwise combinations of independent variables with full datasets. Correlation coefficients (r) ranged between -0.32 and 0.71, were assumed to be independent, and were included in the dataset (Knapp et al., 2003).

The value p_i is the probability of finding the shrimp at location *i*, and is defined as,

$$p_i = \frac{e^{\theta_i}}{1 + e^{\theta_i}}$$

where the linear predictor(*i.e.* the logit line) θ_i is a function of the independent variables. For both shrimp species, the relationship we used for θ was:

$\theta i =$
$\beta_0 + f_1(\text{SILT}) + f_2(\text{AREA}) + f_3(\text{CANOPY}) + f_4(\text{PERIMETER}_{\text{VEG}}) + f_5(\text{UTME, UTMN}) +$
$\text{TILAPIA} + \text{POECILIID} + \text{KSAND} + \text{MLAR} + \text{LU\_PROXIMAL} + \text{LU\_UPSLOPE}$

where θ_0 is the intercept or constant and θ_1 ()..θ_5 () are nonparametric loess smoothing functions that characterize the effect of each continuous independent variable on the probability of

response. Spatial autocorrelation is incorporated as the term θ_5 (UTME,UTMN) which is a smoothed surface of UTM easting and northing (Augustin et al. 1998). The terms TILAPIA, POECILIID, KSAND, MLAR, LU_PROXIMAL, LU_UPSLOPE are categorical binary variables and do not incorporate loess smoothing functions. For the models used to explain *M. lohena* distribution, and additional categorical variable HRUBRA was added to the model. The best combination of independent variables was determined by dropping each term from the model in the presence of all other variables. Analysis of deviance and likelihood ratio tests were used to test the significance of each of the independent variables on the probability of each shrimp species occurrence (Knapp, 2005). Independent variables with significant ($P \leq 0.01$) effects on shrimp occurrence were used to develop a simplified model that could be used to predict shrimp occurrence within anchialine pools.

Table A1: Explanatory factors in generalized additive models

Variable		
Physical		
	AREA	Approximate surface area (m^2)
	SILT	% silt cover on substrate
Fauna		
	TILAPIA (binary)	Presence/ absence Tilapia
	POECILIID (binary)	Presence/ absence poeciliids
	MLAR (binary)	Presence/ absence prawn *Macrobrachium lar*
	KSAND (binary)	*K. sandvicensis*
Vegetation		
	CANOPY	% canopy overhang
	PERIMETER $_{veg}$	% of pool periphery surrounded by vegetation (within 0.5 m)
Land use		
	LU_UPSLOPE (binary)	Yes if urban, resort or residential development within 1km upslope
	LU_PROXIMAL (binary)	Yes if residential or resort development surrounds a pool
Spatial Autocorrelation		
	UTMN,UTMS	X and Y coordinates from GIS
Water quality (examined separately from other variables)		
	Temperature	Celsius
	Salinity	ppt= parts per thousand
	Turbidity	NTU = Nephelometric Turbidity Units
	Chlorophyll *a*	µg/L

CHAPTER 3

Modeling potential shifts in endemic and introduced aquatic species distribution due to sea level rise: An example from Hawaiian anchialine pools

Abstract

Global mean sea levels are expected to rise up to 1.9m by 2100 changing the distribution and community structure of low-lying coastal ecosystems due to flooding, erosion, and salt-water intrusion. Although habitats will be inundated, ecosystems have the potential to shift inland and endemic species may persist if conditions are favorable. Multiple-stressors including invasive species and destructive land-use practices have caused widespread coastal aquatic ecosystem degradation over the last century. Predictions of ecosystem migration due to sea level rise need to account for these stressors, which, even at low levels, may reduce the resilience of these ecosystems. My goal was to predict potential consequences of future sea level rise on groundwater-fed anchialine pool ecosystems in Hawaii by comparing scenarios of marine and groundwater inundation with current patterns of habitat, introduced species, and land use. Results show that current habitats will be increasingly inundated by marine waters. In areas that are not developed, however, new habitat will emerge in the landscape. Because of high subsurface hydrologic connectivity, many endemic species are likely to populate these new habitats by moving through the coastal aquifer. In some areas, rising sea levels will provide surface connectivity between pools currently infested with introduced fishes (tilapia, poeciliids) and up to 46% of new or existing pools that do not contain these fish. Results demonstrate an interdisciplinary approach to examining ecosystem risk due to sea level rise and offer guidance for management and policy actions designed to protect coastal aquatic ecosystems. Successful conservation of coastal aquatic biodiversity and ecosystem services will continue to require current restoration efforts along with protection of potential habitat sites under future climate conditions.

Keywords: groundwater, brackish, coastal, modeling, remote sensing, habitat mapping, fish, invertebrates, alien species, sea level rise

Introduction

Global mean sea level will rise up to 1.9 meters by 2100 (Vermeer and Rahmstorf 2009, Parris et al. 2012). Ecosystem community structure and distribution are expected to significantly change due to flooding, erosion, saltwater intrusion, or a combination of these phenomena (Nicholls and Cazenave 2010, IPCC 2013, Williams 2013). Coastal ecosystems may shift inland if open space is available and conditions are suitable (Woodroffe 1990, Kirwan and Magonigal 2013). Ideally, future potential habitat sites can be targeted for protection and incorporated into restoration efforts so that vulnerable ecosystems and the species associated with them will persist into the future (Hannah *et al.* 2007, Stralberg *et al.* 2011).

Landscape-scale analysis of coastal ecosystem vulnerability and shifts due to sea level change are a relatively new but essential approach for conservation planning (Mawdsley *et al.* 2009). For example, preliminary work on wetlands suggests that in the absence of anthropogenic barriers in the conterminous United States, even complete drowning of existing wetlands may result in only a 22% decrease in potential wetland area because significant upland area could be available for wetland migration (Morris *et al.* 2012). However, this optimistic estimate should be tempered by realities of current and future coastal land use. Spatial analysis of sea level rise impacts on tidal wetland habitat in San Francisco Bay revealed that relatively little area is naturally available to accommodate future marshes, but that removal of levees and other barriers

to tidal action would more than double potential new habitat (Stralberg *et al.* 2011). Evaluation of the landscape where humans will restrict coastal habitat transgression represents a simple and crucial step towards understanding whether these valuable ecosystems will expand or contract with sea-level rise (Kirwan and Magonigal 2013). Furthermore, these types of spatial analyses provide direction for restoration actions, cross-boundary management planning, decisions on future infrastructure development, and ecosystem protection.

Over the last century, multiple-stressors including invasive species, elevated nutrient loads, and destructive land-use practices have caused widespread coastal aquatic ecosystems degradation (Vitousek *et al.* 1997, Paine *et al.* 1998, Foley *et al.* 2005, Halpern *et al.* 2008). Predictions of ecosystem response to changing climate and sea level rise should account for current stressors which, even at low levels, may reduce the resilience of these ecosystems to withstand change (Folke *et al.* 2004, IPCC 2013). Therefore, predictions of habitat and species shifts across the landscape may be most useful if they incorporate stressors such as introduced species or human impacts (Brook *et al.* 2008, Lee *et al.* 2008, Pereira *et al.* 2010, Oliver and Morecraft 2014).

The potential effect of sea level rise on habitat persistence and introduced species dispersal were modeled in relation to Hawaiian anchialine pool ecosystems. Anchialine habitats are tidally-influenced brackish water bodies without surface connection to the ocean (Holthuis 1973). These ecosystems include caves and open pools and are common in tropical coastal areas, such as the Indo-Pacific (Holthuis 1973, Maciolek 1983, Webb 2010), the Yucatan (Sanchez *et al.* 2002), and the Caribbean (Moritsch *et al.* 2014) where porous substrates, such as karst or lava, provide good hydrologic connectivity between the groundwater and ocean. More than 450 new species of anchialine organisms have been discovered and described over the past 25 years highlighting the importance of this ecosystem to biodiversity (Iliffe and Kornicker 2009, Weese 2012). Introduced species and land-use practices appear to be severely degrading some anchialine habitats and threatening rare species within them (Brock and Kam 1997, Iliffe and Kornicker 2009). Future sea level rise will cause some current pool habitats to become inundated as shorelines shift. At the same time there is the potential for new pool habitats to emerge inland in low lying areas (Marrack 2014). There is a high likelihood for these new habitats to be populated by anchialine shrimp and mollusk species because adults and larvae may disperse through subterranean groundwater (Kano and Kase 2004, Craft *et al.* 2008). However, rising sea levels may assist with the dispersal of invasive fishes into existing or future pools that are currently without these taxa.

In Hawaii, anchialine pools support diverse endemic biota (Maciolek and Brock 1974), including seven species listed as candidate threatened or endangered species (USFWS 2011). The dominant species are the aytid shrimp *Halocaridina rubra* and *Metabeteaus lohena*, which are located across the region (Maciolek and Brock 1974). Based on habitat associations, these two species have wide salinity tolerances ranging from 2 to 25 parts per thousand (ppt; Marrack, Chapter 2). Out of 398 pools surveyed on the west coast of the island of Hawaii, tilapia (*Oreochromis mossambicus* and other species) were present in 3.5% and poeciliids (*Poecilia reticulata, Gambusia affinis*) in 24 % of pools in a variety of land-use areas including undeveloped, resort and near urban areas (Marrack, Chapter 2). These fishes prey on endemic anchialine invertebrates and are implicated as a dominant factor causing ecosystem shifts (Brock and Kam 1997, Dalton *et al.* 2013). From a wide range of physical and biologic variables, introduced fishes were the most important variables explaining the lower probability of *H. rubra* and *M. lohena* occurrence during daytime surveys (Marrack, Chapter 2). Other, rarer anchialine

species are present in Hawaiian anchialine pools but their interactions with introduced fishes are not well documented.

In this study, the potential response of groundwater fed anchialine pool habitats to future sea level rise was modeled. Geospatial analyses and field observations were used to determine the extent of pool inundation, formation and infestation by introduced fishes under various sea level rise scenarios. Sea level rise models included 0m, 0.5m, 1m, and 1.5m relative sea level increases along with groundwater heights above mean sea level. Groundwater levels are rarely considered in sea level rise projections but have been shown to more accurately represent flooding in coastal areas with porous aquifers (Rotzall and Fletcher 2013, Marrack 2014). The objectives of this study were to: (1) determine the potential extent of pool inundation and the probable number, location, and size of future pool complexes within different land use types under various sea level rise scenarios, and (2) examine the potential extent to which elevated water levels will aid in the dispersal of introduced fishes from current locations to future pool habitats under various sea level rise scenarios. Results provide predictions of current habitat inundation as well as new habitat creation in both protected and developed coastal areas. Because of high subsurface hydrologic connectivity, many endemic anchialine species are likely move through the coastal aquifer to populate these new habitats. Results also show the potential for introduced fishes (tilapia and poeciliids) to disperse into new habitats due to surface connectivity created by rising sea levels and extreme tides. Outcomes will be used to guide management and planning efforts aimed to conserve anchialine pool habitats and the endemic species that depend on them into the future.

Methods

Study Site

The Hawaiian archipelago is the only place in the United States, other than the territory of Puerto Rico, where anchialine habitats are found, and the study site represents one of the highest concentrations of pool habitats in the Hawaiian island chain (Brock and Kam 1997). Pools are considered subaerial expressions of groundwater and are tidally influenced. Salinities in Hawaiian anchialine pools may range from 0.5 to 30 parts per thousand (Maciolek and Brock 1974). Pools may occur in bare lava substrate with no associated vegetation or on older lava flows surrounded by trees or wetland vegetation (Brock and Kam 1997). Over time pools may become filled in with new lava flows or older sediments which would explain their sparse distribution or absence on older Hawaiian islands (Maciolek and Brock 1974). Pools on the western side of the 1sland of Hawaii are located 13 to 600 m from the shoreline within National Parks, Hawaii state conservation lands, and on private lands under various stages of development (Marrack, Chapter 2). Annual rainfall in the study area ranges from 25 to 50 cm per year (Giambelluca *et al.* 2011). In this study, six sites representing two National Parks, two State Conservation, and two resort development lands were compared (Table 1, Figure 1).

Anchialine Pool Surveys

Data describing the habitat and faunal characteristics of anchialine pools were collected at each study site during daylight hours on single site visits from July 12 to August 10, 2012 and July 2 to July 15, 2013. Methods were based on previous surveys conducted by the National Park Service (NPS) between 2007-2009 (Jones *et al.* 2011, NPS 2012). Data reported in this study

included location, surface area, distance from the shoreline, salinity, and the occurrence of aquatic animal taxa. For pool complexes that connected at high tides, data was collected for the complex as a whole. Therefore, pool numbers reported for habitat surveys are lower than the overall number of pools used for the inundation models. In the case of the Makalawena site (MAKA), additional pools were identified on satellite imagery after the habitat surveys were completed. These pool locations were verified and recorded with a GPS in March, 2014 and are used in the inundation models but are not included in habitat characteristic summaries.

Pool surface area was determined within ESRI's ArcGIS 10.0 using a polygon of the pool perimeter collected in the field with a Trimble GeoXH Global Positioning System (GPS). Surface area for small pools or those with high canopy cover was calculated as pool length x width measured with a transect tape at the high water line. Distance from coastal shoreline was calculated in ArcGIS as the Euclidian distance between the shoreline and the closest edge of each pool. Salinity was collected at the surface of each pool. Previous work has indicated that although pools may exhibit variability in water properties with depth, the surface of each pool remains relatively constant on annual and daily timescales (Bienfang *et al.* 2011, NPS 2012, Marrack Chapter 2).

Endemic pool species as well as introduced fishes were recorded as present or absent based on visual surveys during daylight hours. *Poecilia reticulata, Poecilia mexicana,* and *Gambusia affinis* were present in pools but were not always distinguishable in the field so were combined as poeciliids for statistical analysis. Tilapia species were also grouped together for this study. *Oreochromis mossambicus* probably makes up the majority of tilapia found on the island of Hawaii, but this is not certain since other tilapia species exist on Oahu and Kauai, and they are difficult to identify as juveniles (Mackenzie and Bruland 2012). Most pools were small and shallow enough that it was possible to visually examine the entire water body from the pool edges. Larger pools, where the center and bottom were not visible from the surface, were examined using mask and snorkel.

Modeling Methods

Sea level rise scenarios were combined with current pool locations and conditions at the six sites to determine the extent of ecosystem change expected under future sea level change. Under each scenario, the inundation of existing pools as well as the size, location and number of new pools that will emerge on the landscape were mapped. To model future anchialine pool locations, gridded surfaces of sea level with and without groundwater heights were created using ESRI's ArcGIS 10.1 (Marrack 2014). These water surfaces were then compared to 1 m resolution topographic surfaces (Digital Elevation Models or DEMs) to determine where anchialine pools would be expected to occur. Areas where the water surface was higher than the topographic surface were classified as water bodies. Areas that became flooded in the inundation model but were not connected overland to the ocean were considered potential new anchialine pools. Subsurface hydrologic connectivity between the coastal aquifer and the ocean was assumed to be high (Oki 1999, Bauer 2002, Marrack 2014).

To determine if sea level rise has the potential to aid in dispersal of introduced fishes from infested to uninfested habitats, I examined surface connectivity between pools under sea level rise scenarios at extreme tides. One assumption was that unlike endemic anchialine shrimp and mollusk species, introduced fishes can only disperse over land through surface water connections between pools, but may only need 3 mm of water depth to move (Alemadi and Jenkins 2008). The assumption that fish do not commonly disperse through subterranean

groundwater in the Hawaiian anchialine ecosystem is supported by personal observations of anchialine pools within the study area where uninfested pools are found within 4 meters of pools containing fish, and they have persisted this way for over 10 years. Another assumption was that the current suite of non-native fishes are able to survive in a range of temperature and salinity environments, because they are generalists and are currently found in a wide range of pool habitats (Marrack, Chapter 4).

Sea Level Rise Scenarios

Scenarios of sea level rise are a useful method for illustrating future conditions, because they do not assume a particular timeframe and may incorporate various uncertainties (NRC 2012). Estimates of future sea level carry uncertainty due to a number of global, regional and local mechanisms (IPCC 2013). The rate and magnitude of ice sheet loss, particularly in Greenland and West Antarctica, are a major source of uncertainty for global sea level rise predictions (Vermeer and Rahmstorf 2009, NRC 2012, IPCC 2013). At the regional and local level, sea level rise will be affected by vertical land movement including subsidence or uplift. Maximum water levels will be a result of ocean dynamics including tides, storms and hurricanes (Tebaldi 2012, Ruggiero 2013, Merrifield 2013), and basin wide processes such as the Pacific Decadal Oscillation and ENSO (IPCC 2013, Scafetta 2013). Many of these regional and local factors can only be predicted with high uncertainty for the study area; therefore, a scenario approach was used.

Sea level rise was mapped in 0.5 m increments (0 m, 0.5 m, 1 m, 1.5m). Dates at which these heights are projected to occur ultimately reflect future global carbon emissions (IPCC 2013). For example, based on the Vermeer and Rahmstorf (2009) model, sea levels could rise between 0.3 m to 0.53 m by 2050, and may reach 0.75 m to 1.9 m by 2100. On the island of Hawai'i tide gauges at Kawaihae and Hilo have recorded an average relative sea level rise of 3.5 mm/yr (Vitousek et al. 2009). These data fit the measured global averages of sea level rise (Church and White 2011). However Topex/Poseiden and Jason-1 satellite altimetry data indicate that the global acceleration of sea level rise due to thermal expansion and melting ice has not reached Hawai'i and that the local long-term trend has been approximately 1.5 mm/yr (Meyssignac and Cazenave 2012). Based on this information, the difference between local tide gauge measurements (3.5 mm/yr) and the satellite altimetry measurements is most likely due to island subsidence rates. Subsidence for the island of Hawaii is estimated to be an average of 2.6mm/yr due to loading of the lithosphere by Kilauea volcano (Moore and Clague 1992, Zhong and Watts 2002). Although it is unclear if local subsidence rates and regional oceanographic processes will remain constant, sea level in Hawaii will continue to rise and rates are expected to increase by the middle of the 21st century (Marra *et al.* 2012).

Tides

Tides were incorporated into sea level models because higher tides increase coastal flooding and anchialine pools undergo tidal fluctuations (Marrack 2014). In Hawai'i, tides are semi-diurnal with the highest recorded tide at 0.74 m above Mean Sea Level (MSL) at the local tidal benchmark (Kawaihae -1617433B) in 1993 (NOAA 2012). Some anchialine pools become dry at low tides but are populated by endemic shrimp at higher tides, therefore sea level scenarios used to determine new pool locations were created to reflect local Mean Higher High Water (MHHW) or 0.374 m above MSL (1617433B; NOAA 2012). The value used for the

extreme tide level in this study was 0.7 m above MSL. This elevation is the mean of the six most extreme annual tides observed at the local tidal benchmark from 2001 to 2011 (NOAA 2012).This value concurs with the time-averaged annual maxima water level empirically derived by Merrifield et al. (2013) for the same tide gauge (66.4 cm $\pm$ 3.1 (2 S.E.)).

Groundwater

In coastal regions, groundwater can play an important role in the location and community composition of ecosystems, especially those located slightly inland from shore (Doyle *et al.* 2010, Marrack 2014). In porous, unconfined coastal aquifers, the groundwater table is elevated above mean sea level sloping up and away from the shoreline and typically moves with the ocean surface (Bjerklie *et al.* 2012, Oki 1999). As a result, groundwater may actually exacerbate inundation as sea levels rise (Bjerklie *et al.* 2012, Rotzoll and Fletcher 2013). Along the west coast of the island of Hawaii, Marrack (2014) showed that incorporating observed groundwater levels into models of current sea level improved detection of known anchialine pools up to 37%. The research presented here is the first time groundwater levels have been incorporated into models of future sea level rise for the island of Hawaii.

Theoretically, in a homogeneous unconfined coastal aquifer with constant recharge from an inland source, the groundwater level should be a function of the square root of distance from the coast (Glover 1959). On the west coast of Hawaii, the relationship between observed groundwater heights and distances from shore has been calculated as $h = 0.00989 \, x^{1/2} + 0.16734$, where h is the average groundwater height in meters above MSL and x is the distance from shoreline in meters (R = 0.93; Marrack 2014). This equation was incorporated into sea level rise models by creating a raster representing the Euclidean distance from shoreline (2 m resolution) using ArcGIS Spatial Analyst tools (ESRI 2011). A raster representing mean groundwater height above MSL was then calculated by applying the linear regression equation to each pixel.

A tidal efficiency component was then added to the groundwater raster to incorporate tidal effects on groundwater heights. Tidal effects decay with distance inland from shore and can be represented by the tidal efficiency ratio which is 1 at the shoreline decreasing to 0 inland where there is no tidal effect (Todd 1980). Tidal efficiency represents the ratio of mean daily groundwater tidal range at a site to mean daily ocean tidal range. For the study area, Marrack (2014) used observed ocean and groundwater tide heights to calculate: $\log(y) = -0.00034 \, x - 0.26646$, where y is the tidal efficiency and x is the distance from shoreline in meters (R = -0.92). Raster surfaces representing tidal influence during MHHW and extreme tides were combined with the groundwater surface over MSL raster to create the groundwater models used in subsequent analysis. Individual groundwater models were created at each sea level scenario (0m, 0.5m, 1m, 1.5m) based on the unique shoreline predicted for that sea level.

Because annual rainfall on the island of Hawai'i has decreased in the past century and may continue to do so with climate change (Giambelluca et al. 2011), groundwater levels in the future may be lower (Oki 1999). To account for this potential decrease in future groundwater levels, another set of scenarios were made without groundwater. Within this study, sea level rise scenarios that incorporate groundwater can be considered an upper bound to future flooding due to rising ocean levels while scenarios without groundwater are a lower bound.

<u>Digital Elevation Models</u>

Topographic data were derived from Federal Emergency Management Agency (FEMA) – LiDAR data collected along the coast in 2006 for the Hawaiian Islands (Dewberry and Davis 2007). LiDAR coverage includes the water line to the 15m elevation contour with an average point distance of 0.9 m for bare earth returns. Data were horizontally referenced to the North American Datum 1983 (NAD83) and were reported as horizontally accurate to 0.3 m with 68.2% of laser returns. The North American Vertical Datum 1988 is specific to the Continental US and does not exist for Hawai'i, therefore the vertical datum was referenced to a Local Tidal Datum with 0 m = Mean Sea Level (MSL). For bare earth surfaces the reported mean vertical error for the LiDAR points was 0.03m and for all terrain types was 0.05m (Dewberry and Davis 2007).

Digital elevation models (DEMs) were created from the LiDAR bare earth returns using ESRI's ArcGIS. First, Triangular Irregular Networks (TINs) were created from LiDAR point files. TINs were then converted to a raster format using linear natural neighbor interpolation. This interpolation technique constructs DEMs that retain original peak and valley elevation values which are useful for finding small isolated pits that exist in the lava surfaces (Maune 2007). Prior to subsequent analysis, DEMs were corrected by -0.25 m to account for vertical offsets in the LiDAR data detected during accuracy assessments that compared LiDAR DEM data to National Geodetic Survey benchmark orthometric heights (Marrack 2014).

<u>Analysis</u>

Within AcGIS 10.1, each scenario was compared to the topographic surface (DEMs) of a site. Areas where the water surface was higher than the topographic surface were classified as water bodies and converted to polygons. Polygons within 1m of each other were aggregated. Then, polygons were visually examined over Quickbird true color imagery (USDA 2006) to eliminate ocean surfaces and fishpond embayment features from the anchialine pool category. For each scenario the inundation of current pools was calculated. A pool was considered inundated if it overlapped with an ocean or fishpond surface. The number, surface area, and location of new pools created at each scenario were also calculated. New pools were defined as completely separated from other water bodies at MHHW, were at least 10m from the shoreline, and did not overlap current pool surfaces. Also, inundation that occurred on unnatural surfaces such as paved areas or golf course were not considered potential new pool habitat. All new pool calculations are relative to current land use conditions.

To examine potential dispersal of fish due to sea level rise, sea level scenarios were examined as time steps with current conditions as the first step, 0.5m next and so on. At each step, the extreme tide scenario was used to determine flooding extent. Flooding extent polygons that overlapped with pools containing introduced fish were assumed as potential dispersal routes able to infest fishless pools. If pre-existing pools or newly created pools overlapped with the flood extent polygons they were ranked as a potential fish pool, enumerated, and considered a source of fish for the next sea level step (Figure 2). Ocean surfaces were not included in the flooding extent polygons because tilapia and poeciliids are not observed living in marine conditions in Hawai'i and would therefore not be transported by marine flooding. Fishpond embayments at KAHO connect with narrow channels to the ocean but are lower salinity than marine habitats and contain tilapia and poeciliids (Mackenzie and Bruland 2012). These embayments were considered as potential sources of fish and were included in analysis. For

simplicity, the fish dispersal analysis were only examined using sea level rise models without groundwater and therefore represent a conservative estimate of connectivity.

Results

Current Habitat Characteristics

Across all six sites, 405 pools were mapped with a GPS and 348 pools were surveyed for habitat characteristics. Salinities ranged from 1.3 to 25.6 ppt across all sites with the highest mean salinity of 14.5 ± 3.2 ppt at the KAHO site (Table 2). The lowest salinities were 1.3 ppt in pools from the ABKW site where the mean was 3.7 ± 1.1 ppt. Pool surface areas ranged from less than $1 m^2$ to $7931 m^2$ for one very large pool within the Waikoloa Pond Preserve. This large pool was the reason the mean pool size for the WAIK site ($1466 m^2$) was so much larger than the mean pool size for all other sites ($14 - 124 m^2$). Pool distance to the ocean shoreline ranged from 10 to $600 m^2$ but averaged $40 - 135$ m at all sites.

The most common endemic anchialine species observed during daylight surveys were *Halocaridina rubra* and the candidate endangered species *Metabateaus lohena.* At the ABKW site*, H. rubra* occurred in 76% of 71 total pools while *M. lohena* occurred in 18%. At the MAKA site*, H. rubra* occurred in 50% of 44 total pools while *M. lohena* occurred in 14%. *Halocaridina rubra* occurred in 46% of pools surveyed at PUHO (n=11) and 60% at KAHO (n=184), while *M. lohena* was present in 18% and 12.5% respectively. The lowest percent of pools with endemic shrimp was at MAUNA resort property where *H. rubra* was in 29% of 11 pools. Other endemic anchialine species that were seen across the sites in less than 1% of pools included gastropods (*Nerita picea, Neritina vespertina, Theodoxus cariosus,* and *Thiaridae* species), the endemic prawn *Macrobrachium grandimanus,* the glass shrimp *Palaemon debilis* and the candidate endangered damselfly *Megalagrion xanthomelas.*

Introduced fish were found in pools throughout each site (Table 2). Poecillids were more common than tilapia and occurred in 85 pools across all sites with up to 57% of pools at any one site (MAUNA; Table 2). Tilapia were present in a total of 13 pools across all sites and were at every site but MAUNA.

Endemic shrimp only co-occurred with tilapia in one pool and were in extremely low densities (3 per 10 m^2) during the time of the survey. *H. rubra* co-occurred with poeciliids more frequently and were observed in 35% of the pools with poeciliids. At the time of surveys, *M. lohena* only occurred in 2 pools with poeciliids.

Habitat Inundation

As expected, rising sea levels will inundate current pools at all sites connecting them to the ocean. Projections of pool inundation vary by site and scenario (Figure 3, Table 3). Under the 0.5 m sea level rise scenarios, relatively minor percentages of pools become inundated at all sites (0 -13%) except at the Waikoloa resort site (WAIK; 92%) and the KAHO national park site when groundwater levels are included (32%). At the WAIK site, all but one current pool are within 72 m of the current shoreline and a rise of only 0.5m will cause these pools to connect overland to the ocean (Figure 3). At the KAHO site, incorporating current day groundwater levels in the scenario causes pools currently sitting at the edge of fishpond embayments to merge with fishponds. When groundwater is not part of the scenario, only 8% of pools are inundated. Under the 1m and 1.5 m scenarios, increasing numbers of current pools will become inundated

by marine waters at all sites. For the 1 and 1.5 m scenarios, groundwater causes a large difference in the number of pools inundated at the MAKA and ABKW sites. When groundwater is incorporated into the models, more pools merge with current fishpond embayments (Figure 5b).

Formation of New Pool Habitat

Although current pools will become inundated as sea levels rise, new pools will emerge in the porous basalt substrate (Figure 4c,d). Under all scenarios, the greatest number of new pools will form within sections of ABKW and MAKA as well as in the KAHO national park (Table 4, Figure 3). For example, relative to current conditions at ABKW, up to 238 new pools will form at 0.5m sea level rise, 336 at 1m sea level, and 308 at 1.5m. Once new pools are formed, they may be inundated by subsequent sea level rise, but additional pools form inland in the rugose substrate (Figure 4c,d).

Scenarios incorporating groundwater cause greater inland flooding than the same scenarios without groundwater. As a result, at all sea levels and sites, total pool surface area is higher for scenarios with groundwater compared to the same sea level scenario without groundwater (Table 4, Figure 5a). The only exceptions are at KAHO and MAKA where a 1.5m sea level with groundwater creates 3617 m^2 and 67 m^2 less pool surface area compared to the same scenario without groundwater respectively. This result is due to the fact that when groundwater is incorporated, some pools merge with fishpond embayments (Figure 5b).

Increased pool surface area due to groundwater is not always reflected in pool counts. For example, at MAUNA, MAKA, and PUHO, total pool surface area increases when groundwater is incorporated into 1m and 1.5m scenarios however total pool and new pool counts decrease (Table 4). In these cases, smaller pools in proximity to one another may merge into one pool when groundwater is included in the model.

Land Use Effects

Land use does affect potential pool formation. Within WAIK and MAUNA resorts, increasing sea levels will cause inland flooding but in the models, most of the flooding will occur on golf course turf or paved areas (Figures 1 and 4a,b). Unless these areas were to be converted back to lava substrate, pools will not form in these areas. Some sections of the coastline are not developed but will not be conducive to pool formation because of high elevation cliffs such as the southern section of PUHO.

Dispersal of Introduced Fishes

Rising sea levels will aid in the dispersal of introduced fishes from current infested pools to uninfested existing and future pool habitats (Figure 2). Introduced fishes currently inhabit at least 27% of the existing anchialine pools (n=405) included in this study and are present at all sites (Table 4, Figure 6). Additionally, tilapia and poeciliids occur in fishpond embayments (Figure 1: KAHO, MAUNA) and man-made resort water features (MAUNA, WAIK).With a 0.5 m sea level rise at an extreme tide, fish will have the potential to disperse from current habitats to uninfected pools raising the total percent of pools potentially infested with fish to 38.6%. Percentages range from 27 to 70% pool infestation potential at different sites (Table 4). The percentage of potentially infested pools decreases with further increases in sea level rise, because some of the source areas will become totally inundated by the ocean environment (Table 4). For

example, at all sites but KAHO, potential infestation of pools drops to 0-17% at the 1.5m sea level rise scenario. These results are based on models that do not include groundwater, high wave events, or human transport of fish.

Introduced fishes currently occupy a range of pool sizes but poeciliids are commonly found in smaller pools than those occupied by tilapia (Figure 7). Poeciliids are found in pools as small as 0.6 m^2 with an average surface area of 77 ± 139 (stdev) m^2. Tilapia have been found in pools as small as 6.3 m^2 with an average surface area of 179 ± 223 m$^{2.}$ Both are commonly found in large ponds (> 400 m^2) or fishponds alone or together. A comparison of pool sizes currently occupied by introduced fishes with pools that will be created under future sea level scenarios indicates that new pools will be of the range of sizes currently occupied by both poeciliids and tilapia. In addition, numerous pools will be created that will be smaller than currently observed with tilapia, but will be large enough to support poeciliids.

Discussion

Efforts to conserve coastal systems under changing climates have begun to include geospatial predictions of future habitat so that these land areas can be protected (Mawdsley *et al.* 2009). As sea levels rise, many low elevation coastal ecosystems will become inundated more frequently through the tidal cycle until they are eventually underwater 100% of the time. Ecosystems may gradually migrate inland if conditions are appropriate and open space is available (Doyle *et al.* 2010, Stralberg *et al.* 2011). Results from this study, which examined 405 anchialine pools along 24 km of coastline, show that although current pools will become increasingly inundated as sea levels rise, new pools will form inland. Because there is high subsurface hydrologic connectivity within the coastal aquifer (Oki 1999), there is a high likelihood for these new habitats to be populated by anchialine shrimp and mollusk species which may disperse through subterranean groundwater (Craft *et al.* 2008, Kano and Kase 2004). Additionally some new habitats may be colonized by non-native fishes that disperse through overland surface water connections.

Sea Level Rise Models

This study is one of the few examples incorporating groundwater into predictions of ecosystem shifts under sea level rise (Bjerklie *et al.* 2012, Rotzoll and Fletcher 2013). The methods applied may be useful for examining sea level rise effects on other ecosystems dependent on groundwater in unconfined coastal aquifers. Prior to model construction, the relationship between groundwater level and distance from shoreline should be calibrated to local conditions. In this study, the groundwater models were based on groundwater levels near Kāloko-Hōnokohau National Historical Park, which are assumed to be relatively representative of other areas in the study area (Marrack 2014). Within the study area, groundwater levels may become lower in the future due to increased water withdrawal (Oki 1999, Thornberry-Ehrlich 2011) and decreasing annual precipitation (Giambelluca *et al.* 2011). Therefore, the sea level models that incorporate current groundwater levels in this analysis may be considered an upper bound to future inland flooding. Although the scenarios without groundwater are considered a lower bound to flooding, it is assumed that some groundwater is needed for anchialine ecosystems to exist.

Due to uncertainties in future groundwater levels as well as limitations of the LiDAR data, calculations regarding pool formation, size and placement should be considered estimates

of future habitat extent. Accuracy assessments that examined the ability of LiDAR to detect current pool locations within the study area showed that LiDAR was not able to detect pools in caves or narrow fissures (Marrack 2014). Furthermore, LiDAR point data are sometimes spaced farther apart than pool areas, effectively missing small pools ($<5m^2$) pools 59% of the time. Although the models may under predict the locations of small or cave-like pools, the general patterns of pool inundation and formation along with the locations of expected new pool complexes should accurately reflect future conditions under sea level rise.

Geospatial predictions of coastal change typically include coastal elevation data and local sea level rise scenarios (Gesch 2009), but may also incorporate wave dynamics and erosion models (*e.g.* Reynolds *et al.* 2012). Because anchialine pools are typically found in bedrock and are usually over 15 m inland from the shore, erosion and wave run-up are relatively unimportant for modeling sea level rise impacts to this ecosystem. Anchialine pools closest to the coast may be filled with sediment and ocean water during extreme wave events, but this is usually a temporary impact because groundwater rapidly flushes the system (personal observation).

Anchialine Pool Community Response to Sea Level Rise

For coastal ecosystems that are dependent on groundwater, changes to groundwater heights and salinities may drive shifts in community structure (Doyle *et al.* 2010). Based on anchialine pool surveys along 280 km of coastline on the western and southern shores of the island of Hawai'i, Marrack (Chapter 2) have found that the dominant anchialine shrimp species *Halocaridina rubra* and *Metabeteaus lohena* have fairly wide salinity tolerances and are found in salinities ranging from 2 to 25 ppt. Pool salinities vary by aquifer and may become less saline with increasing distances from the ocean, but the same dominant species are found throughout. These observations indicate that increasing pool salinity due to sea level rise will not necessarily lead to changes in pool community structure unless marine conditions dominate. However, it is unclear if *H. rubra* and *M. lohena* are able to complete their entire life cycle in the full range of salinities measured in pool habitats. It is also unclear how sea level rise will affect the subterranean habitat except that some parts of the aquifer will become more saline. Furthermore, salinity tolerances are unknown for rarer endemic anchialine shrimp and mollusk species found within restricted ranges (Sakihara 2012). Work examining species-specific salinity tolerances is needed to understand how anchialine communities may shift with sea level rise. This is especially important because reduced rainfall and increased withdrawal could lead to lower groundwater levels and elevated salinities in the future.

Results show that sea level rise with extreme tides has the potential to aid in dispersal of introduced fishes from currently infested pools to uninfested habitats. Fish may not disperse immediately, but over time will spread into new habitats. The connectivity models used in this study do not account for human aided or bird aided dispersal, groundwater levels, or wave events that may increase infestation rates. In other freshwater systems it has been well documented that Tilapia (*Oreochromis mossambicus* and other species) and poeciliids (*Poecilia reticulata, Gambusia affinis*) have a strong negative effect on native biodiversity due to predation and habitat modification (Global Invasive Species Database 2010). Because these fish are tolerant to a wide range of ecological conditions, have highly generalist dietary requirements, and have rapid reproductive rates, they have become successfully established in almost every region in which they have arrived (Canonico *et al.* 2005, Deacon *et al.* 2011). Empirical data on the effects of fish predation in anchialine pool systems is limited. However, stable isotope analysis indicates that mosquitofish (*Gambusia affinis*) do eat the dominant endemic grazer (*H. rubra*) in

Hawaiian anchialine pools (Capps *et al.* 2009). Additionally, Marrack (Chapter 2) showed that out of numerous abiotic and biotic factors, tilapia and poeciliids were the most important factor explaining the absence of the anchialine shrimp in pools during daylight surveys. Tilapia and poeciliids already inhabit a range of pool habitats in Hawai'i, and it is likely that if they disperse into new habitats, they will continue to thrive. One exception is that tilapia may be restricted to occupying slightly larger pools therefore the smallest pools ($< 5m^2$) may be refugia from these fish. It would be best to target fish removals in locations where current pools threaten to infest new pools as sea levels rise.

Land-use and Coastal Topography Limit Future Habitat Formation

The lowest numbers of current and future pools relative to coastline length exist at the two resorts (WAIK and MAUNA) as well as at the PUHO national park. At the resorts, low lying land has been converted to paved areas or golf courses and relatively little area exists for new pool formation. Coastal planning should consider utilizing geospatial models of sea level rise to determine where future pool habitats will emerge on the landscape so that these areas can be protected from development.

Not all coastal areas are ideal for anchialine pool formation. The southern portion of the PUHO national park shoreline consists of 10- 15m high cliffs. The only anchialine pool in this southern section of the park consists of an old well set back from the shoreline and dug down to groundwater level. Interestingly, the well contains endemic anchialine shrimp, which suggests that habitat for native biodiversity may be created in some areas by digging down to the groundwater.

Conclusion

As sea levels rise and current pools become inundated, high subsurface hydrologic connectivity will cause future pools to emerge in the rugose lava terrain. Endemic anchialine shrimp and mollusks will be able to populate new pools, because adults and larvae move in brackish coastal groundwater through subterranean cracks (Craft *et al.* 2008). Low lying coastal areas that will become future anchialine habitat should be protected from development. Because sea level rise will provide a mechanism for introduced fishes to disperse from infected to uninfected habitats, fish removals will help protect future ecosystem integrity. Conservation efforts aimed at reducing introduced fish, minimizing groundwater contamination and withdrawal, and protecting low lying coastal area from development will ultimately allow the unique Hawaiian anchialine pool ecosystem to persist in the face of climate change.

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Table 1: Study sites with total number of pools, number of pools with fish, and total length of coastline. Current pools do not include fishponds with direct access to the ocean, man made, or modified pools in which reef fish or koi are maintained.

Study site	Site Name	Land Use	Number of identified pools	Length of Coastline (km)
Waikoloa resorts	WAIK	Resort	12	1
Maunalani resorts	MAUNA	Resort	8	4.5
Anaehoomalu to Keawa Iki	ABKW	Undeveloped (State conservation and private lands)	80	6
Makalawena	MAKA	Undeveloped (State conservation and private lands)	75	4.2
Puuhonua O Honaunau National Historic Park	PUHO	National Park	14	3.9
Kaloko Honokonau National Historical Park	KAHO	Natonal Park and State conservation lands	216	4.1

Table 2: Summary of habitat characteristic data collected at all sites. Salinity, surface area and distance are shown as mean ± standard deviation.

| Study Site	Salinity (ppt)	Surface Area (m²)	Distance to Shoreline (m)	% with poeciliids	% with tilapia	% with H. rubra	% with M. lohena	# Surveyed pools
WAIK	3.5 ± 4.5	1466 ± 3197	43 ± 23	0	18	36	9	11
MAUNA	4.1 ± 2.7	91 ± 96	94 ± 109	57	0	29	14	7
ABKW	3.7 ± 1.1	39 ± 76	135 ± 88	37	7	76	18	71
MAKA	6.1 ± 2.9	124 ± 223	96 ± 52	43	7	50	14	44
PUHO	5.2 ± 6.7	45 ± 78	121 ± 69	18	18	46	18	11
KAHO	14.5 ± 3.2	14 ± 48	113 ± 69	19	0.5	60	12.5	184

Table 2: Percentage of anchialine pools inundated at various sea level rise scenarios within six sites. The total number of current pools known at each site are included in parenthesis. Water level models with groundwater (GW) and without groundwater (no GW) are included.

| Site	Ground-water Model	Percent of Current Pools Inundated under Sea Level Rise Scenarios (m)		
		0.5	1	1.5
WAIK (12)				
	no GW	92	92	92
	GW	92	92	92
MAUNA (8)				
	no GW	13	13	38
	GW	13	13	38
ABKW (80)				
	no GW	0	1	50
	GW	0	36	60
MAKA (75)				
	no GW	0	27	79
	GW	0	62	98
PUHO (14)				
	no GW	0	36	57
	GW	0	36	57
KAHO (216)				
	no GW	8	75	88
	GW	32	82	89

Table 3 : The number and surface area of pools created under sea level rise scenarios at six sites on the western coast of the island of Hawai'i. Pools were enumerated for scenarios with (GW) and without (no GW) groundwater levels. All calculations of new pools are relative to current conditions.

| Site	Sea Level Rise (m)	Number of New Pools		Total Pool Area (m2)		Total Number of Pools		Average Pool Area (Mean ± SD)		Pools with Fish Access (% of total)
		no GW	GW	no GW	GW	no GW	GW	no GW	GW	no GW
WAIK										
	0.5	2	5	784	919	3	6	392 ± 390	184 ± 350	33.3
	1	4	5	1312	1572	5	6	328 ± 404	314 ± 427	20.0
	1.5	5	1	13	28	6	2	3 ± 1	28	16.7
MAUNA										
	0.5	20	15	385	1005	27	22	19 ± 30	67 ± 77	70.4
	1	18	9	811	1120	25	16	45 ± 109	124 ± 237	32.0
	1.5	30	16	2013	2440	35	21	67 ± 239	153 ± 365	11.4
ABKW										
	0.5	196	238	5015	7513	276	318	26 ± 62	32 ± 76	29.7
	1	302	336	18762	25492	381	387	62 ± 236	76 ± 409	11.5
	1.5	288	308	12422	12833	328	340	43 ± 173	42 ± 164	1.2
MAKA										
	0.5	341	362	6464	8248	342	437	19 ± 51	23 ± 57	39.5
	1	475	428	12444	15822	530	457	26 ± 75	37 ± 124	22.6
	1.5	371	374	12310	12243	387	376	33 ± 150	33 ± 169	0.5
KAHO										
	0.5	225	131	3977	5682	423	277	18 ± 44	44 ± 96	31.7
	1	258	122	6622	10819	313	162	26 ± 87	89 ± 304	46.3
	1.5	147	66	11332	7715	173	89	77 ± 417	117 ± 455	32.9
PUHO										
	0.5	34	37	322	484	48	51	10 ± 30	13 ± 41	27.1
	1	46	26	1486	1665	55	35	32 ± 64	64 ± 107	0
	1.5	32	23	1063	1084	38	29	33 ± 74	47 ± 69	0

Figure 1: Location of sites on the island of Hawaiʻi from north to south: Kawaihae tidal Benchmark (BM), Maunalani Resort (MAUNA), Waikoloa Resort (WAIK) Anehoomalu Bay to Keawa Iki Bay (ABKW), Makalawena site (MAKA), Kaloko Honokohau National Historical Park (KAHO), Puuhonua o Honaunau National Historical Park (PUHO). Corresponding site maps (b-g) show locations of current anchialine pools and land cover/land use (NOAA 2011). Land cover/land use types include bare basalt, turf grass, and impenetrable surfaces such as roads and buildings. Unidentified land cover land/land use (white) is a mix of undeveloped tree, shrub and grass cover.
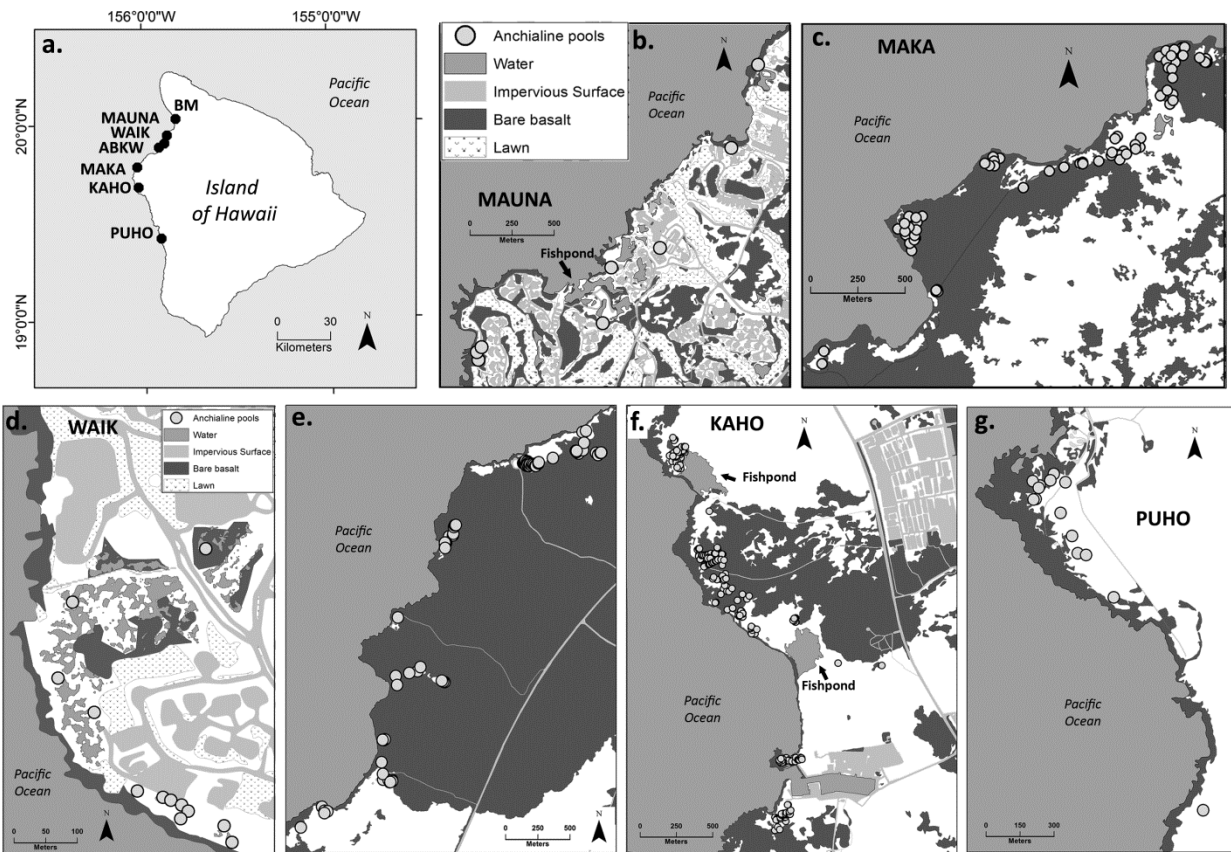
Figure 2: Potential dispersal of introduced fishes due to sea level rise and extreme tides. Time series shows: (a) current pool and introduced fish distribution, (b) connectivity between fish infested pool and uninfested pools at 0.5m sea level rise during an extreme tide, (c) potential distribution of pools and fish at 0.5m sea level scenario at Mean Higher High Tide after an extreme tide event.
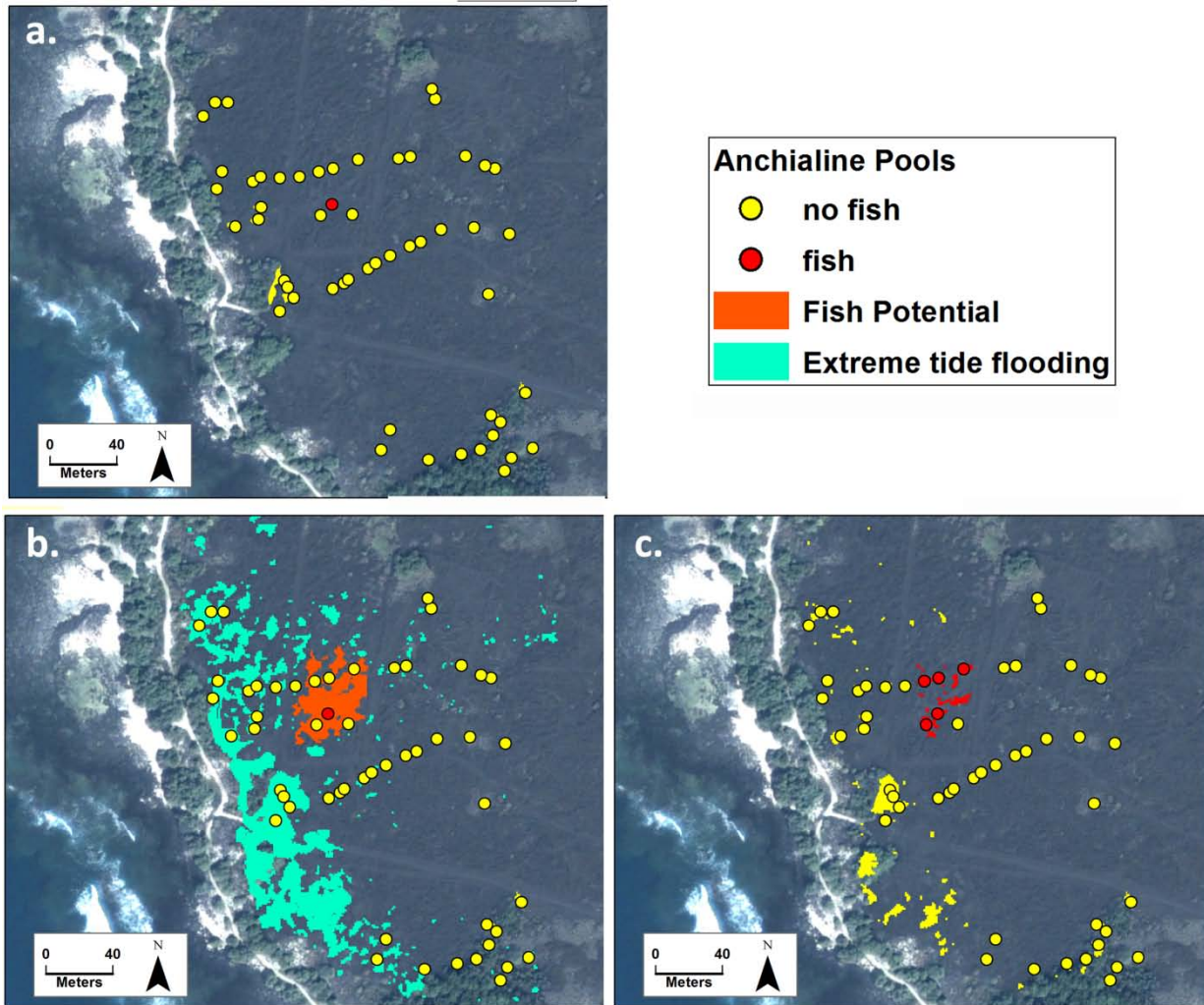
Figure 3: Predicted changes in the number of anchialine pools at six sites under varying sea level rise scenarios. Bar plots include the inundation of existing pools (original) and creation of new pools (new). 0m is the current sea level scenario. Results are from models without groundwater.
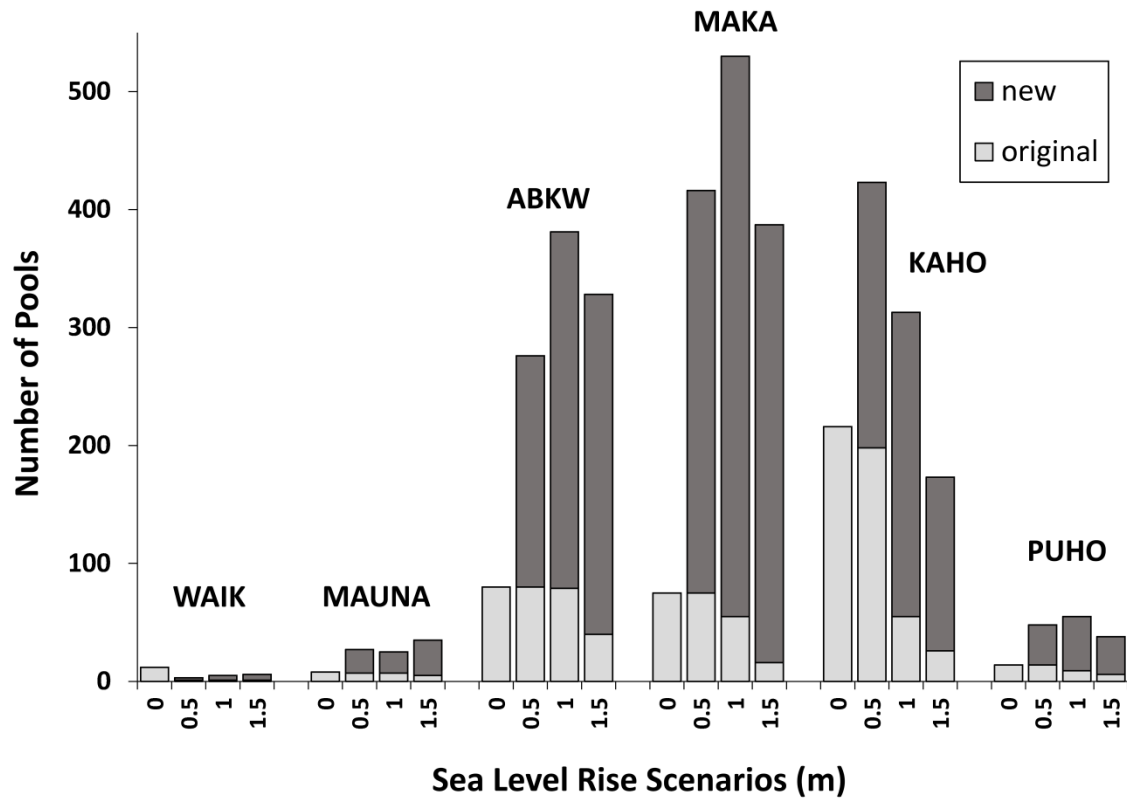
Figure 4: Inundation at two sites due to sea level rise scenarios prior to screening of potential pools by land-use or proximity to ocean surface. (a,b) Waikoloa resort complex at 0 and 1.5m sea level rise showing inundation over parking lots and grass turf; (c,d) Portion of Kaloko Honokohau National Historic Park at 0 and 1m sea level rise. The 0m scenarios show current pool locations.
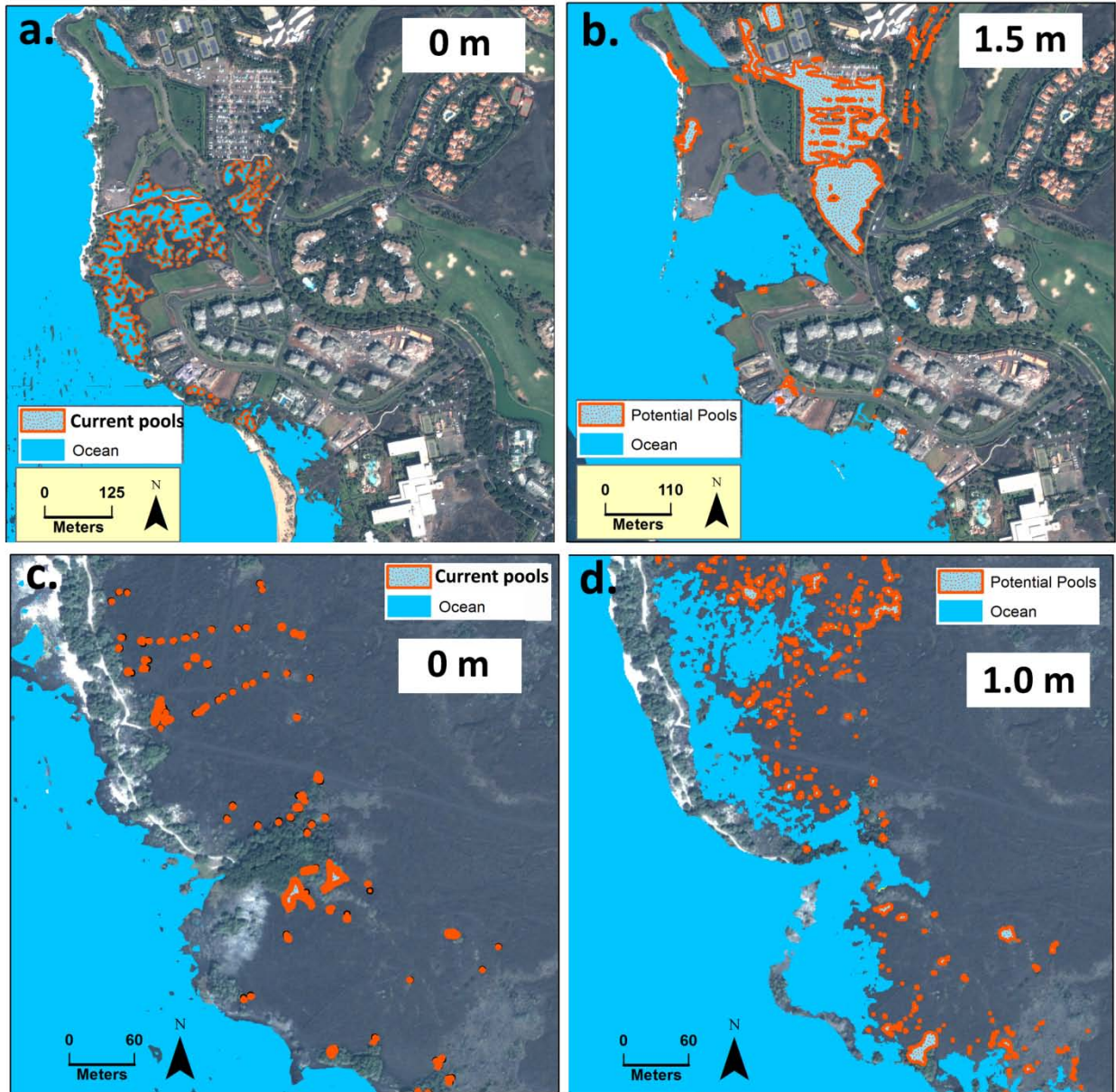
Figure 5: Influence of groundwater on predicted changes to anchialine pool surface area and distribution. (a) Total anchialine pool surface area at six sites under varying sea level rise scenarios. Bars show results from models without groundwater and the additional pool surface area created when groundwater is incorporated. (b) Incorporating groundwater in models increases flooded areas at the edges of a fishpond embayment within Kaloko Honokohau National Historical Park (0.5 m sea level rise at Mean Higher High Water).
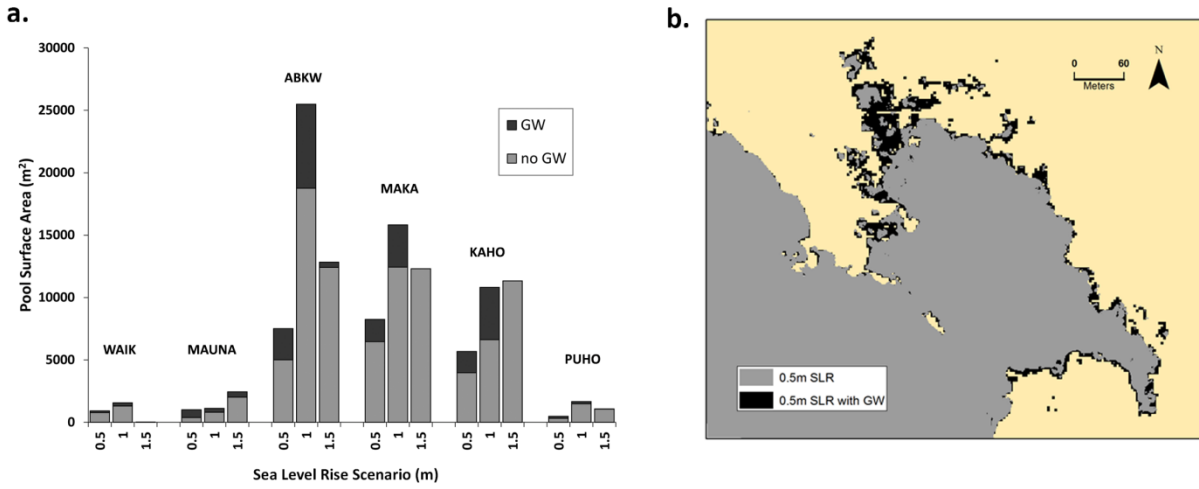
Figure 6: Number of pools that have potential to be infested with introduced fishes as a proportion of the total number of pools after extreme tides under rising sea level scenarios (0m, 0.5m, 1m, 1.5m).
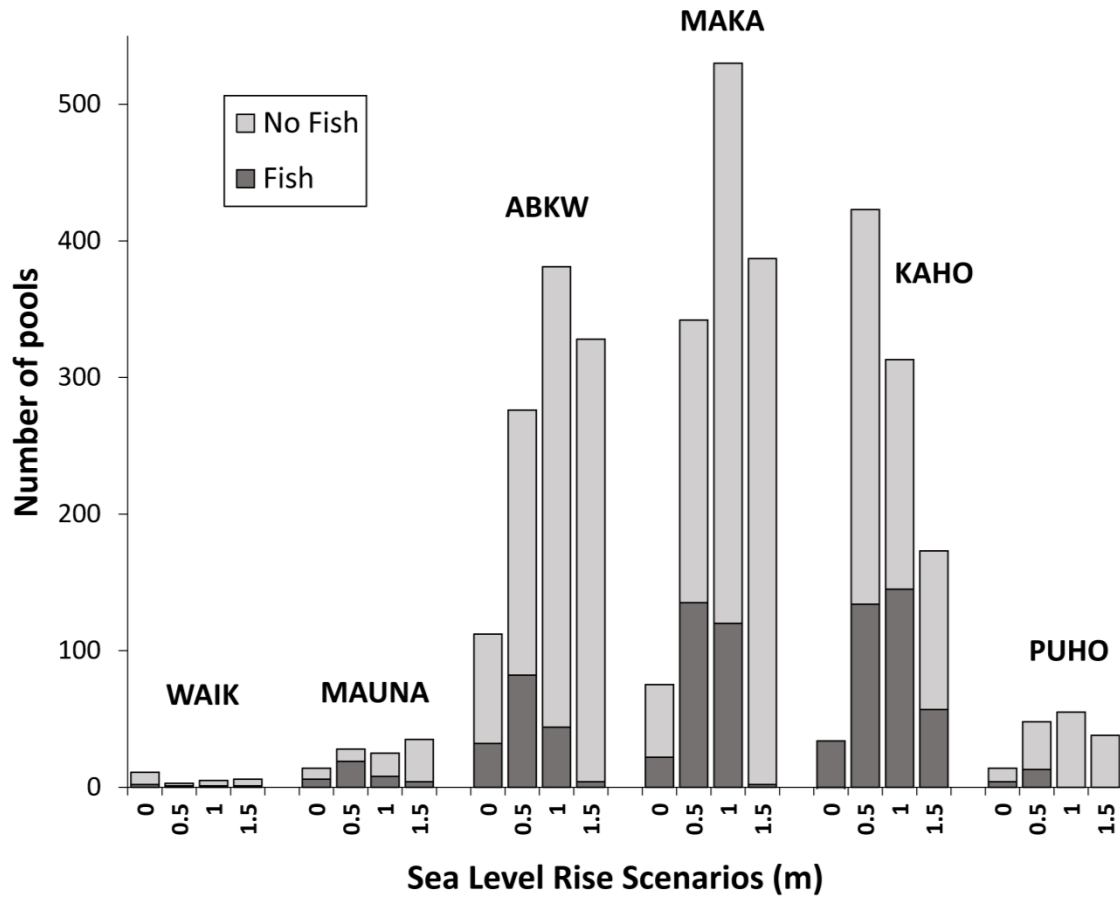
Figure 7: Size distribution of pools currently containing poeciliids (n=102) and tilapia (n=19) compared to predicted pool sizes under sea level rise scenarios with and without groundwater (GW). Pools over 400 m^2 are not included in the plot.
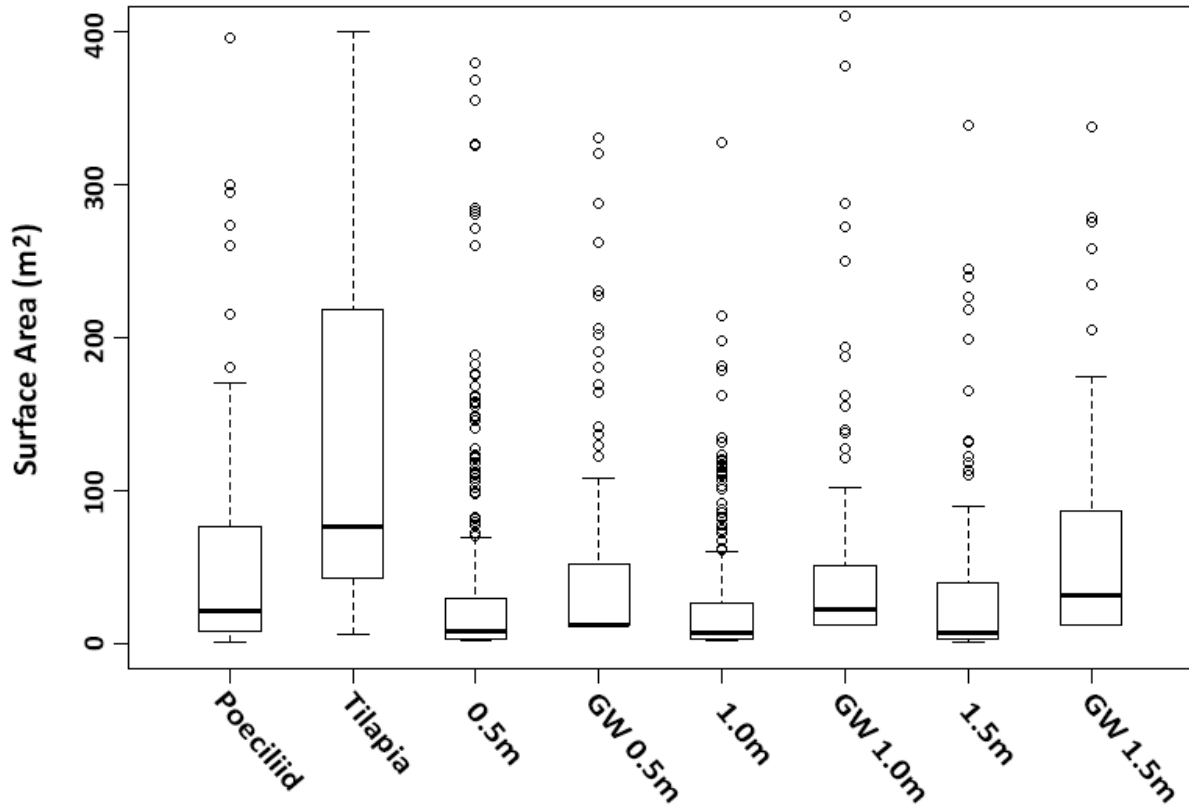
CHAPTER 4

**Comparison of Introduced Species Habitat Associations and Impacts on Anchialine
Ecosystems**

Introduction

Biological invasions are one of the primary conservation threats today and have caused localized species extinctions and degradation in a wide range of terrestrial and aquatic ecosystems (Vitousek *et al.* 1997, Simberloff 2010, Lockwood *et al.* 2013). The negative effects of introduced fish species on native biodiversity and nutrient cycling in aquatic ecosystems have been well documented (Gozlan *et al.* 2010, Cucherousset and Olden 2011). However, not all invasive species have equal effects on biodiversity and habitats (Olden and Poff 2003). Introduced fish that cause the greatest impacts are often prolific reproducers, tolerant to a wide range of environmental conditions, and are generalist feeders able to utilize a wide variety of food resources (Canonico *et al.* 2005, Pyke 2005). Because wide scale removal of introduced fishes is difficult (Britton *et al.* 2011), understanding niche requirements as well as the specific effects of introduced fish on habitats and native biota may be extremely important for management and control purposes.

Introduced tilapia (Canonico *et al.* 2005), *Gambusia affinis* (Global Invasive Species Database 2010) and *Poecilia reticulata* (Deacon *et al.* 2011) are strongly associated with ecosystem declines across the globe due to their high reproduction rates and ability to tolerate a wide range of environmental conditions. All three taxa have been introduced widely for mosquito control or bait, including to anchialine pools in Hawaii (Yamamoto and Tagawa 2000). They are thought to be a primary cause of anchialine pool degradation because they prey on and therefore reduce grazing by the dominant herbivore, the aytid shrimp *Halocaridina rubra* (Brock 1987, Chai 1989). Reduction of grazing by *H. rubra* has been suggested as the primary mechanism for ecosystem phase shifts, resulting in rapid macroalgal accumulation, eutrophication, and pool senescence (Brock 1987, Chai 1989).

Manipulative empirical studies indicate that *G. affinis* do prey on *H. rubra* in Hawaiian anchialine pools (Capps *et al.* 2010). In the presence of *G. affinis* and *P. reticulata*, *H. rubra* shift to predator avoidance behavior by hiding in rocky substrate during the day and emerging at night to feed when fish are inactive (Capps *et al.* 2010, Dalton *et al.* 2013, Sakihara 2012, Havird *et al.* 2013). In comparisons of pools with and without poeciliids, pools with introduced fish had slightly higher mean epilithon biomass, productivity, and nutrient content than pools without fish, indicating non-consumptive effects by introduced fishes (Dalton *et al.* 2013). However, there have been no studies examining potential differences between the effects of tilapia and poeciliids on pool biota or environment.

The objective of this study was to understand habitat associations and ecosystem effects of tilapia and poeciliids within anchialine pool ecosystems. Regional surveys of 398 anchialine pools, diel surveys within a subset of pools, and stable isotope food-web analysis were used to examine the following questions: (a) What habitat and impact factors are associated with tilapia and poeciliid occurrence? (b) How are anchialine grazing shrimp densities impacted by introduced tilapia compared to poeciliids? (c) Are *H. rubra* the dominant prey item for tilapia and poeciliids? Results show similarities and differences in the effects of these two fish taxa on anchialine pool ecosystems as well as differences in their habitat associations.

Methods

Study Site

This study occurred along the arid western coastline of the Island of Hawaii (Figure 1a) where annual rainfall ranges from 25 to 50 cm per year (Giambelluca *et al.* 2011). The study site encompasses one of the highest concentrations of anchialine pools in the world (Brock and Kam, 1997). Pools are considered subaerial expressions of groundwater and are tidally influenced. In Hawaii, salinities may range from 0.5 to 30 parts per thousand (ppt; Maciolek and Brock, 1974). Pools may occur in bare lava substrate with no associated vegetation or on older lava flows surrounded by trees or wetland vegetation (Marrack and Beavers, in prep). Eventually pools may become filled in with new lava flows or older sediments, a progression that would explain their sparse distribution or absence on older Hawaiian islands (Maciolek and Brock 1974).

Regional analysis of habitat associations and impacts of introduced fishes

Data describing the habitat and faunal characteristics of 330 anchialine pools were collected during daylight hours on single site visits from July 12 to August 10, 2012 and July 2 to July 15, 2013. Data for an additional 102 pools were added from previous surveys conducted by the National Park Service (NPS) between 2007-2009 (Jones *et al.* 2011, NPS 2012). Pools were located within private, state conservation, and national park boundaries and were in proximity to a range of land uses including undeveloped, residential, resort, and urban.

Physical attributes including location, surface area, maximum depth, substrate, distance from the shoreline, and water properties were collected. Pool surface area was determined within ESRI's ArcGIS 10.0 using a polygon of the pool perimeter collected in the field with a Trimble GeoXH Global Positioning System (GPS). Surface area for small pools or those with high canopy cover was calculated as pool length $\times$ width. Depth was measured with a weighted line in the deepest part of each pool at the time of the survey. Pool depths fluctuate as a function of tidal oscillations and distance from shore so these measurements represent maximum depth at the time of the survey. Substrate was categorized as percent cover of rock, sand, and silt using visual estimates. Distance from roads was calculated in ArcGIS as the Euclidian distance between a pool and the closest edge of paved or commonly used unpaved roads. Salinity, pH, temperature, dissolved oxygen (DO), turbidity, and Chlorophyll *a* (Chl *a*) were collected at pools with a portable YSI 6500 sonde or a Hydrolab Quanta. Chl *a* measurements were not available for the 102 pools sampled during the period of 2007- 2009. High turbidity and Chl *a* are both indicators of more eutrophic conditions in aquatic systems (Clesceri *et al.* 1998) and were used as proxies for water quality. Water measurements were collected at the surface of each pool to control for depth and changes with the tidal cycle. Previous work has indicated that although water properties may be temporally and spatially variable between pools and within the water column of a single pool, the surface of individual pools remains relatively constant (Marrack, chapter 2).

The endemic dominant grazing shrimp *Halocaridina rubra* as well as introduced fishes were recorded as present or absent based on timed visual surveys during daylight hours. *Poecilia reticulata, Poecilia mexicana,* and *Gambusia affinis* were present in pools but were not always distinguishable in the field so were combined into one group ('poeciliids') for statistical analysis. Tilapia species were also grouped together for this study. *Oreochromis mossambicus* probably makes up the majority of tilapia found on the island of Hawaii, but this is not certain since other tilapia species exist on Oahu and Kauai and they are difficult to identify as juveniles (Mackenzie

and Bruland 2012). Macro-algae was recorded as present or absent. Most pools were small and shallow enough that it was possible to visually examine the entire water body from the pool edges. Larger pools, where the center and bottom were not visible from the surface, were examined using mask and snorkel. Terrestrial vegetation associated with pools was documented including percent canopy cover by species, percent cover of emerging vegetation by species, and percent cover of plants within 0.5 meters of pool periphery by species. Further details regarding survey methodology are described in Chapter 2.

Survey data was used to determine which habitat and impact factors are associated with tilapia and poeciliid occurrence. Habitat factors are defined here as those factors that might limit or promote occurrence of introduced species including pool size, pool deepest depth, salinity, terrestrial vegetation, and distance to roads. Impact factors are defined as those that may be a result of introduced species occurring in pools including turbidity, chlorophyll *a*, percent silt substrate, macroalga occurrence and *H. rubra* occurrence. Continuous and percent factors were compared between pools with no introduced fish, pools with tilapia, and pools with poeciliids using the Kruskal-Wallace test with a significance level of $P \leq 0.05$ (Quinn and Keough 2009). Post-hoc pairwise comparisons are not commonly used on non-parametric data, therefore the Kruskal-Wallace test was used to test for significant differences between all three groups as well as for significant differences between a specific fish group and no fish. The presence/absence categorical variables (*H. rubra*, macroalgae) were also compared with the presence/absence of fish species using the Pearson chi-squared test with Yates correction (χ^2).and a significance level of $P \leq 0.05$.

Comparison of predation effects in diel surveys

To compare effects of introduced species on *H. rubra* densities between day and night conditions, diel surveys were conducted in pools with tilapia (n=4 pools), poeciliids (n=5 pools), both tilapia and poeciliids (n=4 pools), and control pools where none of these potential predators were observed (n=8 pools). To control for differences in *H. rubra* densities in different locations, pools with potential predators were paired with nearby control pools in each location. Three 0.23 cm^2 PVC quadrats were haphazardly placed within each pool and all shrimp within each quadrat were counted. Quadrats were held 15-20 cm above the benthic substrate to eliminate shrimp disturbance. Pools were visited at least once during daylight hours and once the preceding night.

The relationship between *H. rubra* density and predator group was examined using a linear mixed effects model analyzed in R (R Core Team 2012) and *lme4* (Bates, Maechler and Bolker 2012). Predator group (poeciliid, tilapia, both, none) and time of survey (day, night) were included as fixed effects in the model. Individual pools were included as random effects to account for repeated measures at pools. Visual inspection of residual plots initially showed deviations from homoscedasticity therefore shrimp density values were log-transformed and re-inspected prior to analysis to fulfill assumptions of homoscedasticity and normality. P-values were obtained by likelihood ratio tests of the full model with predator group against the model without predator group.

Food web dynamics of introduced fishes using stable isotopes

Stable isotopes (carbon, nitrogen, and sulfur) were used to examine the diet of introduced fish in anchialine pool habitats. Stable isotopes have been used extensively to identify food

sources and trophic positions of organisms within a wide range of aquatic and terrestrial systems (Peterson and Fry 1987, Fry 2006, Boecklen *et al*. 2011). The basis for using stable isotopes in food-web studies is that "You are what you eat (plus a few per mil)" (DeNiro and Epstein 1978). Isotopic signatures are expressed as δ, the ratio of heavy to light isotope, and reported in parts per thousand (per mil). Ratios of carbon isotopes ($\delta^{13}C$) are distinctly different among primary producers with different photosynthetic pathways (*eg*. C3 plants *versus* C4 plants). Because $\delta^{13}C$ values tend to be relatively well conserved up the food chain they can indicate the diet of consumers (Peterson and Fry 1987, Post 2002). Nitrogen isotopes are useful for examining trophic levels because $\delta^{15}N$ becomes concentrated in the consumer versus its diet increasing between 2 to 4 per mil (Vander Zanden and Rasmussen 2001, McCutchan *et al*. 2003). Sulfur isotopic signatures ($\delta^{34}S$) shift less than carbon between consumer and resource and are especially useful for studies that contain marine and terrestrial components because the two systems are usually isotopically distinct (Peterson *et al*. 1986, Fry 2006, Jones *et al*. 2010). All three stable isotopes were considered potentially useful for identifying introduced fish diet in anchialine pools, especially because food resource options are limited to three or four potential items within most pools.

To determine the extent to which introduced fishes are preying on the dominant grazing shrimp *H. rubra* within anchialine pools, fish and their potential food items were collected from 12 pools. The pools sampled represented very simple communities including *H. rubra* and one predator type (poeciliids, tilapia, or the introduced prawn *Macrobrachium lar*). Poeciliids were collected from eight pools where *H. rubra* was present. *H. rubra* are rarely observed in pools with tilapia, therefore only one pool was sampled that contained both tilapia and *H. rubra*. For comparison, the prawn *Macrobrachium lar*, which is thought to feed primarily on *H. rubra*, was sampled from four pools that did not contain fish. To determine the extent to which primary producers may support *H. rubra* and introduced fishes, isotope values of algae and terrestrial leaf litter were also considered.

If pools had associated algae or terrestrial vegetation, samples of primary producer tissue were collected. In all but one pool, pool substrates appeared to be bare lava with no algal film evident. Epiphytic algae is assumed to be the dominant food item for *H. rubra* but was not available in enough quantities to collect for analysis. If present, snails, which feed exclusively on epiphytic algae, were collected because snail $\delta^{13}C$ and $\delta^{34}S$ values can be considered a proxy for algal film stable isotope signatures (Post 2002). Stable isotope values were compared between snail and *H. rubra* found in the same pool.

Carbon (^{13}C), nitrogen (^{15}N), and sulfur (^{34}S) were analyzed by continuous flow triple isotope analysis using a CHNOS Elemental Analyzer interfaced to an IsoPrime100 mass spectrometer located at the Center for Stable Isotope Biogeochemistry (CSIB) at University of California at Berkeley. Long-term external precision for C, N and S isotope analyses within the CSIB is $\pm 0.10‰$, $\pm 0.15‰$, and $\pm 0.40‰$, respectively. When animals were first collected they were kept in cool water for 1-2 hrs then put on ice and kept frozen until analyzed. Prior to spectrometer analysis, tissue samples were freeze dried, ground, and weighed out in tin capsules. For prawn and fish, dorsal and ventral muscle tissue was used for analysis. For snails, foot muscle tissue was used for analysis. Because *H. rubra* are 2-5 mm long, whole shrimp were analyzed.

One common method in stable isotope analysis of muscle tissue is to do a lipid extraction prior to mass spectrometer analysis to correct for lipids in $\delta^{13}C$ values. However a meta-analysis by Boecklen *et al.* (2011) examining the change in $\delta^{13}C$ in tissues after lipid extraction across

numerous studies showed a median change of 0.64 per mil for muscle tissue with a mean of 0.79 per mil for fish muscle. Furthermore, estuarine and freshwater fish median differences were 0.5 per mil. Lipid extraction did cause an undesirable large shift in $\delta^{15}N$ values (-2.11 to 2 per mil). Based on the small shift in $\delta^{13}C$ and large shift in $\delta^{15}N$ due to lipid correction, lipid extraction was not performed on fish muscle tissue prior to analysis.

Individual pools were considered the sample unit. To get estimates of isotope variability among individual specimens from a single pool, two to three *H. rubra*, prawn (*M. lar*) and fish were analyzed separately for a subset of pools. For pools with multiple isotope samples of shrimp or fish, stable isotope values for each pool represent a mean. For other pools, isotope values represent homogenized muscle tissue samples combined from 2-3 individual shrimp or fish.

Variability in *H. rubra* isotope values ($\delta^{15}N$, $\delta^{13}C$, and ^{34}S) between pools were examined for 12 pools distributed across 40 km of coastline. *Halocaridina rubra* stable isotope levels were expected to vary depending on presence/absence of terrestrial vegetation and possibly by aquifer. Next, fish resource use and trophic level were examined by looking at differences between consumer (fish) and resource (*H. rubra*) isotope signatures expressed as Delta (Δ) carbon, nitrogen or sulfur. Delta was used rather than raw stable isotope ratios, because it controls for variability in isotopic signatures between pools. The *a priori* expectation was that poeciliids, tilapia, and prawn are eating *H. rubra*, but when other food sources were available these would also be utilized by the fishes. Evidence for consumption of *H. rubra* would include $\Delta\delta^{13}C$ and $\Delta\delta^{34}S$ values close to zero as well as $\Delta\delta^{15}N$ values of 2 to 4 per mil. If fish are directly consuming plant or algae the $\Delta\delta^{15}N$ would be lower. In pools without terrestrial vegetation, *H. rubra* and snail stable isotope values were expected to be equal because of similarities in diet (i.e., both feed on the same epiphytic algae).

Results

Regional analysis of habitat associations and impacts of introduced fishes

Analysis of survey data from 398 pools test showed that there were significant differences in physical and biological properties of pools with and without introduced fishes (Table 1, Figure 2). The introduced fish were associated with less saline conditions and pools that were larger and deeper than pools without fish (Table 1, Figure 2). Introduced fishes also occurred in pools that were closer to roads, had higher terrestrial vegetation around the pool perimeter, and had higher percent silt substrate. Although turbidity was significantly different between fish and fishless pools this was primarily due to slightly higher turbidity in pools with tilapia where the mean was 3.4 ± 8.8 NTU (versus 0.3 ± 1.7 NTU in fishless pools). Chlorophyll *a* concentrations did not differ between pools with and without fish (p = 0.19).

When pools with tilapia were compared separately to fishless pools, turbidity, pool surface area, and pool depth, were all significantly higher in pools with tilapia while salinity was significantly lower. When pools with poeciliids were compared separately with fishless pools, all factors but turbidity were significantly different than fishless pools. For all factors, mean values observed at poeciliid pools were intermediate between those for fishless and tilapia pools (Table 1, Figure 2). For example, mean salinity for pools without fish was 11.9 ppt, for poeciliid pools mean salinity was 8.9 ppt, and for tilapia pools it was 6.1 ppt. On average, tilapia species were found in less saline, larger and slightly more turbid pools than poeciliids (Table 1).

Overall, *H. rubra* were present in 58% of the 398 pool surveyed, and their presence was influenced by the presence of fish. Contingency table results show that tilapia or poeciliid occurrence was significantly associated with absence of *H. rubra* in pools during daytime observations (Table 2). Specifically, of 14 pools with tilapia, *H. rubra* were evident in only one pool during daylight conditions and in very low densities (3 per m^2). Of 95 pools with poeciliids, *H. rubra* occurred in 33% of pools during daylight conditions. *H. rubra* seen in poeciliid pools during the daytime were of all of the large 3-4 mm length size class.

Visible macroalgae or epilithion was present in only 10% of 398 pools and was not directly correlated with the presence of introduced fishes. Contingency table results showed that macroalgae occurrence was not significantly associated with either tilapia (p = 0.64) or poeciliid (p = 0.053) occurrence.

Comparison of predation effects in diel surveys

A linear fixed effects model that included predator type (poeciliid [n=5 pools], tilapia[n=4], both[n=4], none[n=8]) and time of observation (day, night) suggested that the predator type had a significant effect on shrimp density ($\chi^2(1)$=22.6, p<0.0001). Time also had a significant effect on shrimp density ($\chi^2(1)$=7.55, p=0.006). During daytime surveys, *H. rubra* densities showed little difference between pools with poeciliids compared to control pools (Figure 3). Mean shrimp densities were 17.9 ± 9.2 (standard error of the mean) and 13.0 ± 3 shrimp per 0.23m^2 in poeciliid vs control pools, respectively. In comparison, *H. rubra* daytime densities were very low in pools with tilapia as well as in pools containing both tilapia and poeciliids with a mean of 0.1 ± 0.55 shrimp per 0.23m^2 quadrat in both groups. During night time surveys, shrimp densities increased in pools with fish (poeciliid, tilapia, and tilapia and poeciliid pools). Increases in shrimp numbers during night time surveys were particularly evident in pools with poeciliids where numbers ranged from 10 to 138 shrimp per quadrat with a mean of 44.7 ± 8 shrimp per 0.23 m^2 (Figure 3). In contrast, shrimp densities in control pools with no invasive fish did not differ between night and day. Night time shrimp densities increased slightly in tilapia pools compared to daytime levels but remained low overall ranging from 0 to 5 shrimp per 0.23m^2 quadrat. In pools with tilapia, *H. rubra* were only seen in very shallow areas 4 to 5 cm deep near pool edges or near obvious cracks in the lava but were not seen in deeper areas. The fact that poeciliid pools showed the highest mean densities of *H. rubra* compared to other categories is surprising and reflects the fact that one of the poeciliid pools located at the edge of a wetland had unusually high densities during the day and at night (40 to 250 per 0.23 cm^2).

Food web dynamics of introduced fishes using stable isotopes

Individual specimens of the same taxa (*H. rubra*, prawn, fish) collected within the same pool showed some isotopic variability, but differences between individuals were no more than 1.2 δ^{15}N, 1.2 δ^{13}C, and 1.3 δ^{34}S in all cases except in one pool surrounded by vegetation. The mean differences in isotope values between individual *H. rubra* per pool (n=8 pools) were 0.6 δ^{15}N, 0.3 δ^{13}C, and 0.3 δ^{34}S. The largest differences between individual *H. rubra* occurred in the pool surrounded by terrestrial vegetation and were 1.4 δ^{15}N, 5.95 δ^{13}C, and 2.13 δ^{34}S. The mean difference in isotope values between individual prawn per pool (n=4 pools) were 0.5 δ^{15}N, 0.2 δ^{13}C, and 0.8 δ^{34}S. The largest differences between individuals were 1.2 δ^{15}N, 0.6 δ^{13}C, and 1.3 δ^{34}S. The mean difference in isotope values between individual tilapia per pool was 0.9 δ^{15}N, 1.2 δ^{13}C, and 1.2 δ^{34}S. Isotopic variability of tissues between pools was much greater than within pools.

Halocaridina rubra δ^{13}C and δ^{34}S values were highly variable among the thirteen pools that were sampled. The δ^{13}C values ranged from -13.3 to -25.3 per mil while the δ^{34}S values ranged from 14.1 to 24.3 per mil (Figure 4). *H. rubra* δ^{13}C and δ^{34}S values were distinct for pools with and without terrestrial vegetation (Figure 4) with average -20.3 δ^{13}C and 17.4 δ^{34}S values in pools with terrestrial vegetation and average -14.5 δ^{13}C and 21.4 δ^{34}S values in pools with bare lava substrate. One vegetated pool was an outlier with isotope values falling closer to the rocky pool values (Figure 4). Across all pools, *H. rubra* δ^{15}N values ranged between 3.1 and 7.6 per mil except in two pools located in urbanized Kona. The pool with the highest δ^{15}N value (23.1 per mil) is located between the sewage treatment plant injection well and the ocean. The next highest δ^{15}N value (10.5 per mil) is located between downtown Kona and the ocean. These elevated values indicate that human sewage inputs to groundwater are being transferred into the anchialine food web.

In contrast to stable isotope variability in *H. rubra* tissues among pools, δ^{13}C and δ^{34}S values were relatively consistent in plant and snail tissues. For six different plant species which contributed leaf litter to at least one of five different pools, mean δ^{13}C was -26.3 per mil ± 0.8 (standard error of the mean) and mean δ^{34}S was 18.7 per mil ± 0.8. Snails collected at four different pools had muscle tissue with mean δ^{13}C of -11.5 per mil ± 0.7 and mean δ^{34}S of 18.2 per mil ± 0.6.

Comparison of snails and *H. rubra* found within the same rocky pools (without terrestrial vegetation) show similar δ^{13}C and δ^{34}S values with *H. rubra* lighter in δ^{13}C by -3.5 per mil on average and heavier in δ^{34}S by 4 per mil on average (Figure 6). This comparison indicates *H. rubra* does consume algal film in these pools as expected. However, the differences in isotope ratios do indicate *H. rubra* may incorporate additional materials into their diet or that there are differences in isotope fractionation within the tissues sampled.

Differences in stable isotope ratios between introduced species and the dominant grazing anchialine pool shrimp *H. rubra* do indicate poeciliids, tilapia, and the Tahitian prawn *Macrobrachium lar* are likely consuming *H. rubra* along with other terrestrial or aquatic primary consumers. The mean $\Delta\delta^{15}$N values between consumers and *H. rubra* were 3.8 per mil for poeciliids, 2.5 per mil for *M. lar*, and 2.9 per mil for tilapia, all which indicate these consumers were one trophic level above the grazing *H. rubra*. The lowest and highest $\Delta\delta^{14}$N values occurred within poeciliids collected from pools with terrestrial vegetation.

The δ^{13}C and δ^{34}S values indicate diet and the source of nutrients at each trophic level. These isotope ratios values should be conserved relatively well up the food chain translating to low $\Delta\delta^{13}$C and $\Delta\delta^{34}$S values. At individual pools the mean $\Delta\delta^{13}$C value between poeciliids and *H. rubra* was 2.1 per mil with values ranging between -0.2 to 6.3 per mil at a pool with large amounts of leaf litter. For *M. lar* pools, mean $\Delta\delta^{13}$C was 2 per mil with a range of -0.7 to 4.5 per mil, all occurring in pools with some terrestrial vegetation input. The highest overall $\Delta\delta^{13}$C value of 7.3 per mil was in a pool with tilapia with no terrestrial vegetation. Sulfur isotopes also differ between consumers and *H. rubra* with poeciliids deviating -0.7 to -6.9 per mil from *H.rubra*; *M.lar* deviating -0.7 to -2.8 per mil from *H.rubra*; and tilapia deviating 0.6 per mil. The large delta values within some pools indicate that introduced fishes also utilize food resources other than *H. rubra*.

Discussion

Results of regional and diel surveys show that while both poeciliids and tilapia have an effect on anchialine pool ecosystems, the effects of tilapia are stronger, especially on the

occurrence and densities of the native grazer, *H. rubra*. Unlike fishless pools or pools with poeciliids, *H. rubra* were typically absent from tilapia pools during the day and either absent or at very low densities at night. Pools with tilapia had the greatest turbidity and percent silt substrate. In contrast, *H. rubra* occurred in 33% of poeciliid pools during the daytime surveys. Densities of *H. rubra* in poeciliid pools also increased at night, reflecting predator avoidance behavior during daylight hours. Stable isotope results support the hypothesis that both tilapia and poeciliids are consuming *H. rubra* as part of their diet, but that other food items are probably consumed as well. Stable isotopes also indicate that *H. rubra* have a varied diet and may be a useful bio-indicator of human sewage in groundwater.

While *H. rubra* were absent or observed in very low numbers in tilapia pools, 33% of pools with poeciliids had some *H. rubra* during daylight hours. One clue to the co-occurrence of shrimp and their poeciliid predators was that *H. rubra* observed during the day were of a uniformly large class size while smaller shrimp appeared at night. Poeciliids are probably gape limited in relation to *H. rubra* which would explain their co-occurance during the day. Tilapia are much larger fish than poeciliids and would not be gape limited in relation to *H. rubra* explaining the absence of the shrimp from tilapia pools during the daytime.

While tilapia may have a larger effect on pool biota and water clarity, survey results indicate that they are limited to a narrower range of pool habitats than poeciliids. Tilapia were associated with a smaller range of salinities and larger pools (in terms of area and depth). These factors may limit tilapia distribution in some pools. Elsewhere tilapia are known to be highly tolerant to a range of salinities (Canonico *et al*. 2005). More work on tilapia tolerance levels would help to determine if smaller, saltier pools offer refugia to endemic invertebrate species. Higher turbidity in tilapia pools may be a result of the copious amounts of tilapia fecal matter which was visible on the pool substrate and may build up over time (Marrack, personal observation).

Results from the $\Delta\delta^{15}N$ analysis do partially support the hypothesis that introduced fishes and *M. lar* are consuming *H. rubra*. The $\Delta\delta^{15}N$ values for poeciliids, tilapia, and *M. lar* are all within the 2 to 4 per mil increase expected for consumers in relation to their food resource (McCutchan *et al*. 2003; Fry 2006). If the introduced consumers were purely eating plant litter and/or algal film they would occur at the same trophic level as the *H. rubra*, and $\Delta\delta^{15}N$ values would be close to zero which is not what was observed. However, while $\Delta\delta^{15}N$ values indicate introduced consumers are feeding on *H. rubra*, one of the few prey items available in pools, $\Delta\delta^{13}C$ and $\Delta\delta^{34}S$ values indicate that in some pools the introduced fishes and, to a lesser extent *M. lar,* are utilizing other food resources.

Differences between consumer and resource isotope signatures expressed as Δ (delta) may be a result of a number of processes including multiple food resources and metabolic fractionation within consumers (Fry 2006; Boecklen *et al* 2011). McCutchan et al. (2003) examined isotopic shifts between consumers and food resources and found that the mean isotopic shift for $\delta^{13}C$ was +0.5±0.13‰. The shift for $\delta^{13}C$ was higher when consumer muscle tissue was analyzed (+1.3±0.30‰) than for consumers analyzed whole (+0.3±0.14‰). In this study, mean $\Delta \delta^{13}C$ between *H. rubra* and *M. lar* muscle tissue was 2 per mil with a range of -0.7 to 4.5 per mil. Poeciliid muscle tissue was shifted as much as 6.3 per mil compared to *H. rubra* from the same pool, while tilapia was shifted 7.3 per mil. Additionally, poeciliid tissue deviated up to 6.9 per mil $\delta^{34}S$ from *H. rubra* from the same pool. These shifts do indicate that in some pools, fish and *M. lar* are utilizing food resources other than *H. rubra*. Poeciliids, tilapia, and *M. lar* are known to be generalist consumers (Global Invasive Species Database 2010). Therefore it is not

surprising that once *H. rubra* shift their behavior and become less dense during the day when fish are actively foraging, fish would begin to utilize alternative food sources. Gut content analysis of 183 poeciliids (*G. affinis* and *P. reticulata*) from four anchialine sites supports this hypothesis (Havird *et al*. 2013). At three sites there was no evidence for successful predation of *H. rubra* by the introduced fishes and at the fourth site only 10% of fish guts contained *H. rubra* remains suggesting that the predation avoidance behavior of *H rubra* is successful. Furthermore, poeciliids gut contents contained undigested remains of mites, flies, isopods, arthropods, and other flying Hymenoptera. *G. affinis* were originally introduced to Hawaii to control mosquitoes (Yamamoto and Tagawa 2000) so terrestrial subsidies to fish diets are not surprising. Terrestrial subsidies should be expected for tilapia as well. More adequate sampling of all possible food resources would allow for more rigorous modeling of fish diets within pools.

Reduced grazing by *H. rubra* due to predator avoidance might be expected to release primary producers from top down control leading to algal accumulation. In comparisons of pools with (n= 10 pools) and without poeciliids (n=10 pools), pools with introduced fish had slightly higher mean epilithon biomass, productivity, and nutrient content than pools without fish (Dalton *et al*. 2013). However, my survey results from 398 pools showed that the occurrence of visible macroalgae or epilithion was low (10% of pools) overall and not directly correlated with the presence of introduced fishes. Many pools with poeciliids remained free of macroalgae and visible epilithion indicating that despite reduced grazing time in pools, *H. rubra* may continue to suppress primary producer biomass. Additionally, poeciliids and tilapia may also consume algae. Capps *et al*. (2009) used δ^{15}N stable isotopes to examine the trophic levels of eight *Gambusia affinis* (mosquito fish) from one pool. Results suggested that *G. affinis* were eating *H. rubra* but possibly eating algae as well. Ultimately, macroalgae biomass would reflect the combined grazing pressures of *H. rubra*, fishes and other taxa as well as nutrient levels within pools.

In areas of anthropogenic nutrient loading, algal production rates may be expected to increase and biomass accumulation may occur, especially where introduced fishes decrease *H. rubra* grazing. Groundwater nutrient loading does occur in the west coast of the island of Hawaii in the form of sewage enriched irrigation water, storm water runoff, fertilizers, and septic/cesspool effluent and can be observed as elevated anchialine pool nutrients (Weigner *et al*. 2006, Dalton *et al*. 2013). One very interesting outcome from this project was the clear signal that *H. rubra* tissues are highly elevated in δ^{15}N in the pool located between the sewage treatment plant and the ocean. Dudley *et al*. (2012) also found high nutrient levels in water samples collected at pools in this location. Although macroalgae was not evident in the pool sampled for this study, shrimp were in high abundances (100s per meter square). There were no fish in this pool. If fish were introduced and grazing was reduced, it is possible that the combined top down and bottom up effects may cause rapid algal accumulation and pool degradation. These stable isotope results suggest shrimp tissue δ^{15}N levels could be used as a bio-assessment tool to examine elevated levels of nutrients in pools if algal samples are not available.

The highly variability in δ^{13}C and δ^{34}S values for *H. rubra* tissues from pools along the coastline are likely to be a result of variation in *H. rubra* diet and food availability at different pools. The δ^{13}C values of *H. rubra* ranged from -13.3 to -25.3 per mil and are within the expected range for terrestrial plants and algae. Worldwide, carbon isotope values for C3 terrestrial plants average -28 per mil but range from -22 to -34 per mil (O'Leary 1988). In this study, the average δ^{13}C of terrestrial plants at pool edges was -26.3 per mil. In benthic algae, δ^{13}C values are partly dependent on microenvironment water turbulence and range between -17 $\pm$ 4 (SD) per mil in marine coastal areas to -26 $\pm$ 3 per mil in freshwaters (France 1995). In this

study, the algal film grazed on by snails and *H. rubra* were not in high enough volumes to collect, however snail δ^{13}C can be considered a proxy for algal film stable isotope signatures because snails depend exclusively on this food source in these pools (Post 2002). Snail muscle tissue was -11.5 per mil δ^{13}C on average. In anchialine pools, if algae is approximately -11.5 per mil δ^{13}C and terrestrial plant litter is -26.3 per mil δ^{13}C, the variation of δ^{13}C observed in *H. rubra* tissues from pools with and without terrestrial vegetation reflects variable inputs of these energy sources to the grazer's diet. In pools where *H. rubra* was able to utilize terrestrial plant leaf litter, the shrimp δ^{13}C averaged -20.3 δ^{13}C. In rocky pools without surrounding vegetation, shrimp δ^{13}C were higher (mean -14.5 δ^{13}C) reflecting their reliance on algal biofilms. Expanding the sampling of available food resources along differing pools would help determine *H. rubra* diet with more clarity and would allow use of mixing models.

Management implications

Management strategies aimed at conserving Hawaiian anchialine pools should consider removals of introduced fishes as an important step towards protecting endemic anchialine species. Results from this study suggest that tilapia are a bigger threat to endemic anchialine species and ecosystem health and should be targeted first. While both poeciliids and tilapia have a negative effect on the occurrence and behavior of the dominant grazer *H. rubra*, tilapia appear to have a much greater impact on endemic shrimp causing them to essentially disappear from pools. Tilapia also appear to contribute to greater sedimentation and poorer water clarity in pools. Fortunately, tilapia occur in far fewer pools than poecillids. Removals should be a priority before sea level rise, extreme water levels, or humans disperse fishes into new habitat.

In addition to fish removals, further investigations into the combined effects of introduced fishes and groundwater nutrient loads on anchialine pools are advised. Development along the west Hawaii coastline is ongoing, and anthropogenic nutrient loads into groundwater are expected to increase. Past and current investigations on nutrient levels in anchialine pools have typically focused on dissolved nutrient levels in water samples. However, these measurements are snap-shot views and may not capture pulses of nutrients that are flowing through groundwater-fed ecosystems. Additionally, if nutrients loads are taken up rapidly by primary producers they will not persist in the water column. Our stable isotope results indicate that in areas near urban centers, human sewage is clearly entering the anchialine food web. Increases in nutrients coupled with decreases in native grazing pressure (introduced fish effects on *H. rubra*) may cause major changes in anchialine pool ecosystems.

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Table 1: Summary statistics for factors that show statistically significant differences (Kruskal-Wallace Test, p-value $\leq$ 0.05) when all three anchialine pool groups (with tilapia, with poeciliids, and no introduced fishes) were examined together. Mean, standard deviation, median, minimum value and maximum value are included for pools with poeciliids and tilapia. Perimeter vegetation represents percent cover data. Total number of pools with fish in survey = n. P-value represents Kruskal-Wallace Test results for 2 group comparisons (no fish and tilapia pools ; no fish and poeciliid pools).

Pool Characteristic	Pools sampled	Mean	Stdev	Median	Min	Max	P - value
Tilapia (n=14)							
Turbidity (NTU)	13	3.4	8.8	0	0	32.3	<0.001
Salinity (ppt)	14	6.1	5.2	3.1	1.3	16.07	<0.001
Surface Area (m^2)	14	782.7	2071.9	127.7	7.7	7931.6	<0.001
Maximum Depth (m)	14	1.0	0.8	0.62	0.4	2.5	<0.001
Perimeter Veg (%)	14	40.1	38.1	33	0	100	ns
Silt Substrate (%)	14	36.1	37.3	30	0	95	ns
Distance to Road (m)	14	252.8	445.2	108.7	6.6	1346.9	ns
Poeciliids (n=95)							
Turbidity (NTU)	72	0.2	0.7	0	0	4.1	ns
Salinity (ppt)	89	8.9	4.8	7.0	4.2	18.9	<0.001
Area (m^2)	95	89.2	170.8	18.0	20.8	951.5	<0.001
Maximum Depth (m)	95	0.47	0.41	0.4	0.1	2.5	<0.001
Perimeter Veg (%)	95	31.1	38.8	6	0	100	0.02
Silt Substrate (%)	95	28.8	40.0	0	0	100	<0.01
Distance to Road (m)	95	273.3	650.6	109.9	0	6250.0	<0.001
No Fish (n=)							
Turbidity (NTU)	151	0.3	1.7	0	0	15.8	
Salinity (ppt)	227	11.9	5.9	12.8	1.6	26.6	
Area (m^2)	296	17.3	42.7	6.3	0	500.0	
Maximum Depth (m)	296	0.32	0.7	0.2	0	10.0	
Perimeter Veg (%)	296	27.5	37.7	5	0	100	
Silt Substrate (%)	296	20.3	37.8	0	0	100	
Distance to Road (m)	296	615.2	1301.0	366.9	0	8004.8	

Table 2: Contingency table analysis comparing *Tilapia* and *Poeciliid* presence/ absence with categorical variables. "# of pools" is the number of pools within the category, for example 14 pools had Tilapia. These pools are grouped into "with fish" and "without fish" as % of pools and total number of pools in the category. The χ^2 value is the Pearson's chi-squared test with Yates correction. Significance level is P≤ 0.05. A total of 398 pools were surveyed.

Species	Factor	# of pools	With fish % (total)	Without fish % (total)	x^2	P-value
Tilapia (present in 14 pools)						
	H.rubra presence	230	0.4%(1)	99.6% (229)	13.2	**0.0003**
	Macroalgae presence	40	5.0%(2)	95.0%(38)	0.007	0.63 **(NS)**
Poeciliids (present in 95 pools)						
	H.rubra presence	230	13.5%(31)	86.5%(199)	31.0	**< 0.0001**
	Macroalgae presence	40	37.5%(15)	62.5%(25)	3.75	0.053 **(NS)**

Figure 1: Maps of sampled pools for: (a) regional survey, (b) diel surveys, (c) stable isotopes.
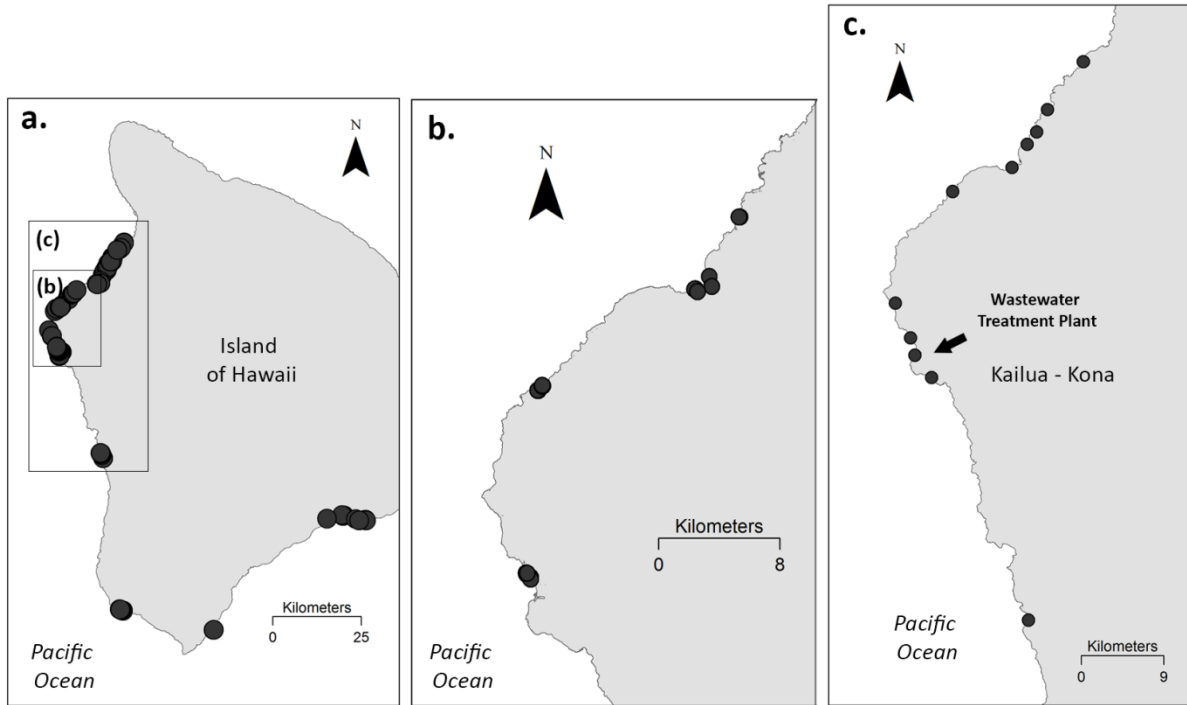
Figure 2: Boxplots comparing pool characteristics for pools with no introduced fish present (none) , poeciliids present, and tilapia present during daytime surveys. Kruskal – Wallis test p-values are at the top right of each plot. If P > 0.05 there is no significant difference (NS) between groups.
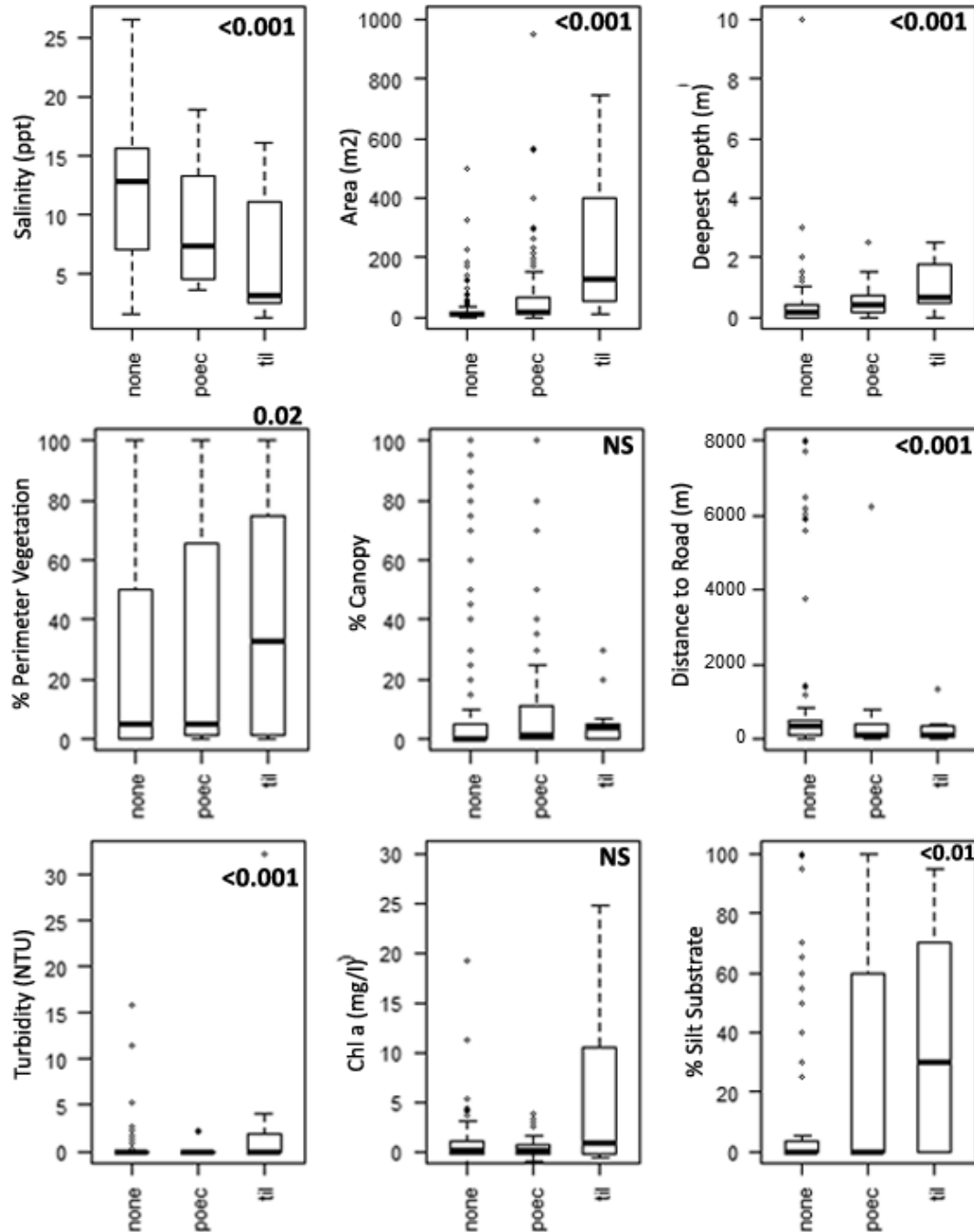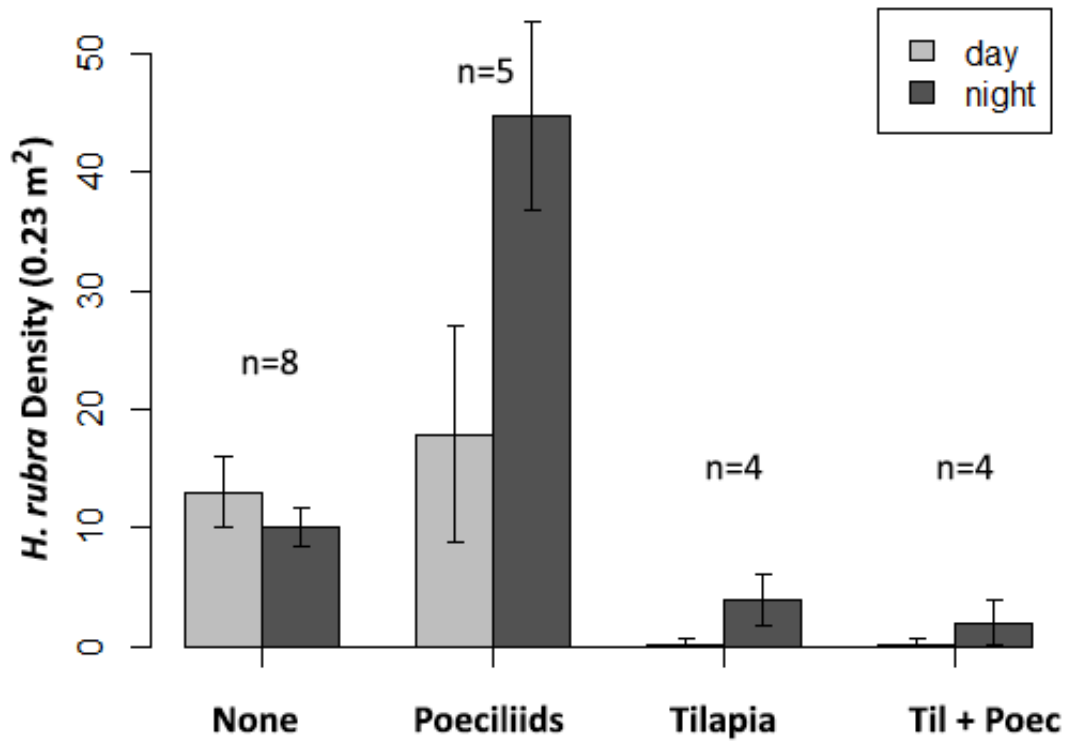
Figure 3: Comparison of *Halocaridina rubra* densities during day and night surveys in anchialine pools with different predator types (poeciliids, tilapia, both, and none). Error bars represent standard error of the mean. Number of pools surveyed for a group are indicated by "n".

Figure 4: Average stable isotope values (δ^{15}N, δ^{13}C, and δ^{34}S) for *H. rubra* at 12 anchialine pool locations. Pools include those with some terrestrial vegetation available as litter and those in non-vegetated lava substrate.
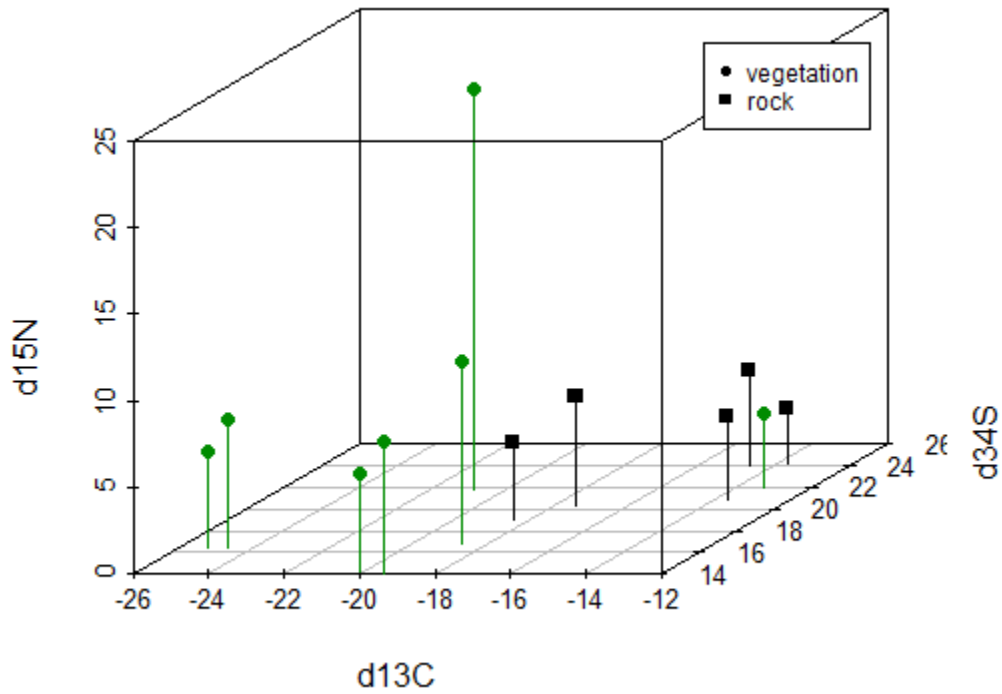
Figure 5: Differences in stable isotope values (δ^{15}N, δ^{13}C, and δ^{34}S) between consumers (poeciliids, tilapia, and the Tahitian prawn *Macrobrachium lar*) and the grazing anchialine pool shrimp (*H. rubra*) denoted as Δ. Pools with and without associated terrestrial vegetation are indicated. A value of 0 means no difference between consumer and shrimp.
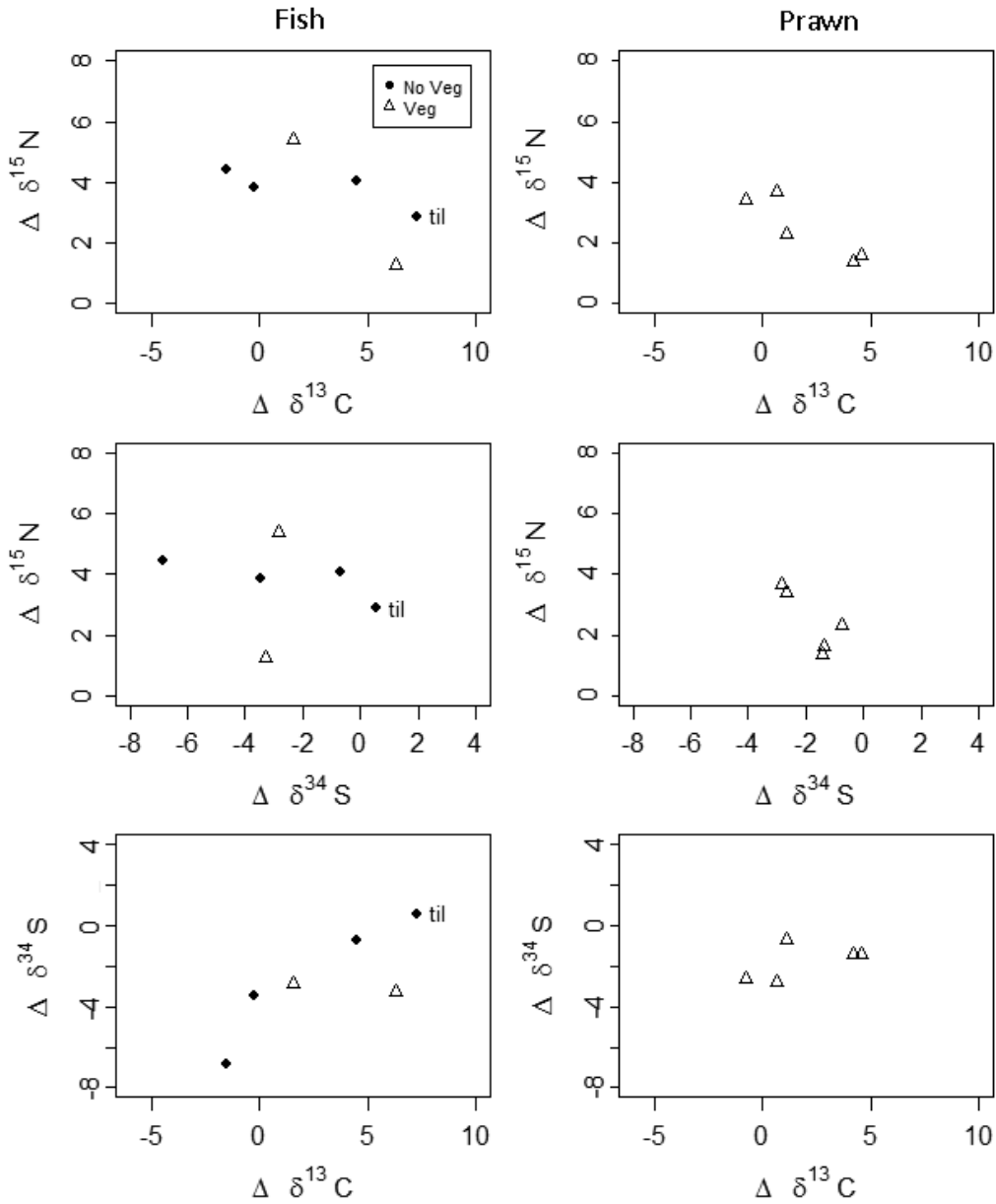
Figure 6: Comparison of mean snail and *H. rubra* δ ^{13}C and δ ^{34}S values from 4 pools where they co-occur. Error bars are standard error of the mean.
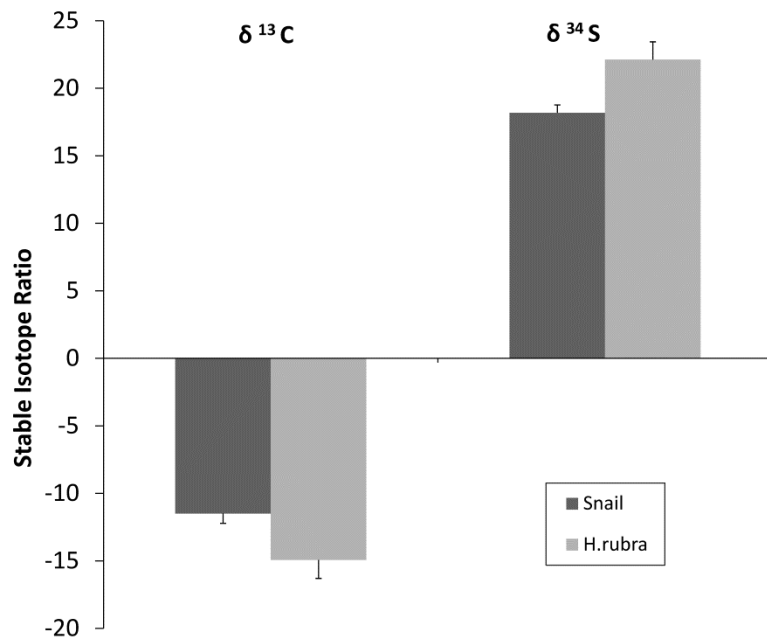
CHAPTER 5

Conclusions

Current anthropogenic stressors are eroding ecosystem resilience and this degradation will make it more difficult for natural systems to adapt to future climate change (IPCC 2013). Ideally, predictions of climate change impacts to ecosystems should include current stressors to best inform conservation management efforts. Introduced species and groundwater pollution may be driving some of Hawaii's unique coastal anchialine pool ecosystem to degraded states. Sea level rise will compound degradation of this habitat by facilitating dispersal of introduced fishes and inundating some pools. The goal of this dissertation was to document the status of anchialine pool habitats along the western and southern coastlines of the Island of Hawaii and to provide data and tools to assist managers and planners with protection of this unique ecosystem and the organisms that depend on it. Predictions of sea level rise impacts on anchialine pool habitats would be most helpful to resource managers and planners if models included current pool condition assessments and future invasive species dispersal pathways.

Hawaiian anchialine pools support diverse endemic biota, including seven species listed as Candidate Threatened or Endangered Species (US FWS 2011). Although anchialine ecosystems exist worldwide, cave and pool systems in Hawaii represent the only anchialine habitat in the United States other than the caves of the territory of Puerto Rico. Past studies examining the ecology and threats to pool ecosystems have been limited in geographic scope (2-20 pools) (Capps *et al*. 2009, Carey *et al.* 2010, Sakihara 2012, Dalton *et al.* 2013) or have been descriptive inventories (Maciolek and Brock 1974, Brock and Kam 1997). Research for this dissertation accomplished habitat mapping at over 400 anchialine pools to assess ecosystem condition at a regional scale (chapter 2); performed quantitative examination of impacts to anchialine ecosystems by introduced species, land-use and sea level rise (chapters 3 and 4); and developed fine scale sea level rise scenarios for 280 miles of coastline on the Island of Hawaii (chapter 1). Results and future directions are summarized below.

Habitat mapping and condition assessments

Chapter 2 presents the first regional perspective on anchialine pool habitat characteristics on the Island of Hawaii since the 1970's. Over 400 pools were surveyed for biotic and abiotic features along the west coast and at some southern sites on Hawaii. Results show that the endemic anchialine shrimp *H. rubra* and *M. lohena* are located across the study area, with rarer species of anchialine mollusks, shrimp, and fish in restricted locations. The introduced fishes tilapia and poeciliids were present in ~ 25 % of pools surveyed and had a strong negative impact on shrimp occurrence. Based on their habitat associations, *H. rubra* and *M. lohena* have wide tolerances for a number of physical and biological characteristics of anchialine pools including salinity and temperature. However, there is a negative association between endemic shrimp occurrence and human land-use. Turbidity and chlorophyll *a* levels were very low in 98.5% of pools observed while visible macroalgal growth occurred in approximately 10% of pools. Algal occurrence was not associated with decreased occurrences of *H. rubra* or *M. lohena*.

Over time, pools may become filled in with sediment as surrounding basalt bedrock develops into soil. Out of 398 pools, 17% had fine organic sediment covering 80 - 100% of the substrate, and high sediment cover was negatively associated with shrimp occurrence. Each pool

with high sediment cover had associated native or introduced vegetation which strongly supports the assumption that vegetative litter speeds the process of pool infilling. However vegetation also has a positive association for some anchialine pool species such as the candidate endangered damselfly *Megalagrion xanthomelas* (Tango *et al.* 2012) and candidate endangered shrimp *M. lohena*. Current anchialine pool restoration efforts often involve the removal of fine benthic sediments and clearing of surrounding terrestrial vegetation. Results indicate that removal of sediments may increase the probability that shrimp will occur in pools. However, removal of terrestrial vegetation may have a mixed effect on pool biota. A more refined understanding of the effect of native versus introduced plants on both anchialine pool species and rates of pool sedimentation would be helpful to managers interested in vegetation removal.

Surveys need to be extended to more remote and less well documented sections of the coastal corridor where pools are known to exist but have not been surveyed since the 1970s (Maciolek and Brock 1974) or have never been formally surveyed. Expanding the data set will allow for a more comprehensive regional understanding of habitat condition and will allow for a better understanding of the biogeography of rarer species. In addition, sea level rise models can be applied to sections of coastline that have not yet been surveyed to determine expected inundation and pool creation under differing scenarios. Finally, current and future pools can be protected only if we know their locations or can predict where they may form.

Response of Anchialine Ecosystems to Sea level Rise

Project outcomes of chapter 3 include the first geospatial analysis of anchialine ecosystem response to future sea level rise. Sea level rise scenarios were created for 280 km of coastline along the Ala Kahakai National Historic trail (Marrack and O'Grady 2014). Current pool locations identified during the habitat surveys were assessed for inundation under various scenarios. Although current pools will become increasingly inundated as sea levels rise, new habitat will emerge in undeveloped low-lying lava substrate. Future coastal development needs to avoid building on low-lying areas so as to avoid flooding of infrastructure and to allow aquatic habitat such as anchialine pools, wetlands and fishponds to shift inland.

Geospatial models of sea level rise were created to visualize inundation under various scenarios (0.5m, 1m, 1.5m, and 1.9m) both with and without groundwater. In unconfined coastal aquifers, the groundwater table is elevated above mean sea level sloping up and away from the shoreline and typically moves with the ocean surface (Oki 1999). As a result, sea level rise models without groundwater levels may under-predict coastal flooding. Groundwater was incorporated into sea level rise scenarios using the methods of Rotzoll and Fletcher (2013) and Marrack (2014). Because annual rainfall on the Island of Hawai'i has decreased in the past century and may continue to do so with climate change (Giambelluca *et al.* 2011), future groundwater levels may be lower. Increasing human extraction from aquifers is likely to exacerbate lowering groundwater levels (Oki 1999). Within this study, sea level rise scenarios that incorporate current groundwater levels can be considered an upper bound to future flooding due to rising ocean levels while scenarios without groundwater are a lower bound.

These scenarios have been shared in a GIS format and through presentations with staff at the five National Parks on the Island of Hawaii, the Hawaii County Planning Department, The Nature Conservancy, Kamehameha Schools, Fish and Wildlife staff, the Pacific Island Climate Change Cooperative (PICCC), the Hawaii State Department of Land and Natural Resources and various other community stakeholder groups such as the Hui Aloha Kiholo and the Kohala Center. The goal is to encourage stakeholders to utilize sea level rise scenarios in their planning

process and share knowledge with groups about the value of anchialine pools and the expected response due to climate change. Furthermore PICCC intends to add the GIS sea level scenarios to an online mapping tool allowing users to create their own inundation maps for a variety of natural and cultural coastal features.

Future work is needed to refine sea level rise models. The groundwater data used to create sea level models were collected in a 2 km radius area around Kaloko-Honokohau National Park. An obvious next step is to deploy groundwater level loggers in pools and low elevation wells elsewhere along the coast so as to refine groundwater slopes in these areas. Another future direction for examining ecosystem response to sea level rise is to map scenarios using a probabilistic approach incorporating uncertainty from global, regional and local mechanisms. Sources of uncertainty in sea level rise models include the rate and magnitude of ice sheet loss (NRC 2012, IPCC 2013); coastal subsidence; groundwater recharge rates; ocean dynamics including tides, storms and hurricanes (Ruggiero 2013, Merrifield *et al.* 2013); and basin wide processes such as the Pacific Decadal Oscillation and ENSO (IPCC 2013, Scafetta 2013). All of these processes will affect sea level rise, and likelihood estimates of each could be combined visually in a map for conservation planning purposes.

Finally, prior to total inundation, sea level rise will modify anchialine habitats by making them increasingly saline. Currently, the dominant anchialine species in Hawaii (*H. rubra* and *M. lohena*) are found in a wide range of salinities (1 to 30 ppt). However, it is not understood if these species are able to complete their entire life cycle within these salinity ranges. There is also no knowledge of the tolerances of rarer shrimp and mollusk species. Knowledge of species specific salinity tolerances will be important for understanding the response of brackish coastal ecosystems across the globe.

Introduced fishes

While both tilapia and poeciliids strongly impact Hawaiian anchialine invertebrate communities, tilapia appear to have a greater effect on individual pools. We examined a wide variety of physical and biological pool attributes and introduced fishes (tilapia, poeciliids) were the most important variables explaining the lower probability of *H. rubra* occurrence during daytime surveys within 398 pools. Results of both regional and diel surveys show that tilapia have a greater effect on *H. rubra* occurrence and densities. Unlike fishless pools or pools with poeciliids, *H. rubra* were typically absent from tilapia pools during the day and either absent or emerging in very low densities at night. Pools with tilapia were also slightly more turbid probably due to copious amounts of tilapia fecal matter which build up over time (Marrack, personal observation). Although poeciliids did affect *H. rubra* occurrence and densities, shrimp were still evident in pools with poeciliids both during the day and night. In pools with poeciliids, larger *H. rubra* were evident during the day indicating that poeciliids are gape limited. Although poeciliids may not have as strong of an effect on shrimp occurrence in individual pools, they have a larger effect on a regional scale. Poeciliids occurred in 24% of pools surveyed while tilapia only occurred in 3.5% of pools. Because *H. rubra* and *M. lohena* move within subterranean groundwater and emerge in pools at night when fish are inactive, fish removal efforts should result in rapid recovery of native shrimp in pool habitats. Fish removal efforts are resource intensive (Britton *et al.* 2011), therefore targeting the worst offender may be the most cost effective strategy. Because tilapia may have the largest effect on shrimp occurrence and sediment accumulation, they should be a priority for removal efforts.

Further studies on removal techniques of both fish groups will help managers attempting to conserve anchialine pool endemic species. Sea level rise models show that increasing water levels will provide connectivity between pools allowing introduced fishes to disperse from current locations into areas where they were previously absent. These connectivity maps may be used to prioritize removal efforts by targeting areas where a few pools are projected to be the source of infestation for numerous other habitats. Ecological questions regarding the non-consumptive impacts of introduced fishes, especially acting synergistically with groundwater nutrient loading from human sewage or fertilizers, are also important to consider as human development along the coastline continues.

Groundwater Contamination

Although evidence strongly suggests groundwater pollution could be an important mechanism for anchialine ecosystem decline, invasive fishes are typically considered the primary reason for pool degradation (Brock and Kam 1997). Eutrophication caused by excessive inputs of nutrients (nitrogen, phosphorus) is one of the most common causes of impairment of surface waters in the United States (Carpenter *et al*. 1998, U.S. EPA 2004). Elevated nutrients, especially when combined with loss of grazer capacity, often results in increased primary producer biomass (Gruner *et al.* 2008) and major shifts in ecosystem structure and function (Jackson *et al.* 2001, Folke *et al.* 2004). On the west coast of Hawaii Island where the majority of the State of Hawaii's pools are located, rapid development has occurred in coastal and upslope areas over the past thirty years and substantial urbanization is planned for the future. Enriched irrigation water (*i.e.,* sewage effluent diluted with coastal well water), storm water runoff, fertilizers, and septic or cesspool effluent can leach through porous basalt substrate into groundwater and flow into anchialine pool ecosystems. Although pool nutrient levels may naturally vary, studies show that pools in proximity to developments have had significant increases in nutrients (*i.e.,* nitrates, phosphates) after project build out (Brock *et al.* 1987, Weigner *et al.* 2006). Measurements of nutrient levels in pools both pre- and post-golf course development show increases in nitrates, phosphates, and ammonium of 98%, 55%, and 135% respectively over pre-development conditions (Jackson and Rosenlieb 1989). In a comparison of twenty anchialine pools located within and outside of resort complexes, pools with human development on their immediate periphery had significantly higher concentrations of ammonium, dissolved inorganic nitrogen, and soluble phosphorus (Dalton *et al.* 2013). Stable isotope analysis of shrimp tissues from a pool located down flow from the Kona sewage treatment plant injection well show δ^{15}N values over 500% higher that shrimp from pools elsewhere along the coast. Elevated δ^{15}N indicates a source of sewage is making its way into the food web. Furthermore, although water is clear and algae are not visible, the high shrimp densities indicate high rates of primary productivity. Because groundwater flows through pools and out to wetland and coral reef ecosystems (Knee *et al.* 2008), broad-scale groundwater contamination is also expected to affect other ecosystems.

The long-term effects of elevated nutrients in anchialine pools are presently unknown. It is possible that in most areas, pools have not reached a threshold of nutrient loads that would lead to eutrophic conditions. Because groundwater moves through pools to offshore areas (Knee *et al.* 2008), this constant flow is likely to reduce nutrient buildup in pools with good hydrologic connectivity (Dudley et al., 2013). Future increases in development along the coast will increase anthropogenic nutrient inputs to groundwater and could potentially lead to greater numbers of pools in eutrophic conditions. Ensuring that native grazers are abundant would be one way to help conserve pool integrity.

Future of Anchialine Ecosystem Research in Hawaii

In Hawaii, ecological and conservation work has focused on anchialine pools as individual units and not fully considered that the bulk of the ecosystem may actually be the unexplored subterranean portion of the coastal aquifer connected to pools. In the Caribbean, Eastern Europe, and Australia, anchialine ecosystems consist primarily of extensive caves that can only be accessed by scuba divers (Iliffe and Kornicker 2009). Few accessible anchialine caves have been identified in Hawaii, but clearly anchialine mollusks and shrimp utilize subsurface cracks and crevices in the porous bedrock, often on a daily basis. This raises the question, what is the biological importance of the surface pool versus the subsurface habitat for anchialine organisms? Population genetic work on the anchialine shrimp *H. rubra* points to larval dispersal between pools and even islands with genetic lineages determined by barriers to movement such as non-porous parts of aquifers or unfavorable ocean currents (Craft et al. 2008). We know very little regarding the way Hawaiian anchialine species use the subterranean habitat. A few chance observations indicate there is more complexity than we realize. For example, gravid female *H. rubra* are not observed in pools, but biologist David Chai (personal communication) describes finding hundreds of gravid females in water that was near ocean salinities (32 ppt) and pumped from 75ft depths out of a test well on the Kona Coast. Personally, I have observed *H. rubra* and *Macrobrachium* prawns deep in caves where groundwater receives no sunlight. Are Hawaiian shrimp able to exist completely underground like related taxa in caves in the Caribbean? Are anchialine aytid shrimp such as *H. rubra* utilizing sulphide-oxidising chemoautotrophic bacteria like related taxa in Australia? Or are sunlit pools and the photosynthetic producers in them essential sources of energy for the entire anchialine community? Few surface pools exist on the older islands, but should we expect to find anchialine organisms in subterranean habitats like the karst caves existing under urban Honolulu? With so little understood about the anchialine ecosystem, we might consider shifting the focus from protecting individual pool units to protecting the aquifer as the ecosystem unit. Protection of groundwater quantity and quality is clearly essential for sustaining anchialine ecosystems.

Summary

As sea levels rise and current pools become inundated, high subsurface hydrologic connectivity will cause future pools to emerge in the rugose lava terrain. Endemic anchialine shrimp and mollusks will be able to populate new pools, because adults and larvae move in brackish coastal groundwater through subterranean cracks (Craft *et al.*, 2008). Low lying coastal areas that will become future anchialine habitat should be protected from development. Because sea level rise will provide a mechanism for introduced fishes to disperse from infected to uninfected habitats, fish removals will help protect future ecosystem integrity. Conservation efforts aimed at reducing introduced fish, minimizing groundwater contamination, and protecting low lying coastal area from development will ultimately allow the unique Hawaiian anchialine pool ecosystem to persist.

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