

Assessment of coral settlement distributions and environmental conditions

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Summary

The patterns of coral recruitment along environmental gradients in relation to coral and fish communities, in reference to historical, sedimentation, and water quality data were determined. Changes on the reef in relation to changes on the watershed were evaluated. From our evaluation of past, present and projected future condition of the coral reefs of Pelekane Bay we find that the historical reef decline has been subsiding, offering support of local action strategies including regulatory initiatives and watershed restoration. Abundance and diversity of reef fishes has increased since 1996 and coral decline has stabilized. Coral recruitment patterns show substantially lower levels in inshore waters. This is supported by manipulative lab experiments showing larval settlement blockage under very low levels of fine sediments. Results of water quality analysis and field assessment suggest no substantial change in offshore water quality from 2010 to 2014. Moreover, greater observed coral settlement offshore remained steady across years suggesting no immediate threat from land-based sedimentation. The potential threat from existing mud deposits adjacent to excellent coral reefs appears to be minimal.

Baselines have been set for 34 sites within the Kawaihae/Pelekane region that will be valuable in evaluation of changes in the future in response to further natural and anthropogenic impacts and management strategies. This highly successful project produced five peer-reviewed journal articles. Outreach components include 12 venues that reached members of science, academia, and management. All goals and objectives proposed have been met or exceeded.

1. Problem Statement

The marine environment of Pelekane Bay has been severely impacted by the construction of the neighboring Kawaihae Harbor in the 1950's and subsequent changes in land use throughout the bay's watershed. Sedimentation and other forms of land-based pollution have led to declines in water quality and coral reef ecosystem health over the last two decades (Tissot 1998). The Kohala Watershed Partnership was awarded \$2.69 million from NOAA's Restoration Center as part of the American Recovery and Reinvestment Act (ARRA) of 2009 to stabilize soil and improve land use practices on the Pelekane Bay watershed. This work has been completed and various upland watershed management activities are ongoing that will reduce land-based sources of pollution into Pelekane Bay. There is a need to determine the efficacy of land restoration and reef recovery. The emerging South Kohala Conservation Action Plan (SKCAP) has identified a number of "Target" areas that will require scientific input on the condition of the reefs.

2. Goals and Objectives

A number of questions must be answered in order to (1) evaluate the effectiveness of the terrestrial watershed remediation efforts in relationship to reef recovery; (2) to understand the potential of the local marine ecosystem to recover; and (3) to understand the potential threat that existing mud deposits pose to adjacent, relatively pristine coral reef ecosystems. This project made use of an extensive existing database coupled with additional work on coral recruitment patterns to address these questions and establish a framework to evaluate the success of restoration efforts. The results of this program provide resource managers with information relevant to other watershed restoration efforts currently being planned in neighboring watersheds. All anticipated results and deliverables have been completed in accordance with the proposal work plan.

3. Management Relevance

This project addresses the following goals and objectives as described in local, state and national coral reef management documents. It addresses the Hawai'i's Coral Reef Strategy Objective 1: Reduce key anthropogenic threats to two priority nearshore coral reef sites by 2015 and five by 2020 using *ahupua'a* based management. The extensive database from 34 stations within Pelekane Bay is crucial to creating initial baseline data on marine coral, algal and fish communities and will serve to evaluate watershed restoration efforts for development of management strategies in the Kawaihae/Pelekane *ahupua'a*. It also addresses Hawaii's LAS-LBPS Goal: Reduce land-based pollution to improve coastal water quality and coral reef ecosystem function and health, Objective 1: Reduce pollutant load to surface water and groundwater through site-specific actions and best management practices. This research meets this objective by determining the pattern of recruitment as a viable indicator of recovery by examining patterns of coral recruitment along environmental gradients in relation to coral and fish communities throughout the area in reference to historical, sedimentation, and water quality data. A focus on documenting change on the reef in relation to changes on the watershed can support management strategies to improve water quality. In addition it addresses NOAA's Coral Reef Conservation Program Goal 1: Reduce pollutant loading from watersheds to priority coral reef ecosystems, Objective 1.3: Implement watershed management plans and relevant local action strategy within priority coral reef ecosystems and associated watershed to improve coral reef ecosystem resilience. This research occurred within one of the local action strategy priority regions and will add to the foundational evidence needed to develop sound management decisions.

This project is also directed at meeting some of the priority needs of the South Kohala Conservation Action Plan (SKCAP). The database and other information that we have collected as part of this project will allow us to provide the information required by the following SKCAP "Target Areas": 1. Coastal-marine Food Resources, 2. Coral Reef Ecosystems, 3. Native Reef Herbivores and 4. Native Reef Predators. Restoration of the Pelekane Bay watershed and recovery of the adjacent reef is a key element of the SKCAP discussions. This research can help meet the needs of SKCAP for a scientific assessment of the resource while laying the foundation for future assessments of the efficacy of conservation measures.

4. Project Description

This project is directed at establishing past, present and future condition for reefs of Pelekane Bay and south Kohala, Hawai'i. The PI and his associates have developed a large database on this region over the past two decades through a series of research programs in this area. This includes studies associated with the construction of the small boat harbor and coral transplantation at Kawaihae from 1996 through 1998 (Jokiel et al. 1999). In 1999, the Coral Reef Assessment and Monitoring Program (CRAMP) set up long-term permanent baseline transects off Kawaihae to determine any changes over time where monitoring continues. Rapid assessment transects in Pelekane Bay were conducted in 2002. In addition, an extensive survey of the region was undertaken to ground truth satellite images for the NOAA coral reef mapping program (2000-2008). In 2009, a collaborative project was initiated in collaboration with NMFS to evaluate the effect of sedimentation on reef fisheries (DeMartini et al. 2013). The PI in collaboration with USGS undertook a major 1-year Hawai'i Coral Reef Initiative (HCRI) project involving detailed measurement of biological and physical characteristics of the Pelekane region.

This sediment transport and water quality work (Storlazzi et al. 2012) along with the biological results (DeMaritini et al. 2013) have recently been published. We have now compiled extensive data on the biology of Pelekane Bay and South Kohala which includes growth rates of corals, rates of coral mortality, distribution and abundance of corals and fishes throughout the region in relation to sedimentation, and impact of sediment on fish recruitment.

5.1 Objective (1): To evaluate the effectiveness of the terrestrial watershed remediation efforts in relationship to reef recovery.

a) Photo Documentation

Conditions at Pelekane Bay following a January 2014 heavy rain event were assessed through photo documentation and shoreline surveys. Aerial images of the Bay and adjacent areas were obtained through helicopter surveys. Interviews with NPS rangers concerning the January storm flood and impact on the reef were conducted.

b) Data Synthesis and Resurveys

For a historical reference we synthesized a large amount of data on sedimentation and water quality. Using this data and revisiting previously established transects, we have published on 30 years of change in Pelekane Bay. Historical studies describing the Pelekane Bay coral reef communities (Chaney et al. 1977, Tissot 1998) were resurveyed using similar methodology to document changes over time (Fig. 1). Recent surveys help to determine the efficacy of land restoration and reef recovery in the watershed. Resurveys were conducted and results submitted to a peer reviewed journal that was subsequently published in PeerJ during the project period (see full article: Appendix I).



Figure 1. Study sites in Pelekane Bay surveyed in 1977, 1998, and 2012. Sites F1-8 depicts Demartini et al. 2013 sites.

Stender Y, Jokiel PL, and Rodgers KS. 2014. Thirty Years of Coral Reef Change in Relation to Coastal Construction and Increased Sedimentation at Pelekane Bay, Hawai'i. PeerJ DOI 10.7717/peerj.300.

Abstract: Coral reefs are being critically impacted by anthropogenic processes throughout the world. Long term monitoring is essential to the understanding of coral reef response to human impacts and the effectiveness of corrective management efforts. Here we reevaluated a valuable coral reef baseline established in Pelekane Bay, Hawai'i during 1976 and subsequently resurveyed in 1996. During this time interval substantial impacts occurred followed by extensive corrective measures. Coral and fish communities showed dramatic declines from 1977 to 1996 due to massive harbor construction and suboptimal land management practices on the watershed. More recently, corrective measures in the form of watershed stabilization and fishing regulations have been implemented. Consequently our 2012 survey reveals that coral cover since 1996 has increased slightly accompanied by a significant increase in fish abundance, diversity, and evenness. This improvement can be attributed to lower fishing pressure since 1996 due to reduced shoreline access, tighter fishing regulations and increased monitoring of legal and illegal fishing activities. Stabilization of the coral community can be attributed partially to reduced sedimentation resulting from watershed restoration that included installation of sediment check dams, control of feral ungulates, controlled grazing and replanting of native vegetation. Insight into the mechanism that removes sediment from reefs was provided by a major storm event and a tsunami that remobilized and flushed out sediment deposits. The increase in herbivorous fishes probably played a role in reducing algal competition in favor of corals. The data suggest that the precipitous reef decline in this area has been arrested and offers support for the corrective actions previously undertaken.

Summary of Findings

Results show fish assemblage abundance, richness, and diversity in Pelekane Bay has improved over the past 16 years following a severe decline between 1976 and 1996. Our data also show an increased abundance of herbivores. This pattern is supported by results of a 2005 survey by U.S. National Park Service Inventory and Monitoring Program (Beets et al. 2010). Species composition has shifted relative to the 1976 survey but remains similar to that observed in 2005. Results of the present survey are also in agreement with the findings of DeMartini et al. (2013) who demonstrated a significant positive effect of improved habitat (lower sediment accumulation and greater availability of branching corals) on the density of juvenile parrotfishes (Fig. 1). The same pattern of increasing fish abundance along a gradient of improving habitat was shown in our study as well as the study by Beets et al. (2010).

This study showed stabilization and perhaps a slight increase in coral cover since 1996 following a substantial reduction between 1976 and 1996. The increase in herbivorous fishes has likely helped the coral population by reducing algal competition in favor of corals. Since 1996 there have been substantial changes at Pelekane Bay that may explain the increases in fish populations. A public county road that formerly ran along the coastline was realigned at a higher elevation in

1996 in order to restore the shoreline to conditions that existed at the time when the historic Pu'ukoholā temple was dedicated. Removal of the road limited shoreline accessibility. New rules restricted camping to Spencer Beach Park at the south end of Pelekane Bay, which resulted in, lowered fishing pressure in the study area. In addition, a new NPS visitor information center was built in 2007. The visitor center is located close to the bay with an overlook complete with telescopes that allows for constant observation of the reefs by visitors and rangers. Rangers now conduct patrols along the shoreline as part of their duty. Access to Pelekane Bay from the harbor area to the north was further restricted in 2011 due to increased harbor security under the Homeland Security Program at Kawaihae Harbor following the terrorist attack of Sept. 11, 2001. The establishment of nearby marine protected areas designated by the State of Hawai'i in 1998 may also have contributed to the increase in fish populations. In select regions, the West Hawai'i Fisheries Management Areas (FMAs) and Fisheries Replenishment Areas (FRAs) were designed to limit high take methods of fishing, create fish reserves. Marine protected areas (MPAs) act as fish refuges with research demonstrating an increase in the number and size and connectivity within and between reserves (Friedlander et al. 2010). Areas adjacent to reserves benefit as fishes move in and out of the area and "spill-over" into nearby regions (Birkeland and Friedlander 2001). The "spill-over" effect was particularly significant for resource fishes including parrotfishes in Hawai'i (Stamoulis and Freidlander 2012). Although fishing is still permitted by law, Pelekane Bay has developed into a de facto marine protected area due to more limited access.

A seasonal effect among the three survey periods is most likely minimal relative to inter-annual differences in the overall fish abundance. For example, inter-annual variability of recruit abundance in Hawai'i is greater than the seasonal variability (Walsh 1987). Lunar differences in recruitment and spawning periodicity have been reported for several species in Hawai'i (Walsh 1987), but the three surveys used in the present analysis were conducted on multiple days with varying moon phases within each year. The potential effect of lunar phase on overall fish abundances were averaged and not biased towards new or full moon when recruitment and spawning are reported to occur for some species.

Results of the extensive studies by Storlazzi et al. (2013) and DeMartini et al. (2013) indicated that the turbidity, sediment cover and sediment accumulation rate are highest near the sediment source (stream mouth) and decrease on the reef with increasing distance from the stream mouth. Our study is in agreement with these observations. Biotic factors show an inverse relationship to this sediment pattern with the lowest rugosity, coral cover, coral richness, fish abundance, fish diversity, and evenness increasing with distance from the stream mouth. Pelekane Bay has a long history of chronic land-based influences including sedimentation and resuspension, which has affected coral reef recovery. Substantial sediment accumulation between 1928 and 2011 has occurred in Pelekane Bay (Storlazzi et al. 2013). Comparison of bathymetry over this time period revealed that 22,489 to 37,483 m³ of sediment was deposited that resulted in a shoaling of 0.41 to 0.61 m during this time interval. Nevertheless natural resilience of reef ecosystems can facilitate recovery (Nyström and Folke 2000). Full recovery to pre-disturbance levels may be an extended process, requiring many more decades. Even though the reefs have been damaged, our data show that further decline can be stopped and recovery can begin once stressors are reduced. Such damaged reefs may be prime candidates for restoration activities

because at this point on the degradation curve a slight improvement in the environment may result in a greater improvement in coral and fish assemblages than might be observed from similar restorative effort on a mildly stressed reef. Our conclusion is that watershed restoration projects, reduced fishing pressure, and increases in marine protected areas in adjacent regions have allowed for partial recovery of fish populations since the Tissot (1998) surveys.

The community structure of the Pelekane Bay reef over the past two centuries apparently has changed in a manner that results in tolerance resistance to severe impacts including storm events and land-based sedimentation. Results of this survey show that the Pelekane Bay reef has the ability to absorb severe disturbance while continuing to maintain functional capacities. Factors that can affect reef resilience include improved water and substrate quality (Wolanski et al. 2004), herbivore abundance, stable coral cover, and species and habitat diversity (McClanahan et al. 2012). These factors have all improved since the previous survey. Recent change in the reef community of Pelekane Bay exemplified the positive effects of an integrated approach of watershed management and acute wave disturbances on mitigating local human impacts. The long-term data set that now exists for Pelekane Bay will be valuable in the future for continued assessment of reef community response to environmental change and improved management strategies. Continued monitoring and expansion of the original dataset will allow evaluation of relationships between abiotic and biotic factors. These data can be used to examine ecological trends and patterns in response to human and natural impact.

c) Statewide Monitoring Efforts

Our continued efforts in documenting the changes on the reef in relation to changes on the watershed have culminated in a publication on long-term monitoring.

Rodgers KS, Jokiel PL, Brown EK, Hau S, and Russell Sparks R. 2014. Over a Decade of Change in Spatial and Temporal Dynamics in Hawaiian Coral Reef Communities. *Pacific Science Early View*.

Abstract: The Hawai'i Coral Reef Assessment and Monitoring Program (CRAMP) was established in 1999 to describe spatial and temporal variation in Hawaiian coral reef communities in relation to natural and anthropogenic factors. In this study, we analyze changes over a 14 year period (1999 to 2012) based on data from 60 permanent reef stations at 30 sites in the main Hawaiian Islands. Overall mean statewide coral cover, richness, and diversity did not vary significantly since initial surveys, although local variations in coral cover trends were detected. The greatest proportion of stations with significant declines in coral cover was found on the island of Maui (0.40) while Hawai'i Island had the highest proportion of stations with significant increases (0.58). Trends in coral cover at some stations varied over time due to acute (e.g. crown of thorns outbreak) and chronic (e.g. sedimentation) disturbances. Stations with increasing coral cover with the potential for recovery from disturbances were identified for possible management actions in the face of future climate change. The Hawaiian archipelago, located in the center of the subtropical Pacific, has experienced a temporary reprieve of slight cooling due to a downturn of temperature since 1998 at the end of the last cycle of the Pacific Decadal Oscillation (PDO). However, temperatures have been steadily increasing over the past several decades and models predict more severe bleaching events to increase in frequency and

intensity in coming decades with concomitant decline in Hawaiian corals. Trends reported in this study provide a baseline that can later be used to test this predicted decline associated with future warming.

Summary of findings in the Pelekane/Kawaihae area

This study focused on station-specific trends since CRAMP was started in 1999 (Fig. 2). Identifying stations that are improving or stable despite perceived natural and anthropogenic variations will be crucial to direct management strategies in the face of future climate change. The main Hawaiian Islands occupy a unique geographic position in an area of the north-central Pacific that has escaped major bleaching events (Burke et al. 2011) as well as rapid sea level rise (Leuliette 2012) over the past decade. The long-term trend of increasing water temperature in Hawaiian waters, however, indicates that Hawai'i may not be buffered indefinitely from these climatic events. In addition, projected changes in the ocean chemistry due to ocean acidification will have profound effects on reef areas globally and in Hawai'i unless carbon emissions are reduced substantially (Hoegh-Guldberg et al. 2007). Consequently, it is imperative that reefs be identified that appear to be more resistant and/or resilient to these perturbations. Several of the stations in this study such as many of the shallow stations on Hawai'i Island appear to fit these criteria and could act as source populations.

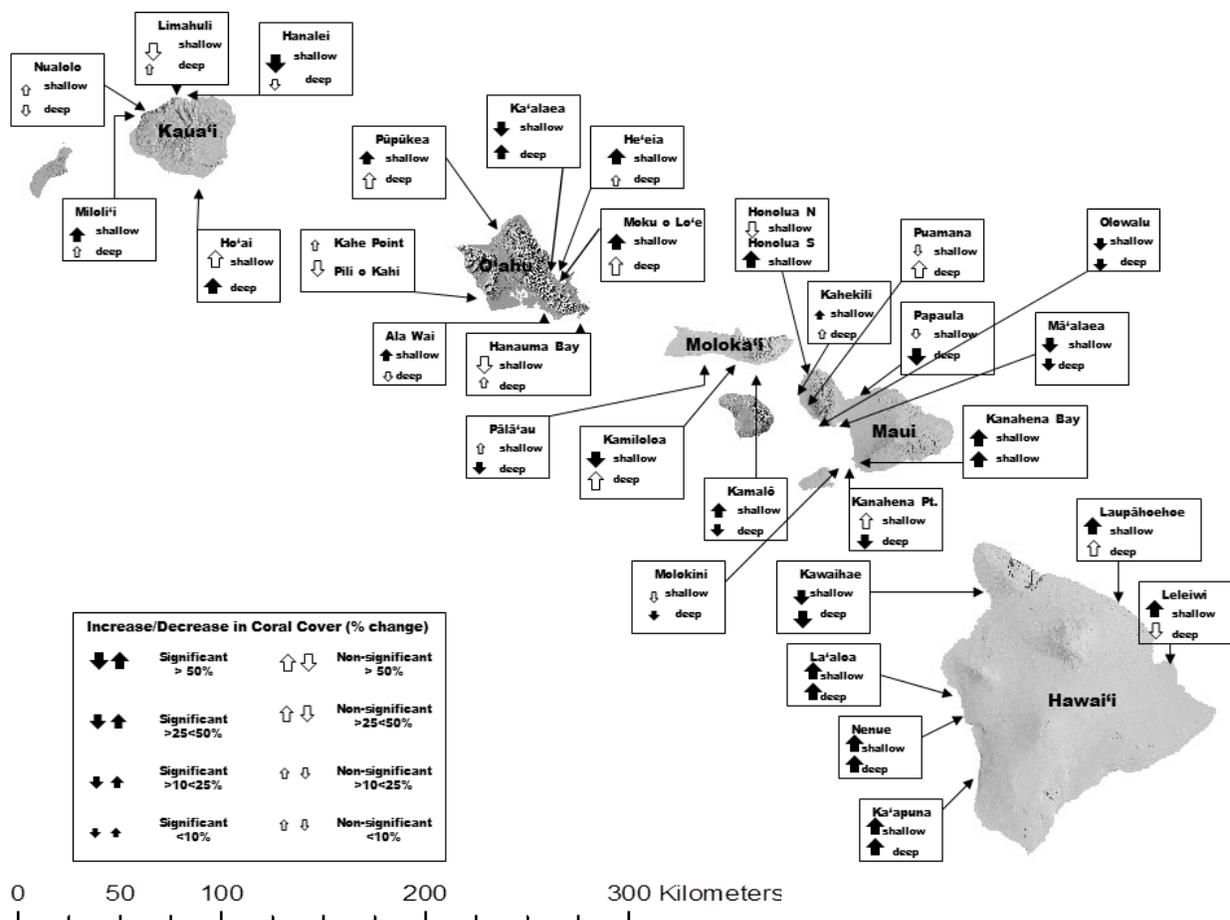


Figure 2. Map of CRAMP sites in the state of Hawai‘i. Solid arrows indicate statistically significant trends. Size of arrows are correlated with the size of the change in coral cover. Direction of arrow indicates the direction of the change (up arrow shows increase).

Many stations on the island of Hawai‘i experienced an overall increase in coral cover during the study period as indicated by the positive regression slopes in percent coral cover (Fig. 2). The exceptions were the two stations at Kawaihae along the northern section of the West Hawai‘i coastline. These results are in agreement with data from the Division of Aquatic Resources (DAR) West Hawai‘i Aquarium Project (WHAP) that has developed extensive spatial and temporal data coverage at 24 sites along the West Hawai‘i coastline. WHAP results showed a significant decline in coral cover since 2003 at six of their seven northern sites that encompass the West Hawai‘i coastline (Walsh et al. 2009). In addition, DAR and the Nature Conservancy found drastic declines in reef fishes and associated coral habitat when reviewing historical and recent data at sites near Kawaihae, West Hawai‘i (Minton et al. 2012). Minton et al. (2012) found that contributing factors included a decrease in vegetation cover in the adjacent watersheds due to a reduction in rainfall over the past nine years that increased sediment deposition on nearshore reefs. Survey plots in the Pelekane Bay Watershed above the Kawaihae site also showed a decline in vegetation as drought conditions progressed (The Kohala Center 2011). Major sedimentation events occurred during periods of high rainfall (USGS 2006, 2013).

The 1999–2000 CRAMP baseline established reliable reference points to evaluate coral cover statewide over time. In addition, comparative studies at the onset (e.g. Brown 2004, Brown et al. 2004) enabled the program to examine earlier temporal data sets at a larger spatial than had been previously attempted. This present study documented the trends at individual stations and found similar levels of improving and declining reefs suggesting that overall statewide coral cover and diversity has remained relatively stable since the initial CRAMP survey. The key strategy will be focusing management efforts on the stations that have been declining in a chronic fashion. Even though many of these reefs may have already been in a degraded state when CRAMP was initiated, the current results will set a new baseline for assessing future declines and potential recovery at reefs targeted for management actions.

5.2 Objective (2): To understand the potential of the local marine ecosystem to recover.

a) Coral recruitment patterns along a sediment gradient

One of the best short-term indicators of environmental change and recovery is the pattern of coral recruitment in relation to land-derived sedimentation. Coral larvae and recruits are sensitive to sediment impacts and other anthropogenic changes in addition to natural variability. Larval production, settlement, and recruitment are crucial biological processes maintaining the population structures for the preservation of coral reefs. A major focus of this study is therefore quantifying coral settlement and environmental factors influencing coral recruitment to assess (1) early settlement patterns along environmental regimes, (2) how settlement rates may vary between years, and (3) how early settlement patterns may be related to characteristics of existing benthic habitat and community. This data will help establish information on early settlement patterns along environmental regimes, how settlement rates vary temporally, and how early settlement patterns may be related to characteristics of established communities.

Coral settlement and recruitment are crucial processes for long-term preservation and integrity of coral reef ecosystems. Successful settlement and recruitment depend upon habitat quality and environmental factors such as sedimentation, available light, salinity, temperature, substrate, surface rugosity, and current patterns. Early settlers and recruits are especially vulnerable to environmental degradation and unsuitable habitats impacted by human-induced processes. Reef habitat and water quality in Pelekane Bay has been subjected to major alteration and multiple stressors including human-induced changes in water circulation and land-based sedimentation. In our previous study, the greater number of early coral settlers was found on the offshore reef than on the inshore reef at where water is poorly circulated and murky near the stream mouth. Percentage of live tissue and growth rate of corals that are commonly found in Pelekane Bay also decreased closer to the stream mouth where water quality is not favorable. We repeated the coral settlement studies to better understand patterns of Hawaiian coral settlers, their response to human impacts and environmental conditions, and to continue monitoring as long-term information is essential to the effectiveness of corrective management effort in the South Kohala region.

Methods

The primary study area includes the Pelekane Bay and Kawaihae areas (Fig. 3). Eight stations were established at a mean depth of 1.5, 5, and 15 m. Six of these stations were established primarily in the vicinity of USGS geologic instrument locations deployed between the winter of 2010 and 2011 along the sediment gradient. These stations included five sampling sites within a radius of approximately 250 m from the instrument package. Two nearest stations to the shoreline included six and four sites. Ten of these 40 sites were established and surveyed by The Nature Conservancy in 2010. Sites were accessed from both shoreline and from a small vessel.

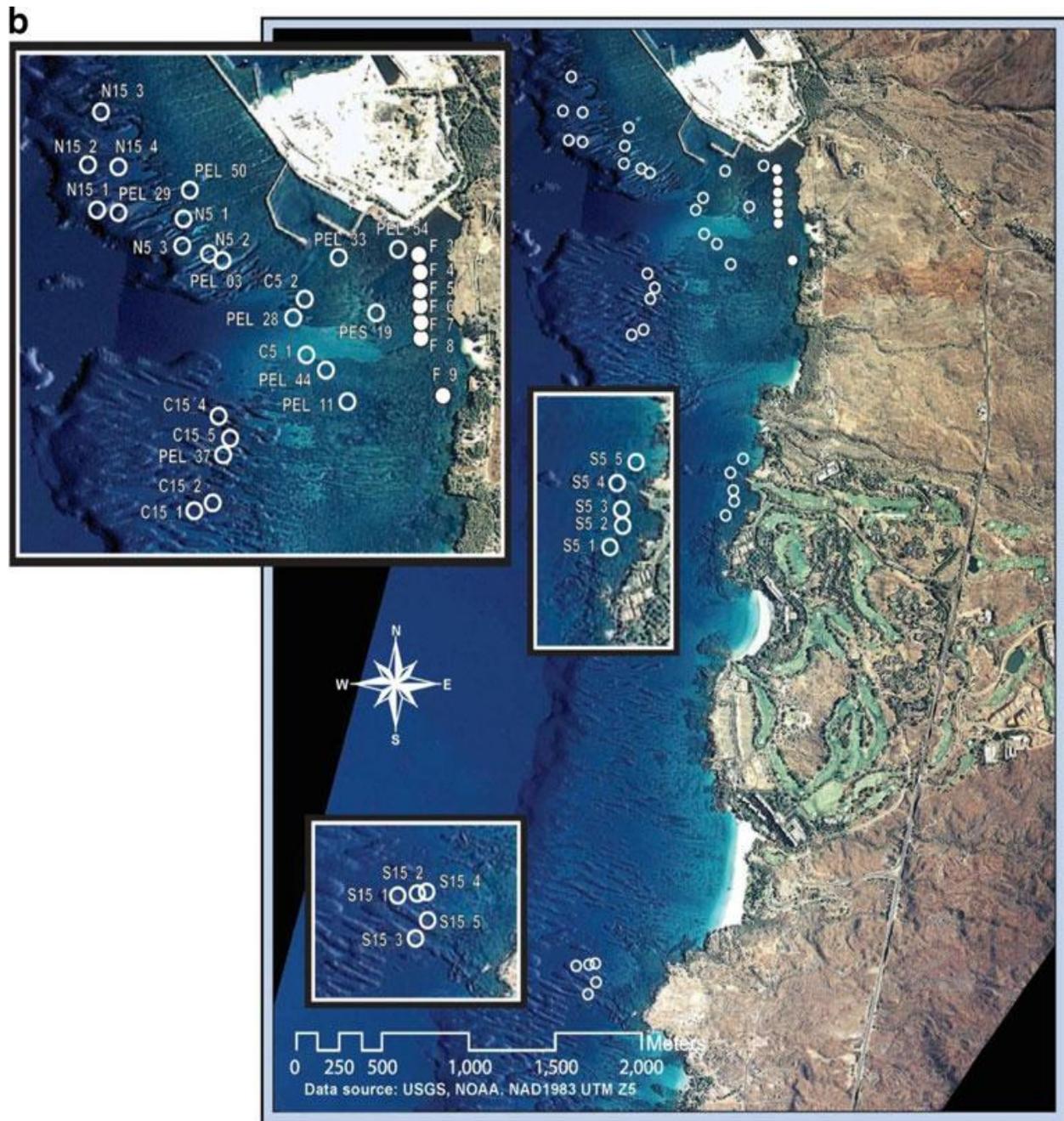


Figure 3. Map of sampling stations with detailed inset of stations within Pelekane Bay and Puakō where recruitment arrays were deployed, surveys conducted, and water quality measurements taken in 2011 and 2014.

Environmental Conditions

Sediment and water quality data were collected to define a gradient of habitat conditions upon the deployment and retrieval of settlement tiles in 2011 and again prior to and following tile deployment and removal in 2014. Water quality parameters collected in 2011 included pH, temperature, salinity (conductivity), dissolved oxygen and turbidity and Photosynthetically

Active Radiation (PAR), while PAR and turbidity were measured in 2014. Water quality parameters were measured with a multi-parameter meter YSI 6920 V2 SONDE at deployment sites above the sea floor during sample collection. PAR was measured using a portable light meter LI-COR LI-250A with an underwater quantum-sensor. Bulk sediment samples were collected manually for composition and grain size analysis at each deployment site if sediment was present. Additionally PAR and suspended solid concentration were measured at each of 37 sites in 2014. Two 1L-seawater samples were manually collected near the seafloor at each site in May and September, 2014. Samples were vacuum-filtered through pre-weighed Whatman 47mm GF/F 0.7 μ m glass microfiber filters immediately following sampling. Filters were then air-dried for at least a week and weighed on a Mettler Toledo X54035 microbalance on three separate days to obtain an average weight.

Coral Settlement

Settlement data were collected by using the following methods in 2011 and were replicated in the 2014 study. A set of two unglazed terracotta tiles (10 cm x 9.7 cm) was assembled and attached to a PVC post (Fig. 4). Recruitment arrays were deployed at 34 randomly selected sites stratified by depth (ranging between 1.5 and 15 m) and proximity from the stream mouth (Fig. 3) prior to the start of the summer reproductive season (June-August).



Figure 4. Unglazed terracotta tiles assembled in an array as a settlement platform at each of the 34 sampling stations.

Three arrays were placed at each sampling site along a 25-m transect in each year (n=204). To replicate the recruitment study in 2011, arrays were deployed in late April in 2014, and retrieved in September of 2014. Retrieved tiles were processed following Brown et al. (2007) to remove sediment and fleshy tissues of settled organisms by soaking tiles in 10% household bleach solution for 24 hours. Tiles were gently rinsed with flowing fresh water then air-dried for subsequent visual examination. Analysis of settlement tiles was conducted in the laboratory using a Carl Zeiss Stemi 2000-C stereomicroscope to determine the abundance of settlers and their positions on the plate surfaces. Individual coral settlers were counted and identified to genus level according to morphological characteristics of skeletons (Fig. 5). An individual was

recorded as unidentified when its skeletal structure was not developed enough for positive identification. A settler, which did not follow the skeletal morphology of a known genus, was also recorded as an unidentified individual.



Figure 5. Coral recruit as seen under dissecting microscope.

Data Analysis

Data sets collected between 2010 and 2014 were integrated and analyzed for this study. A gradient of environmental conditions was characterized and established by use of a Principal Component Analysis (PCA) using a linear combination of correlated water quality and habitat metrics. Descriptive statistics of coral settlement were summarized using data from horizontally-oriented tile sets retrieved at 42 sites across years. Settlement data collected in 2011 and 2014 from 34 sites were statistically analyzed using a Generalized Linear Model (GLM) with the negative binomial distribution (Zuur et al. 2009) in R version 3.1.1. This was to examine the distribution pattern in relation to environmental conditions and variation between years, accounting for non-linearity and the appearance of frequent zeros in the count data. Performance of four non-linear statistical models, including a Poisson GLM (PGLM), Negative Binomial GLM (NBGLM), Zero-inflated Poisson mixture model (ZIP), and Zero-inflated NB mixture model (ZINB), were first compared to evaluate the assumption of no overdispersion (the variance and mean are equal for the Poisson distribution) and a relative importance of zero counts using values of the overdispersion parameters and Akaike Information Criterion (AIC). Settlement data from Puako (five sites of S15 in 2011 and three sites in 2014) were not included in the statistical tests as no associated environmental data for S15 sites were available and settlement arrays were either missing or had been rearranged. The spatial distribution of coral settlers was visually represented using ArcGIS 10.1.

Results

Environmental Conditions

The first three principle components explained about 77% of the variability among study sites. These sites were separated into two primary environmental regimes along the first principle component (PC1). Temperature, salinity, a light extinction coefficient, and depth were strongly correlated with PC1, which explained 43% of the variation in the environmental data collected at

study sites. Temperature made the greatest contribution followed by salinity, light extinction coefficient, and depth. Turbidity, pH, and rugosity were correlated to the second principle component (PC2) accounting for 17% of the remaining variation. Turbidity was the greatest contributor in relation to PC2. Rugosity and pH correlated with the third component accounting for about 17% of the remaining variation. Sites located relatively close to the stream mouth were clustered while sites distant from the shoreline formed another cluster along PC1 and PC2. Shallow (< 2.5 m) inshore sites were generally characterized by warmer temperature, lower salinity, higher light extinction coefficient, higher turbidity, and lower pH than deeper (3-15 m) offshore sites. Sites were aggregated and will hereafter be referred as “inshore” and “offshore” sites (Table 1) based on this analysis for the remainder of this document.

Table 1. Primary sampling sites for coral settlement characterized by environmental types in Pelekane and Kawaihae area in 2011 and 2014. Geographic coordinates of sites are expressed in decimal degree (dd).

Site	Station	Environment	Latitude (dd)	Longitude (dd)
F3	C2	Inshore	20.02656	-155.82463
F4	C2	Inshore	20.02601	-155.82456
F5	C2	Inshore	20.02540	-155.82452
PEL_54	C2	Inshore	20.02673	-155.82540
PES_19	C2	Inshore	20.02432	-155.82522
PES_33	C2	Inshore	20.02647	-155.82748
F6	F	Inshore	20.02495	-155.82452
F7	F	Inshore	20.02445	-155.82447
F8	F	Inshore	20.02396	-155.82447
C15_1	C15	Offshore	20.01864	-155.83183
C15_2	C15	Offshore	20.01838	-155.83248
C15_4	C15	Offshore	20.02137	-155.83166
C15_5	C15	Offshore	20.02069	-155.83124
PEL_37	C15	Offshore	20.02016	-155.83146
C5_1	C5	Offshore	20.02335	-155.82859
C5_2	C5	Offshore	20.02453	-155.82906
PEL_11	C5	Offshore	20.02189	-155.82708
PEL_28	C5	Offshore	20.02512	-155.82868
PEL_44	C5	Offshore	20.02287	-155.82786
N15_1	N15	Offshore	20.02783	-155.83611
N15_2	N15	Offshore	20.02926	-155.83644
N15_3	N15	Offshore	20.03094	-155.83603
N15_4	N15	Offshore	20.02919	-155.83538
PEL_29	N15	Offshore	20.02775	-155.83534
N5_1	N5	Offshore	20.02761	-155.83302
N5_2	N5	Offshore	20.02654	-155.83209
N5_3	N5	Offshore	20.02628	-155.83160
PEL_03	N5	Offshore	20.02673	-155.83305

PEL_50	N5	Offshore	20.02853	-155.83280
S5_1	S5	Offshore	20.00961	-155.82716
S5_2	S5	Offshore	20.01034	-155.82672
S5_3	S5	Offshore	20.01084	-155.82675
S5_4	S5	Offshore	20.01171	-155.82694
S5_5	S5	Offshore	20.01241	-155.82624

Coral Settlement

Total number of coral settlement was 761 individuals across all existing sites between 2010, 2011, and 2014. About 75-85% of total coral settlement occurred on the bottom surface of lower tiles and edges of tiles in 2011 and 2014 across all sites (Fig. 6). In 2011 and 2014, predominant genus included *Porites*, *Pocillopora*, and *Montipora*. Poritids accounting for about 55 – 80% of total settlement in both inshore and offshore environments (Fig. 7).

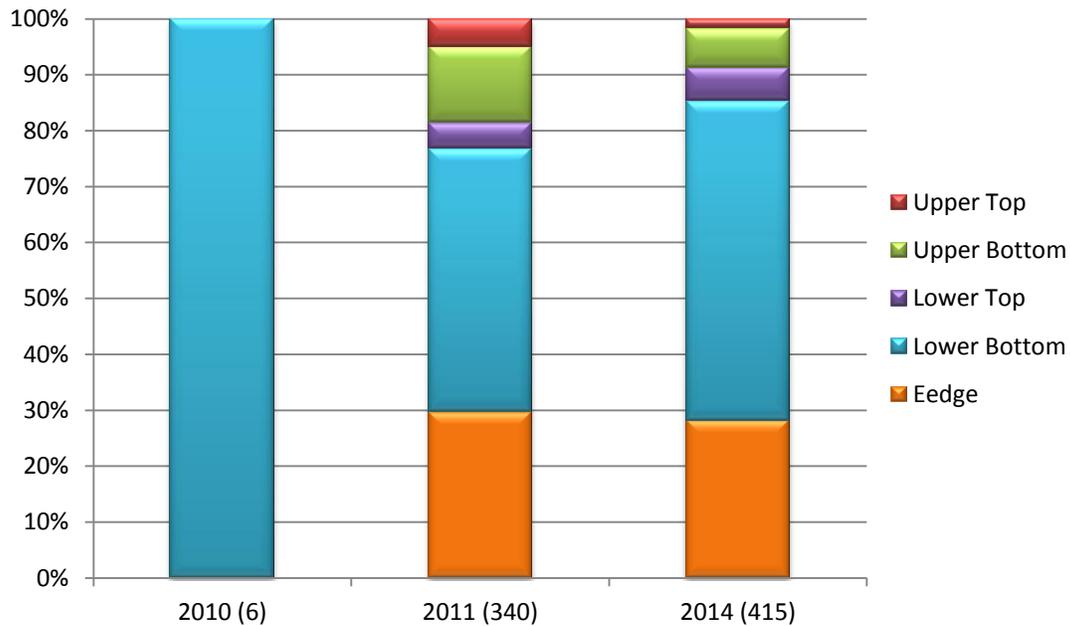


Figure 6. Proportion of settlers on different tile surfaces. Total number of settlers are indicated on the X axis in parentheses.

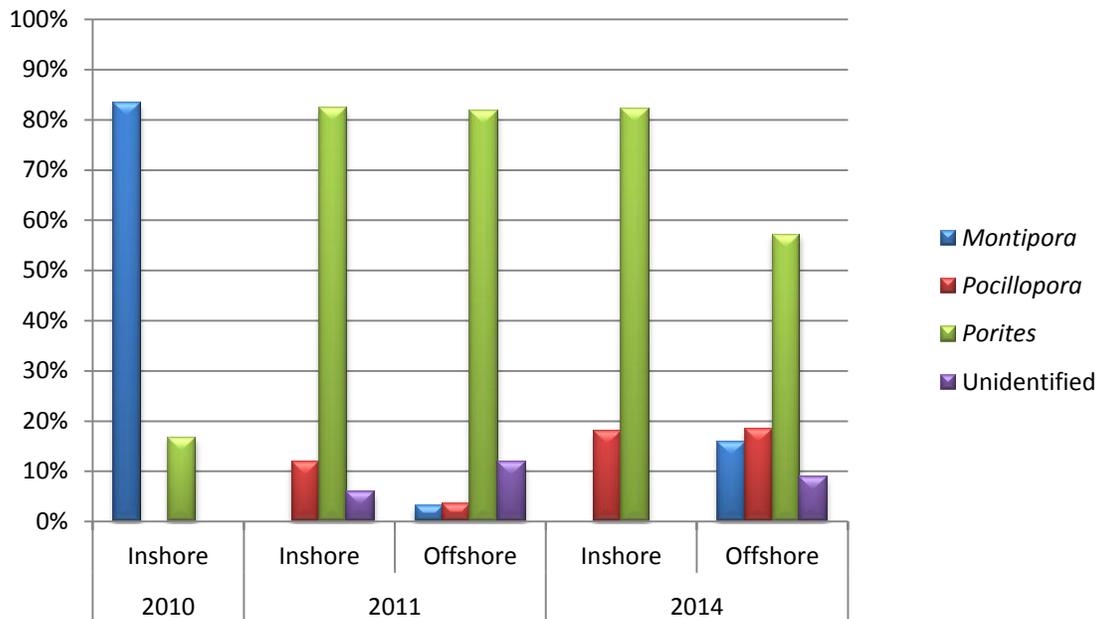


Figure 7. Proportion of settlers by genus, environment, and year.

Overall, the average coral settlement rate was 58.8 ± 62.9 s.d.m. $m^{-2}year^{-1}$ for the South Kohala region including Pelekane Bay, Kawaihae, and Puakō areas. Considerable differences in coral settlement were observed between inshore and offshore environments (Fig. 8) regardless of large Coefficient of Variation (Table 2). Total number of individuals and mean settlement were substantially less for inshore (51 and $14.3 m^{-2}year^{-1}$) than offshore environment (710 and $78.3 m^{-2}year^{-1}$). A small difference in total number of individuals and mean settlement was found between 2011 and 2014 (Table 3). Coefficient of Variation was similar between environmental conditions within a same year while there were some variations between 2011 and 2014 (Table 4).

Table 2. Descriptive statistics summary of coral settlement aggregated by environmental conditions. The unit of values is $m^{-2}year^{-1}$.

Environment	N	Total settlement	Min mean	Max mean	Grand Mean	CV (%)
Inshore	25	51	0.0	61.2	14.3	110
Offshore	57	710	0.0	251.7	78.3	84

Table 3. Descriptive statistics summary of coral settlement aggregated by year. The unit of values is $m^{-2}year^{-1}$.

Year	N	Total settlement	Min mean	Max mean	Grand Mean	CV (%)
2010	7	6	0.0	40.8	7.3	209

2011	39	340	0.0	251.7	52.2	123
2014	36	415	0.0	251.7	76.0	81

Table 4. Descriptive statistics summary of coral settlement aggregated by year and environmental conditions. The unit of values is $m^{-2}yr^{-1}$.

Year	Environment	N	Total settlement	Min mean	Max mean	Grand Mean	CV (%)
2010	Inshore	7	6	0.0	40.8	7.3	209
2011	Inshore	9	17	0.0	34.0	12.8	101
	Offshore	30	323	0.0	251.7	63.9	108
2014	Inshore	9	28	6.8	61.2	21.2	81
	Offshore	27	387	0.0	251.7	94.2	64

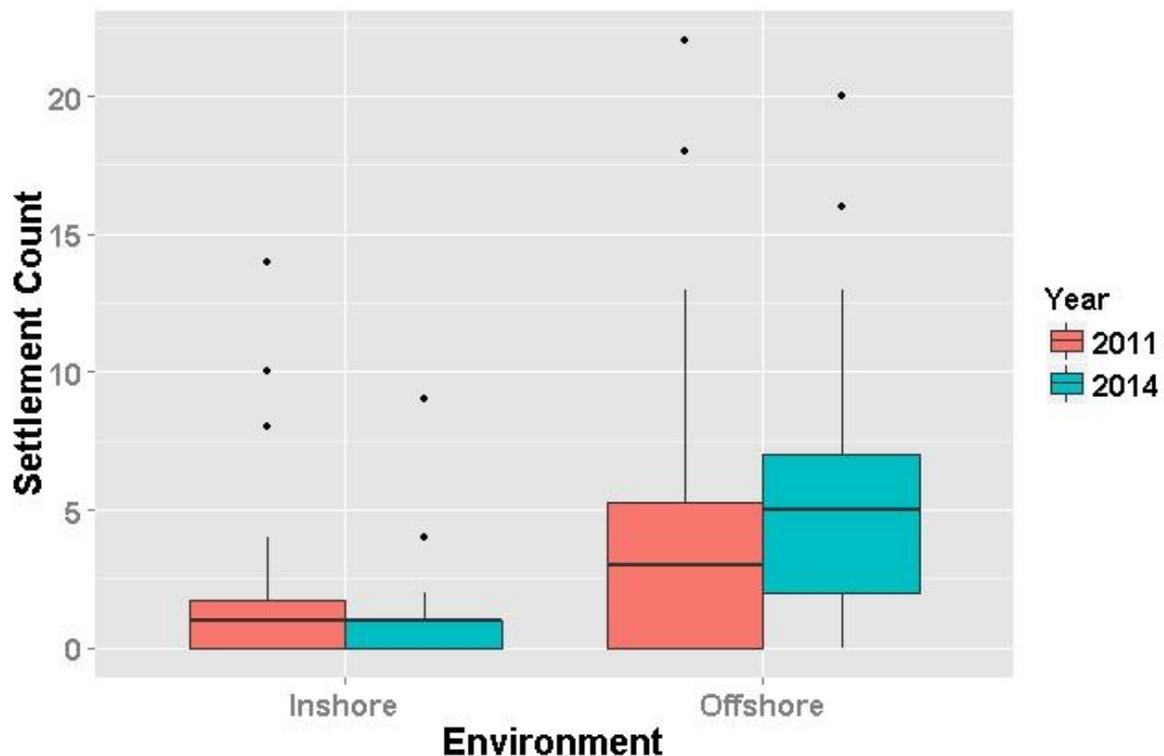


Figure 8. A boxplot of the average coral settlement count by environmental conditions and year.

While the Poisson Generalized Linear Model (PGLM) indicated a considerable overdispersion shown by the highest parameter value, a negative binomial Generalized Linear Model (NBGLM) resulted in the preferred model with the smallest Akaike Information Criterion (AIC) and overdispersion (Table 5). A likelihood ratio test also resulted in a preference of NBGLM ($\chi^2 = 280$ (1), $p < 0.0001$) when compared to PGLM. Zero-inflated negative binomial Model (ZINB) indicated an improvement from Zero-inflated Poisson Model (ZIP), but did not show a

substantial support for a high probability of excess zeros coming from the separate binomial distribution, different from a Poisson process. Effects of environmental regimes and year were then assessed based on NBGLM. While the effect of environmental regimes was statistically significant ($\chi^2 = 37.1$ (1), $p < 0.0001$) the effect of year and interactions were not.

Table 5. Summary of AIC and overdispersion parameter values for a Poisson GLM (PGLM), Negative Binomial GLM (NBGLM), Zero-inflated Poisson mixture model (ZIP), and Zero-inflated NB mixture model (ZINB).

Model	AIC	Overdispersion
PGLM	1202	4.38
NBGLM	923	1.17
ZIP	1050	2.17
ZINB	923	1.24

Spatial distributions of coral settlement were similar among years 2010, 2011, and 2014 (Figs. 9, 10). Greater total settlement of individuals is observed for sites that are distant from the stream mouth than sites near a stream and away from the shoreline.

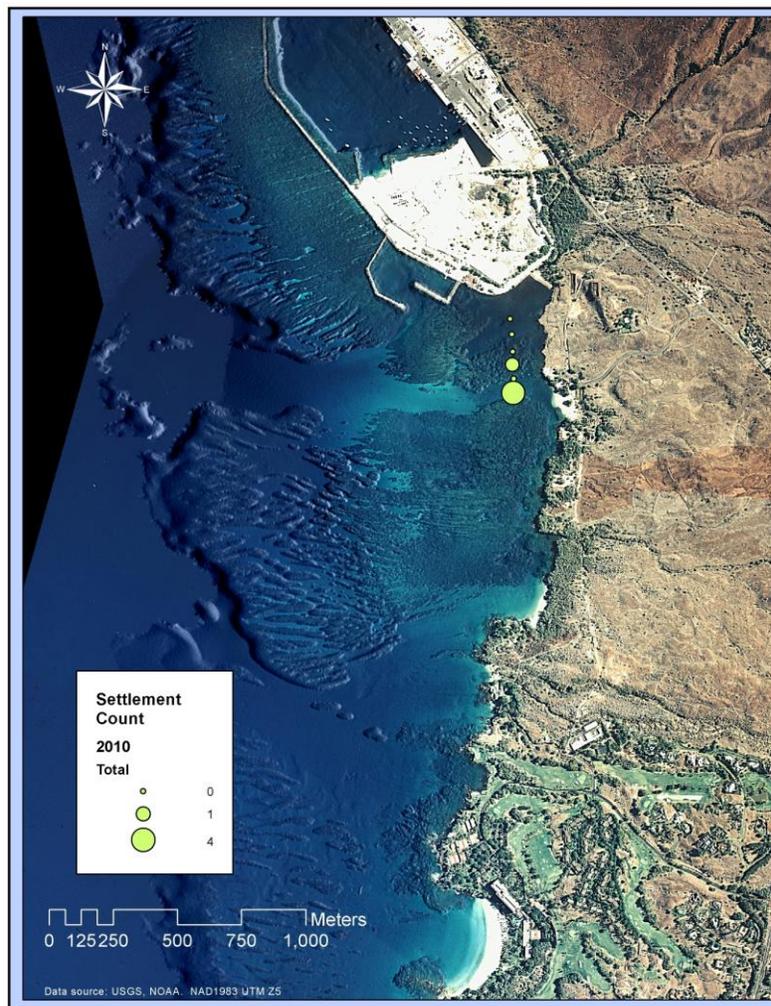


Figure 9. Total numbers of coral settlers at six sites in Pelekane Bay along a sediment gradient in 2010.

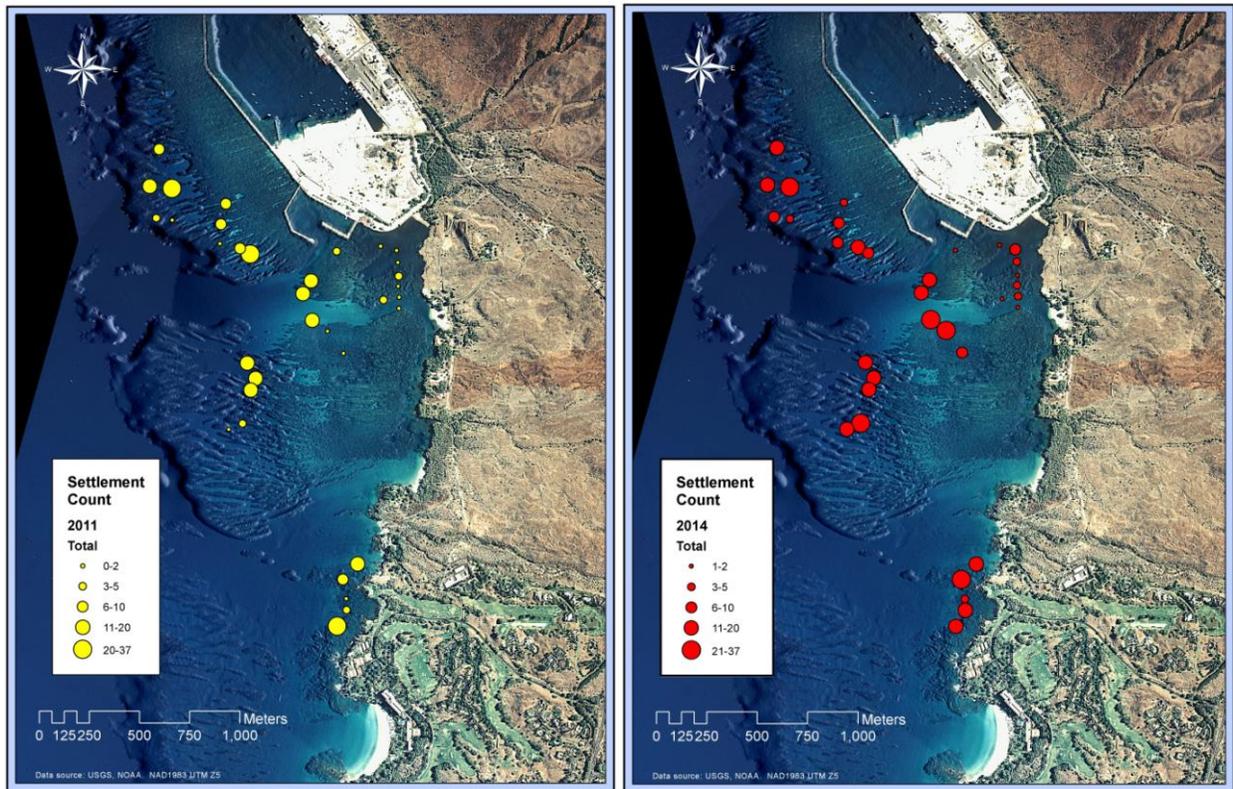


Figure 10. Total number of coral settlers at 34 sites in Kawaihae, Pelekane Bay, and Puakō in 2011 (left panel) and 2014 (right panel).

Results suggested that coral settlement is strongly affected by environmental conditions. On average, coral settlement is extremely lower in the inshore environment than the offshore environment. There is no large statistical variation between years. Although overall variability of coral settlement has been known to be typically high in time and space, there was a considerable difference between the abundance and distribution of settlers by environmental conditions and habitat characteristics.

The distribution pattern of coral settlement was comparable to the size-frequency distribution of *Porites lobate*, one of dominant species in Pelekane Bay and Kawaihae. The distribution of colony size was significantly related to surface turbidity values (Minton et al. 2011). Smaller colonies (0-5cm) were more frequent in less turbid surface water while larger colonies (5-80cm) were associated with greater turbidity (Minton et al. 2011). Colony size of *P. lobata* sampled further inshore attained >50 – 150cm (DeMartini et al. 2013). The turbidity is relatively high inshore, and can exceed a minimum value of turbidity by three orders of magnitudes (1.6 – 1525 NTU, USGS 2013) during the flood and large wave events. Although large colonies have been surviving with partial mortality in the turbid environment (DeMartini et al. 2013), very few coral settlements occurred under this condition during the present study. Survey sites with frequent small colonies coincided with settlement study sites in the offshore environment where greater settlement was observed. Observed small colonies in the offshore environment may include

successful recruits of early coral settlers in addition to colonies established by asexual fragmentation and fission.

The range and average recruitment rate of the present study was similar to reported values for Waiakailio Bay and Puakō in Martin and Walsh (2014). These two DAR monitoring sites are positioned north and south of Pelekane Bay and Kawaihae. Average recruitment rates were substantially higher at Waiakailio Bay and Puakō when compared to seven other southern locations along the West Hawai‘i coast, therefore recruitment rates for Pelekane and Kawaihae should be high as well. Topography of Pelekane and Kawaihae is relatively complex, characterized by basalt pavement and rock. Fossil finger coral beds and other calcified structures on the geologic foundation provide abundance of suitable micro habitat for coral settlement. Episodic large waves observed in this area help clear accumulated sediment. Coral reef recovery is potentially rapid if sediment sources are controlled with improvements to inshore hydrodynamics.

b) Low levels of sediment can block coral recruitment

Fine red terrigenous sediments as are found in Pelekane Bay (Fig. 11) were used in laboratory experiments to determine settlement and survival rates of the Hawaiian coral *Pocillopora damicornis* planulae. These results were revisited and published in the peer reviewed journal PeerJ to better understand sediment patterns in the Pelekane area.

K. Perez III, K.S. Rodgers, P. L. Jokiel, C. Lager, D. Lager. 2014. Effects of terrigenous sediment on settlement and survival of the reef coral *Pocillopora damicornis*. PeerJ 2:e387; DOI 10.7717/peerj.387.

Abstract: Survival and settlement of *Pocillopora damicornis* larvae on hard surfaces covered with fine (<63 μm) terrigenous red clay was measured in laboratory Petri dishes. The dishes were prepared with sediment films of various thicknesses covering the bottoms. Coral larvae were incubated in the dishes for two weeks and the percent that settled on the bottom was determined. There was a statistically significant relationship between the amount of sediment and coral recruitment on the bottom, with no recruitment on surfaces having a sediment cover above 0.9 mg cm^{-2} . Experimental conditions for the delicate coral larvae were favorable in these experiments. Total survival over the two week settlement tests expressed as the sum of coral recruits and live larvae at the end of the experiment did not show a significant decline, so the major impact of the sediment was on successful settlement rather than on mortality. Larval substrate selection behavior was the primary factor in the observed result.

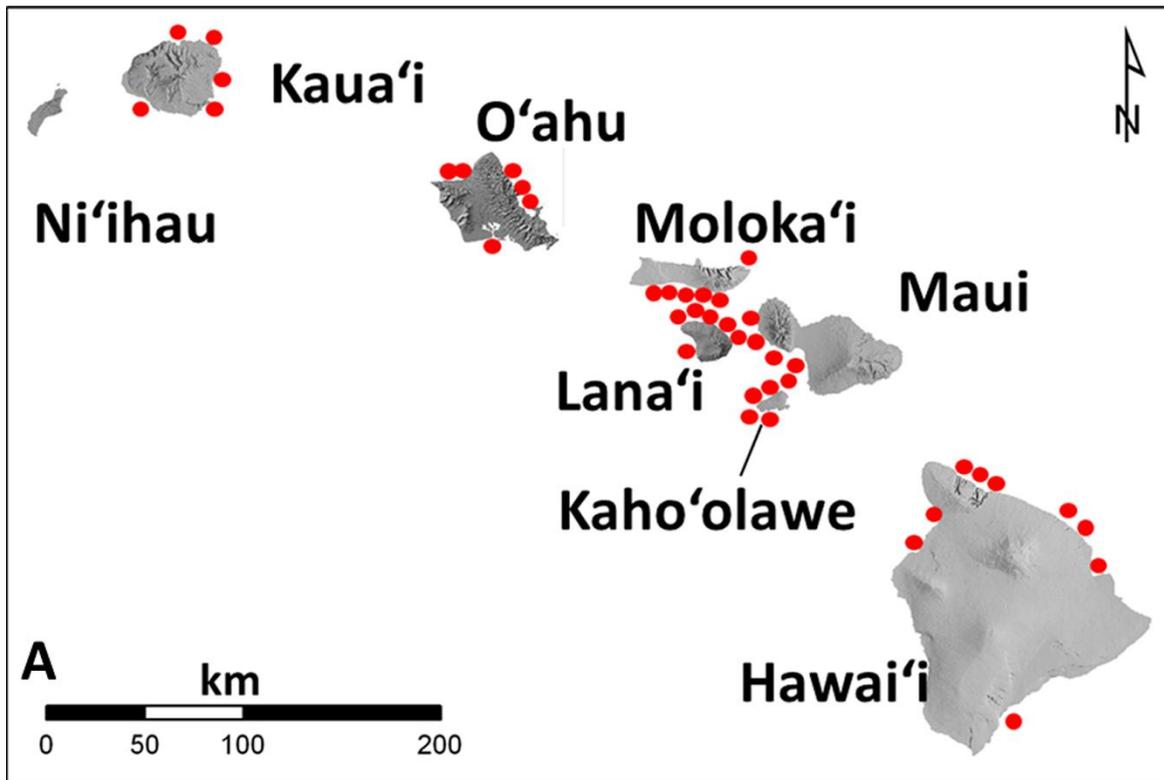


Figure 11. A. Map of the main Hawaiian Islands showing areas with heavy red mud deposits including Pelekane Bay in West Hawai'i.

Findings: Our laboratory results should be used with caution in applying the results to field situations. However, the value of this research is that it shows that an extremely thin film can block recruitment. For further details see Appendix IV.

In summary, the results of the present investigation support and amplify the findings of previous investigations:

- Although a variety of settling cues have been shown, it is possible that a thin film of sediment can override these cues blocking larval settlement.
- Recruitment rate of larvae in sediment experiments is very low. Te (1992) recorded 2% to 3% settlement of *Pocillopora damicornis* larvae over a two week period. Babcock & Davies (1991) report a mean of only 15% settlement in a two day experiment using larvae of the coral *Acropora millipora*.
- Larval behavior is an important factor in determining settling success and survival. Larvae will seek a suitable settlement site (Harrigan, 1972) and will find areas that are free of sediment. Hodgson (1991) conducted larvae settlement experiments on *P. damicornis* on glass plates with sediment layers of 0 to 500 mg cm⁻², but the sediment covering the glass settling plates was not uniform, having some areas clear of sediment. The corals were able to find and settle in open areas not covered with sediment.

- A relatively thin uniform coating of land-derived sediment can prevent coral recruitment. Hodgson (1991) reports a larval settlement threshold for *P. damicornis* of 536 mg/cm^{-2} over patchy horizontal surfaces that blocked 95% of coral settlements. Results of this study refine this cutoff to a lower value of 1 mg/cm^{-2} , for a uniform sediment film of fine muds.

c) Corals can survive and grow in highly turbid areas

Manipulative field experiments were conducted along a sediment gradient to determine how corals are affected. This research relates to recovery of marine ecosystems throughout the Hawaiian Islands. For more detailed information see Appendix V.

Jokiel PL, Rodgers KS, Storlazzi CD, Field ME, Lager CV, Lager D. (2014) Response of reef corals on a fringing reef flat to elevated suspended-sediment concentrations: Molokai, Hawaii. PeerJ 2:e699 <https://dx.doi.org/10.7717/peerj.699>

Abstract: A long-term (10 month exposure) experiment on effects of suspended sediment on the mortality, growth, and recruitment of the reef corals *Montipora capitata* and *Porites compressa* was conducted on the shallow reef flat off south Molokai, Hawaii. Corals were grown on wire platforms with attached coral recruitment tiles along a suspended solid concentration (SSC) gradient that ranged from 37 mg l^{-1} (inshore) to 3 mg l^{-1} (offshore). Natural coral reef development on the reef flat is limited to areas with SSCs less than 10 mg l^{-1} as previously suggested in the scientific literature. However, the experimental corals held at much higher levels of turbidity showed surprisingly good survivorship and growth. High SSCs encountered on the reef flat reduced coral recruitment by one to three orders of magnitude compared to other sites throughout Hawaii. There was a significant correlation between the biomass of macroalgae attached to the wire growth platforms at the end of the experiment and percentage of the corals showing mortality. We conclude that lack of suitable hard substrate, macroalgal competition, and blockage of recruitment on available substratum are major factors accounting for the low natural coral coverage in areas of high turbidity. The direct impact of high turbidity on growth and mortality is of lesser importance.

Findings:

- At the end of a 10 month growth period it was apparent that the growth platforms had recruited different amounts of macroalgae. All macroalgae was removed from each platform, rinsed dried and an ash-free dry weight was determined. When total coral mortality plus partial mortality is plotted against macroalgae dry weight a significant relationship is revealed. Therefore a large amount of the mortality observed in this experiment can be attributed to competition with macroalgae rather than sediment effect.
- Likewise, coral growth was quite good in spite high turbidity. Growth was excellent in the sites at Kamiloloa that were farthest offshore.
- Coral growth at Transect H (Kamiloloa) showed a strong relationship with increasing distance from shore while transect E (Kawela) did not show a strong trend.
- Measures of coral recruitment produced the greatest surprise, with levels of coral recruitment one to three orders of magnitude lower than other reefs measured with the same technique at locations throughout the Hawaiian Islands. This result is explained by

the dramatic impact of thin layers of fine red sediment on coral larval settlement recently documented by Perez et al. (2014).

Our research on sediment levels that can block coral recruitment is highly relevant to conditions at Pelekane Bay. A thin film of sediment was shown to block coral settlement of *Pocillopora damicornis* larvae. Fine muds as were used in this experiment are found throughout Pelekane Bay's benthic habitat. This prevents coral recruits from establishing. However, the large colonies previously established are continuing to survive and grow even under these turbid conditions as were documented in our south Moloka'i study. The levels of fine sediment at Pelekane are comparable to those in south Moloka'i (Rodgers 2005). Although survivorship and growth are negatively correlated with sediment levels, increasing along a sediment gradient, corals can still survive in highly turbid waters as exist in Pelekane Bay.

5.3 Objective 3): To understand the potential threat that existing mud deposits pose to adjacent, relatively pristine coral reef ecosystems.

a) Quantification of fish community factors

Fish biomass and abundance were quantified for 57 observations (34 inshore and 23 offshore environments) to characterize the assemblage using the standard visual belt transect approach (Brock 1954; Brock 1982). A diver swam along two to five 25 m x 5 m transects (125 m²) at each site. Species, quantity, and total length of fishes were recorded. All fishes were identified to the lowest taxon possible. The same individual quantified fishes for all samples to eliminate observer variability. Total length (TL) of fish was estimated to the nearest centimeter in the field. The estimated length was converted to biomass density estimates, metric tons per hectare (t ha⁻¹), with length-mass fitting parameters. Length estimates were converted to mass using estimated fitting parameters available from the Hawai'i Cooperative Fishery Research Unit (HCFRU) or FishBase (www.fishbase.org). If a specific fitting parameter is not available, a congener of similar shape within the genus was used.

Table 6 summarizes overall means and the Coefficient of Variation by environmental regimes. While mean biomass, abundance, and species richness were lower for inshore than the offshore environment, a variation was high within each environmental condition. Total biomass of reef fishes was found to be greater at offshore sites (809 g/m²) among 16 families than inshore environments (350 g/m²) among 19 families (Table 7). Acanthurids accounted for the highest total biomass for both inshore and offshore sites. Acanthuridae, Labridae, Mullidae, Scaridae, and Lutjanidae consisted about 85% of total biomass for inshore. About 88% of total biomass included Acanthridae, Labridae, Scaridae, Serranidae, and Lethrinidae, which includes a single species, *Monotaxis grandoculis*, in Hawai'i, in the offshore environment.

Table 6. Overall means and Coefficient of Variation by environment.

Environment	Biomass		Abundance		Richness	
	Mean	CV (%)	Mean	CV (%)	Richness	CV (%)
Inshore	11.3	99.2	64.9	84.0	12.5	39.5
Offshore	33.7	80.6	84.3	49.7	13.5	24.6

Table 7. Total biomass, means of total biomass, and Coefficient of Variation of fish by family. The sample size (n) indicates the number of transects for observed families.

Environment	Family	Total biomass (g/m ²)	Mean	CV (%)	n
Inshore	Acanthuridae	135.7	4.1	82.8	33
	Blenniidae	0	0.0	NA	3
	Carangidae	8.7	1.5	97.3	6
	Chaetodontidae	14.1	1.3	54.1	20
	Gobiidae	0	0.0	NA	23
	Holocentridae	0.9	0.3	66.7	3
	Labridae	35.8	1.1	91.8	33
	Lutjanidae	19.7	1.2	80.4	17
	Mugilidae	1.2	1.2	NA	1
	Mullidae	40.1	1.8	166.9	22
	Ostraciidae	0.3	0.0	222.7	17
	Pomacentridae	17.8	0.5	200.4	33
	Scaridae	66.1	2.3	155.2	29
	Serranidae	9.4	4.7	51.2	2
	Synodontidae	0.3	0.2	47.1	2
Tetraodontidae	0.1	0.1	NA	1	
Sub total		350.2			
Offshore	Acanthuridae	319.5	13.9	79.3	23
	Aulostomidae	0	0.0	NA	1
	Balistidae	11.8	1.5	63.0	8
	Blenniidae	0	0.0	NA	2
	Chaetodontidae	35.2	2.0	91.5	18
	Cirrhitidae	4.4	0.4	66.1	12
	Labridae	105.5	4.6	58.9	23
	Lethrinidae	114.8	114.8	NA	1
	Lutjanidae	0.6	0.6	NA	1
	Monacanthidae	4	4.0	NA	1
	Mullidae	28.5	1.7	69.5	17
	Ostraciidae	0.1	0.1	141.4	2
	Pomacanthidae	1.7	2.0	NA	5
	Pomacentridae	12	0.7	122.6	18
	Scaridae	84.4	5.3	172.0	16
	Serranidae	83.8	10.5	80.2	8
	Synodontidae	0.6	0.6	NA	1
	Tetraodontidae	0.6	0.2	86.6	3
Zanclidae	1.2	1.2	NA	1	
Sub total		808.7			

Grand total 1158.9

The total number of individual reef fishes was found to be greater offshore (2177) than inshore (1969) (Table 8). Scarids accounted for the highest number of individuals inshore while Labrids were the most abundant offshore (Table 8). Acanthuridae, Labridae, Mullidae, Scaridae, and Pomacentridae consisted about 91% of the total number of individuals inshore. About 93% of the total number of individuals included species from the Acanthridae, Chaetodontidae, Labridae, Pomacentridae, and Scaridae offshore.

Table 8. Total abundance. Means of total biomass, and Coefficient of Variation of fish by family. The sample size (n) indicates the number of transects conducted.

Environment	Family	Total abundance	Mean	CV (%)	n
Inshore	Acanthuridae	534	16.2	82.1	33
	Blenniidae	3	1.0	0.0	3
	Carangidae	11	1.8	63.8	6
	Chaetodontidae	45	4.3	43.4	20
	Gobiidae	72	3.1	85.8	23
	Holocentridae	3	1.0	0.0	3
	Labridae	452	13.7	84.3	33
	Lutjanidae	34	2.0	86.6	17
	Mugilidae	1	1.0	NA	1
	Mullidae	87	4.0	171.2	22
	Ostraciidae	21	1.2	45.5	17
	Pomacentridae	258	7.8	80.5	33
	Scaridae	651	22.4	99.7	29
	Serranidae	2	1.0	0.0	2
	Synodontidae	2	1.0	0.0	2
Tetraodontidae	1	1.0	NA	1	
Sub total		2177			
Offshore	Acanthuridae	1010	43.9	74.9	23
	Aulostomidae	2	2.0	NA	1
	Balistidae	9	1.1	31.4	8
	Blenniidae	2	1.0	0.0	2
	Chaetodontidae	56	3.1	57.2	18
	Cirrhitidae	26	2.2	61.7	12
	Labridae	514	22.3	62.2	23
	Lethrinidae	22	22.0	NA	1
	Lutjanidae	1	1.0	NA	1
	Monacanthidae	1	1.0	NA	1
	Mullidae	42	2.5	68.8	17
	Ostraciidae	2	1.0	95.7	2

Pomacanthidae	7	1.4	39.1	5
Pomacentridae	140	7.8	94.8	18
Scaridae	115	7.2	124.8	16
Serranidae	13	1.6	45.8	8
Synodontidae	1	1.0	NA	1
Tetraodontidae	5	1.7	69.3	3
Zanclidae	1	1.0	NA	1
Sub total	1969			
Grand total	4146			

There were total of 76 species observed on all transects, and 28 of those species were present in both inshore and offshore environments. Table 9 and 10 summarize the 10 highest ranking species of fishes in total biomass and abundance inshore and offshore.

Table 9. Top 10 ranking fish species for total biomass ($\text{g}\cdot\text{m}^{-2}$) in inshore and offshore environments.

Rank	Inshore	Offshore
1	<i>Acanthurus nigrofuscus</i>	<i>Acanthurus nigrofuscus</i>
2	<i>Chlorurus spilurus</i>	<i>Monotaxis grandoculis</i>
3	<i>Mulloidichthys flavolineatus</i>	<i>Cephalopholis argus</i>
4	<i>Thalassoma duperrey</i>	<i>Thalassoma duperrey</i>
5	<i>Lutjanus fulvus</i>	<i>Chlorurus spilurus</i>
6	<i>Cephalopholis argus</i>	<i>Ctenochaetus strigosus</i>
7	<i>Abudefduf abdominalis</i>	<i>Acanthurus olivaceus</i>
8	<i>Caranx melampygus</i>	<i>Acanthurus blochii</i>
9	<i>Naso lituratus</i>	<i>Chaetodon ornatissimus</i>
10	<i>Parupeneus multifasciatus</i>	<i>Acanthurus leucopareius</i>

Table 10. Top 10 ranking fish species for total number of individuals in inshore and offshore environments.

Rank	Inshore	Offshore
1	<i>Chlorurus spilurus</i>	<i>Acanthurus nigrofuscus</i>
2	<i>Acanthurus nigrofuscus</i>	<i>Thalassoma duperrey</i>
3	<i>Thalassoma duperrey</i>	<i>Ctenochaetus strigosus</i>
4	<i>Abudefduf abdominalis</i>	<i>Chlorurus spilurus</i>
5	<i>Scarus psittacus</i>	<i>Chromis vanderbilti</i>
6	<i>Gomphosus varius</i>	<i>Gomphosus varius</i>
7	Gobiidae spp.	<i>Oxycheilinus unifasciatus</i>
8	<i>Mulloidichthys flavolineatus</i>	<i>Stegastes marginatus</i>

9	<i>Acanthurus triostegus</i>	<i>Acanthurus blochii</i>
10	<i>Stethojulis balteata</i>	<i>Paracirrhites arcatus</i>

Four species were commonly shared between inshore and offshore environment within the 10 highest ranking species for both total biomass and total number of individuals. The five most frequently occurring species inshore were *Thalassoma duperrey*, *Acanthurus nigrofuscus*, *Abudefduf abdominalis*, *Chlorurus spilurus*, and *Scarus psittacus*, and *Thalassoma duperrey*, *Acanthurus nigrofuscus*, *Ctenochaetus strigosus*, *Gomphosus varius*, and *Oxycheilinus unifasciatus* in the offshore environment. While *Monotaxis grandoculis* ranked second highest for total biomass in the offshore environment, it was an uncommon transient species. Fish biomass and abundance are highly variable making the impact of land-based sedimentation on the offshore reef fish community difficult to evaluate.

b) Water Quality Analyses to Characterize Environmental Regimes

The relative difference in the extent of sedimentation and water quality was reevaluated during field operations between late April and early May 2014, incorporating water quality data collected in 2011. Water chemistry parameters were measured to characterize environmental regimes in Pelekane Bay using a multi-parameter water quality meter and data logger at the time of recruitment array deployment. Environmental variables measured at each station included temperature, pH, salinity, turbidity, and photosynthetic active radiance (PAR) at deployment sites above the sea floor during sample collection. The light extinction coefficient was calculated using PAR and depth values.

Table 11 summarizes medians and the inter quartile range of water quality variables. There were numerical differences in median temperature and salinity between inshore and offshore environments. Turbidity was highly variable inshore while it was relatively consistent in the offshore environment.

Table 11. Summary of medians for water quality variables by environmental conditions. n= number of sites. Values in parentheses indicate the inter quartile range.

Environment	n	Temperature (°C)	Salinity (ppt)	Turbidity (NTU)	pH
Inshore	10	27.21(1.67)	34.09(0.4)	1.06(0.99)	8.17(0.13)
Offshore	25	25.36(0.30)	34.99(0.11)	0.01(0.23)	8.21(0.07)

Relatively high values of the light extinction coefficient were found in the inshore environment in both the spring and fall seasons (Fig. 12). The light extinction coefficients were more highly variable for inshore sites than across depths (3 m and 15 m) (Fig. 13). Ranges of the coefficients were distinct between inshore and offshore environments with overlap across years.

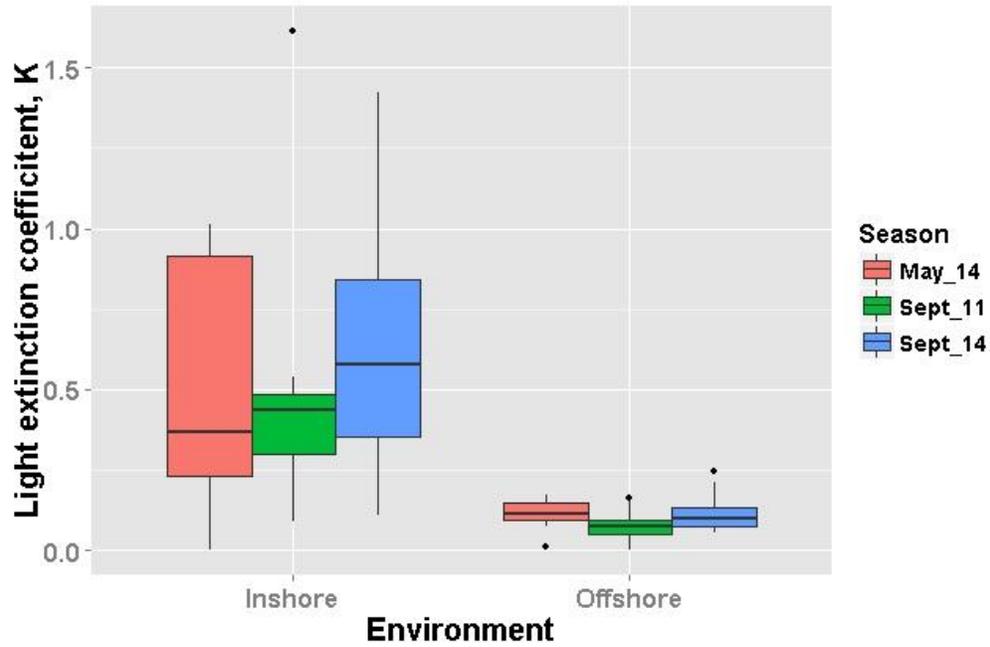


Figure12. Variations in the light extinction coefficient by environmental regimes (inshore vs. offshore).

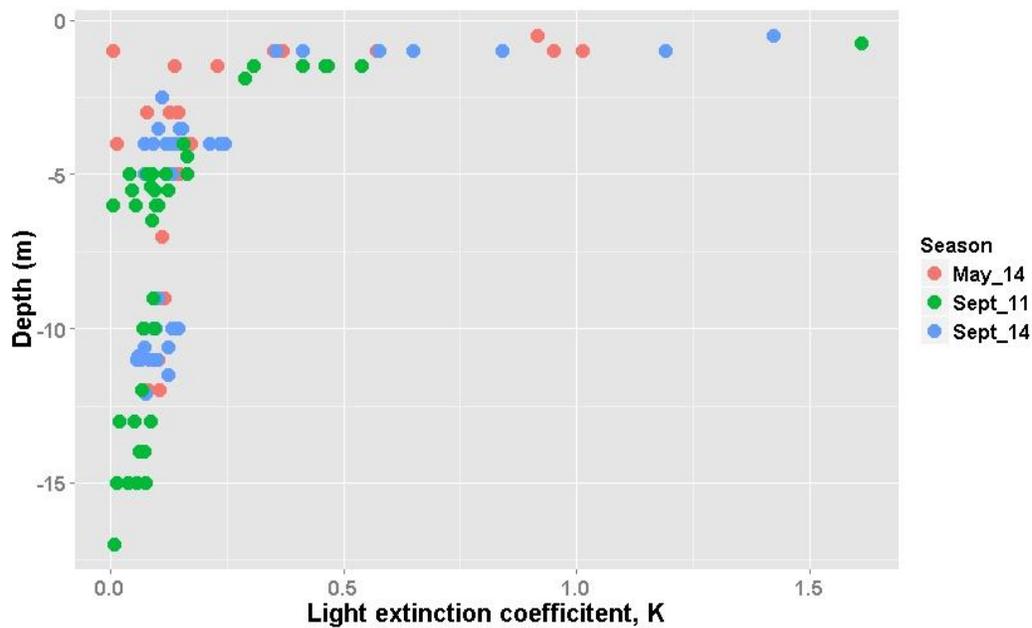


Figure 13. Distribution of the light extinction coefficient along depth.

Median Suspended solids concentration (SSC) is slightly lower offshore than inshore (Figure 14) with high variability.

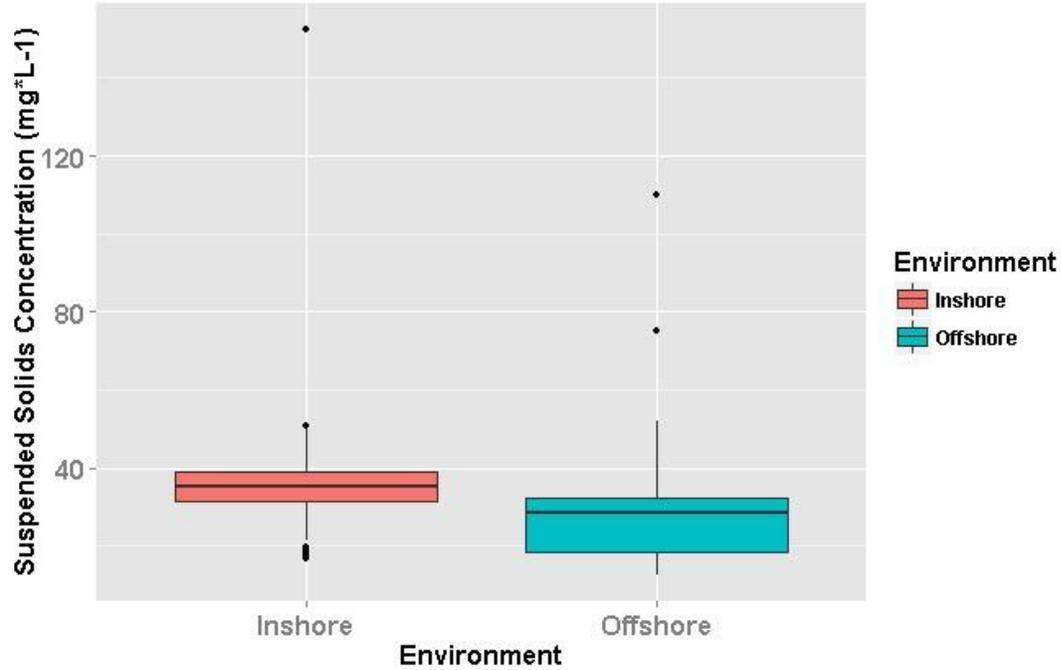


Figure 14. Suspended solids concentration by environment.

SSC appeared to be numerically lower in March and April than in June and Spring months across years. (Figure 15, Table 9).

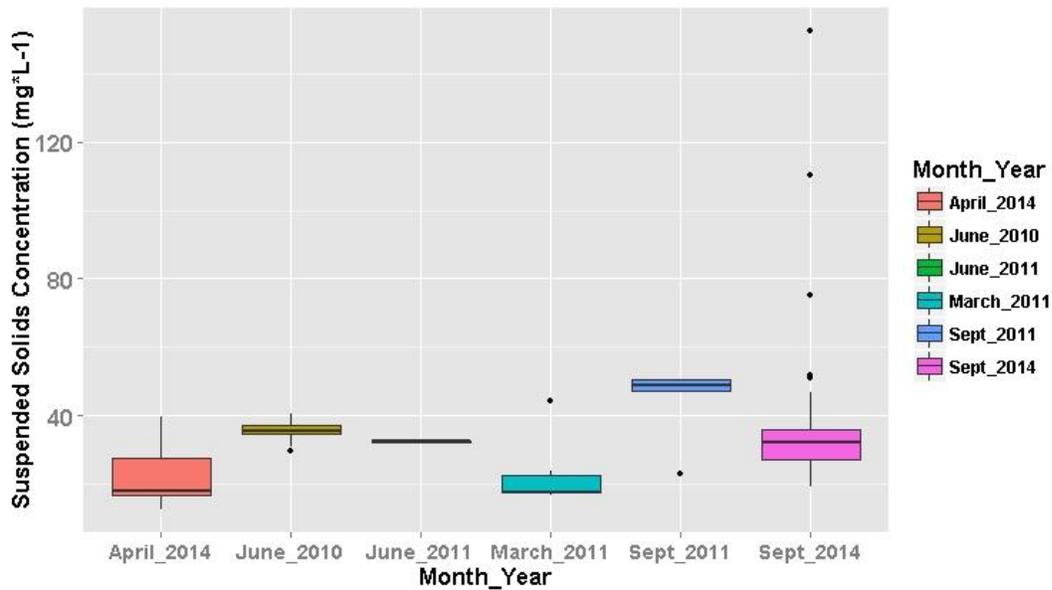


Fig. 15. Suspended solids concentration by month and year.

Table 12. Suspended Solid Concentration ($\text{mg}\cdot\text{L}^{-1}$) by Season and Environment. N = number of sampling sites, Geometric s.d.m. = Geometric standard deviation; IQR = Inter quartile range.

Month_Year	Environment	N	Geometric mean	Geometric s.d.m.	Median	IQR
June_2010	Inshore	23	35.5	1.1	35.4	3.1
June_2011	Inshore	2	32.5	1.0	32.5	1.0
March_2011	Inshore	4	23.9	1.5	20.9	16.5
March_2011	Offshore	2	17.1	1.0	17.2	0.5
April_2014	Inshore	13	24.5	1.4	19.8	18.6
April_2014	Offshore	30	19.3	1.3	17.8	2.7
Sept_2011	Inshore	6	43.4	1.4	49.1	3.5
Sept_2014	Inshore	18	38.8	1.5	37.2	7.0
Sept_2014	Offshore	58	31.0	1.4	31.2	9.7

While there was no substantial difference in median SCC values between inshore and offshore in 2014, colors of sample filters indicated different types of suspended materials. Colors of filtered inshore samples were dark brown, indicating that suspended matter included terrigenous silt. Colors of filtered offshore samples were very pale, translucent, or clear, indicating absence of substantial amounts of silt. Suspended materials such as colloids, flocculent organic particulates and plankton likely comprised the mass of filtered offshore samples. Visual assessment of sediment samples collected during spring and fall 2014 from settlement sites suggested no substantial change in composition. The spatial extent of terrigenous mud observed during field sampling in 2014 was similar to the field assessment in 2011 and 2012. The extent of terrigenous sediment was limited to the inshore environment while carbonate sediment predominated offshore. Results of water quality analysis and field assessment suggest no substantial change in offshore water quality since 2010. Moreover, greater observed coral settlement offshore remained steady across years suggesting no immediate threat from land-based sedimentation. The potential threat from existing mud deposits adjacent to coral reefs in excellent condition appears to be minimal.

c) Benthic Habitat Map Updates

We are collaborating with the NOAA Coral Reef Ecosystem Division to update benthic habitat maps including shallow reefs in the South Kohala region. We have provided benthic imagery data from our study sites to NOAA, maps have been generated, and data are currently being analyzed.

6. Discussion

The data analyzed suggests that the precipitous reef decline in the Pelekane area has been arrested. This success offers support for actions of various local management initiatives involving fishing regulations and watershed stabilization. This long-term data set will be

valuable in the future for assessing changes in biota in response to environmental change and management strategies. Continued monitoring and expansion of the original dataset allows evaluation of relationships between abiotic and biotic factors. These data can be used to examine ecological trends and patterns in response to human and natural impact. The research conducted on impacts of sedimentation on Hawaiian corals can assist in planning management strategies based on sound scientific findings.

7. Key Findings

- The existing and new data analyzed suggests changes in reef communities occurred in the last 30 years in the Pelekane area.
- Reef fish abundance and diversity increased since 1996.
- Decline of live coral cover has stabilized since 1996 following a substantial reduction between 1976 and 1996.
- Coral settlement was substantially lower inshore where there is more impact by sedimentation than at offshore reefs in both 2011 and 2014.
- No strong temporal variation was observed in coral settlement between years.
- Recent episodic seasonal large wave events demonstrate that natural processes remove accumulated sediment deposits on coral reefs to deeper offshore waters.
- Threats from mud deposits to offshore reefs that will affect habitat quality are minimal.
- Although a variety of settling cues have been shown, it is possible that a thin film of sediment can override these cues, blocking larval settlement.
- A uniform sediment film of fine muds as low as 1 mg/cm^{-2} can block recruitment.

8. Project Evaluation

Outputs (products) and Outcomes.

We produced an evaluation of past, present and projected future condition of the coral reefs of Pelekane Bay. We focused on the best short-term indicator of environmental change, which is the pattern of coral recruitment in relation to land-derived sedimentation. We measured coral recruitment during 2010-2011 and 2014 along a sediment gradient in Pelekane Bay. Although coral recruitment is highly variable from year to year the pattern of recruitment can be a good indicator of recovery. This study was directed at patterns of coral recruitment along environmental gradients in relation to coral and fish communities, in reference to a historical, sedimentation, and water quality data, however, other research surrounding sedimentation were explored. Changes on the reef in relation to changes on the watershed were evaluated. During June 2012 we successfully resurveyed the Pelekane transects (Ball 1977, Cheney et al 1977, Tissot 1998) to give us insight into changes over the past 35 years. Manipulative experiments on the impact of sediment on inshore reefs and larval settlement were conducted.

Evaluation of Success

As researchers our long term criteria of success is publication in peer reviewed journals (see citations below) followed by citation of our work. In the short term we can evaluate success by completion of the tasks, production of a final report, evaluation of the interest of managers and scientists to the project (e.g. inclusion in the State of the Reef Reports), outreach venues, successful training of a Ph.D. candidate (Ms. Yuko Stender) who will use this study as a basis of a dissertation, and finally through the acceptance and support of these efforts by the general public in programs such as the South Kohala Conservation Action Plan (SKCAP). We have accomplished all of these measures of a successful project including five articles published in 2014 in peer reviewed journals (see Appendices for full articles).

- 1) Stender Y., P. L. Jokiel, K. S. Rodgers. 2014. Thirty Years of Coral Reef Change in Relation to Coastal Construction and Increased Sedimentation at Pelekane Bay, Hawai‘i. PeerJ. v2013:11:960:1:0.
- 2) Stender Y., M. Foley, K. S. Rodgers, P. L. Jokiel, A. Singh. 2014. Evaluation of the nearshore benthic habitat, marine biota, and water quality adjacent to Kahului Commercial Harbor, Maui, Hawai‘i. UH Engineering Report pp 27.
- 3) Perez III K, K.S. Rodgers, P. L. Jokiel, C. Lager, D. Lager. 2014. Effects of terrigenous sediment on settlement and survival of the reef coral *Pocillopora damicornis*. PeerJ 2:e387; DOI 10.7717/peerj.387.
- 4) Rodgers KS, Jokiel PL, Brown EK, Hau S, and Sparks R. 2014. Hawai‘i Coral Reef Assessment and Monitoring Program: Over a Decade of Change in Spatial and Temporal Dynamics in Coral Reef Communities. Pacific Science. Early View.
- 5) Jokiel PL, Rodgers KS, Storlazzi CD, Field ME, Lager CV, Lager D. 2014 Response of reef corals on a fringing reef flat to elevated suspended-sediment concentrations: Moloka‘i, Hawai‘i. PeerJ 2:e699 <https://dx.doi.org/10.7717/peerj.699>

Data management and dissemination of results

We will continue to use the data management system developed by Dr. Eric Brown early in the development of CRAMP that has now been expanded to include all NPS monitoring data and data from other sources. This data base is moving toward integration with NMFS, UH and other groups. CRAMP has and will continue to archive all data and images at NOAA’s National Ocean Data Center under the direction of Mr. Pat Caldwell as we have since 1998.

Dissemination of results during this study includes the five peer reviewed journal articles listed above and attached as appendices.

Outreach

Twelve outreach venues were conducted to present research findings from this project. These conferences and meetings were well attended by students, researchers, educators, and managers in the marine community.

- a. February 23, 2014 Ocean Science Meeting, Honolulu, HI. “Thirty Years of Coral Reef Change in Relation to Coastal Construction and Increased Sedimentation at Pelekane Bay, Hawai‘i.” Yuko Stender presenter
- b. March 12, 2014 The 39th Albert L. Tester Memorial Symposium, Honolulu, HI. “Thirty Years of Coral Reef Change in Relation to Coastal Construction and Increased Sedimentation at Pelekane Bay, Hawai‘i.” Yuko Stender presenter
- c. May 5, 2014 South Kohala Coastal Partnership Core Team Meeting, Waimea, HI, Paul Jokiel presented findings on sediment impacts.
- d. July 10, 2014 Biol 403 Field Problems in Marine Biology Class PPT Presentation on watershed and reef connections Ku‘ulei Rodgers
- e. July 17, 2014 Biol 403 Lecture State of the Hawai‘i’s Coral Reefs Ku‘ulei Rodgers
- f. July 15 2014 Hawai‘i Conservation Conference “Response of Coral Reefs to Extreme Turbidity on the South Moloka‘i Reef Flat”. Ku‘ulei Rodgers presenter.
- g. Sept 3-4, 2014. Kona Integrated Ecological Assessment Program. Kona Hawaii, King Kamehameha Hotel. “Recent Insights into Effects of Sedimentation on Kona Reefs” presentation by Paul L. Jokiel
- h. Jan 23, 2015 The 23rd Hawaii Conservation Conference, Hilo, HI, August 3-6, 2015 “Assessment of Coral Settlement Distribution and Environmental Condition in Pelekane Bay, Hawai‘i” Abstract submitted by Yuko Stender
- i. Jan 28, 2015 Zoology 410 Corals and Coral Reefs PPT presentation watershed/reef connection
- j. February 1, 2015 UH Sea Grant Reef Talk, Kaloko-Honokohau National Park Visitor Center. Impacts of Sedimentation on the Coral Reef Community in Pelekane Bay, Hawai‘i. Yuko Stender presenter
- k. Feb 24, 2015 IS 203 Windward Community College Ahupua‘a class PPT presentation Mauka/ Makai Connections. Ku‘ulei Rodgers presenter
- l. March 31, 2015 Oceanography Ridge to Reef Class PPT Ridge to Reef Connections Ku‘ulei Rodgers presenter

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APPENDIXES

Appendix I

Stender Y, Jokiel PL, and Rodgers KS. 2014. Thirty Years of Coral Reef Change in Relation to Coastal Construction and Increased Sedimentation at Pelekane Bay, Hawai'i. *PeerJ* DOI 10.7717/peerj.300.

Appendix II

Rodgers KS, Jokiel PL, Brown EK, Hau S, and Russell Sparks R. 2014. Over a Decade of Change in Spatial and Temporal Dynamics in Hawaiian Coral Reef Communities. *Pacific Science* Early View.

Appendix III

K. Perez III, K.S. Rodgers, P. L. Jokiel, C. Lager, D. Lager. 2014. Effects of terrigenous sediment on settlement and survival of the reef coral *Pocillopora damicornis*. *PeerJ* 2:e387; DOI 10.7717/peerj.387.

Appendix IV

Jokiel PL, Rodgers KS, Storlazzi CD, Field ME, Lager CV, Lager D. (2014) Response of reef corals on a fringing reef flat to elevated suspended-sediment concentrations: Moloka'i, Hawai'i. *PeerJ* 2:e699 <https://dx.doi.org/10.7717/peerj.699>

Appendix V

Use of Integrated Landscape Indicators and development of Biocriteria to Evaluate the Health of Linked Watersheds and Coral Reef Environments in the Hawaiian Islands
Ku'ulei S. Rodgers, Michael H. Kido, Paul L. Jokiel, Jason S. Rodgers

PowerPoint Presentation at Hawai‘i Conservation Conference 2013

Appendix VI

Response of reef corals to extreme turbidity on the south Moloka‘i reef flat.

Ku‘ulei Rodgers and Paul L. Jokiel PowerPoint Presentation at Hawai‘i Conservation Conference 2013

Appendix VII

The 23rd Hawaii Conservation Conference, Hilo, HI, August 3-6, 2015 “Assessment of Coral Settlement Distribution and Environmental Condition in Pelekane Bay, Hawai‘i” Abstract submitted by Yuko Stender

Appendix VIII

UH Sea Grant Reef Talk, Kaloko-Honokohau National Park Visitor Center. 2015 Impacts of Sedimentation on the Coral Reef Community in Pelekane Bay, Hawai‘i. Yuko Stender presenter

Thirty years of coral reef change in relation to coastal construction and increased sedimentation at Pelekane Bay, Hawai'i

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ABSTRACT

Coral reefs are being critically impacted by anthropogenic processes throughout the world. Long term monitoring is essential to the understanding of coral reef response to human impacts and the effectiveness of corrective management efforts. Here we reevaluated a valuable coral reef baseline established in Pelekane Bay, Hawai'i during 1976 and subsequently resurveyed in 1996. During this time interval substantial impacts occurred followed by extensive corrective measures. Coral and fish communities showed dramatic declines from 1977 to 1996 due to massive harbor construction and suboptimal land management practices on the watershed. More recently, corrective measures in the form of watershed stabilization and fishing regulations have been implemented. Consequently our 2012 survey reveals that coral cover since 1996 has increased slightly accompanied by a significant increase in fish abundance, diversity, and evenness. This improvement can be attributed to lower fishing pressure since 1996 due to reduced shoreline access, tighter fishing regulations and increased monitoring of legal and illegal fishing activities. Stabilization of the coral community can be attributed partially to reduced sedimentation resulting from watershed restoration that included installation of sediment check dams, control of feral ungulates, controlled grazing and replanting of native vegetation. Insights into the mechanism that removes sediment from reefs was provided by a major storm event and a tsunami that remobilized and flushed out sediment deposits. The increase in herbivorous fishes probably played a role in reducing algal competition in favor of corals. The data suggest that the precipitous reef decline in this area has been arrested and offers support for the corrective actions previously undertaken.

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Keywords Coral reefs, Land-based impacts, Hawai'i, Long-term monitoring, Sedimentation

INTRODUCTION

Coral reefs have been impacted by anthropogenic processes on a global scale (*Bryant et al., 1998; Richmond et al., 2007; Halpern et al., 2008; Wilkinson, 2008*). Direct impacts of global climate change on coral reefs is a great concern (*Hughes et al., 2003; Hoegh-Guldberg, 2011*), but indirect local effects such as altered hydrological processes (*Fletcher, 2010*) also impose land-based threats to coral reefs. Deforestation, uncontrolled grazing and

other destructive practices accelerate erosion with a concomitant increase in delivery of terrigenous sediments, associated nutrients and pollutants to coral reefs (*Syvitski et al., 2005; Maina et al., 2013*). Habitat degradation and or loss from anthropogenic activity impairs the ability of corals to recover from perturbations (*Wolanski et al., 2003; Richmond et al., 2007*). Sedimentation has long been known to be one of the major threats to coral reefs worldwide (*Johannes, 1975*), and appears to be the main stressor in Pelekane Bay. Sediments interfere with ecological functions (*Rogers, 1990; Richmond, 1993; Fabricius, 2005; Johansen & Jones, 2013*). Quantitative and comprehensive studies substantiate the negative effects of sedimentation on coral growth, morphology, and development at all coral life stages (*Grigg & Birkeland, 1997; Te, 2001*). Extensive research has been published on lethal and sublethal effects of sediment including reduced reproductive output, lower recruitment rates (*Birkeland, 1977; Rogers, 1990*), decreased calcification (*Randall & Birkeland, 1978*), morphological changes (*Dustan, 1975; Brown, Howard & Le Tissier, 1986*), metabolic changes (*Te, 2001*), behavioral alterations (*Brown & Howard, 1985; Rogers, 1990*), and increases in diseases and bleaching (*Brown & Howard, 1985*). Researchers have identified detrimental impacts to corals from toxins associated with sediment such as chemicals and heavy metals. These toxins adsorb onto sediment and even at low concentrations can produce adverse secondary effects in corals (*Glynn et al., 1986; Glynn et al., 1989*).

Pelekane Bay, located on the south Kohala Coast of the island of Hawai'i, has historically been subjected to major alterations (*Fig. 1*). Since the early 1800s there have been extensive large-scale modifications of the Kawaihae watershed that drains into the bay (*Greene, 1993*). Introduction of cattle by Captain Vancouver in 1793 and the harvest of sandalwood (*'iliahi*) from the upper reaches of the Kawaihae watershed decimated this once lush forest and caused increasing sedimentation and alteration of natural water flow patterns. Early historical accounts on effects of deforestation and grazing describe a nearly barren landscape with a cessation of perennial streams by 1830 (*Kelly, 1974*). Subsequent impacts continued with dredge and fill operations that removed a large fringing reef to create the adjacent Kawaihae Harbor in 1959 (*Fig. 1*). Long-shore currents were disrupted by construction of breakwaters and a large filled area to the north of Pelekane Bay. Massive explosive charges were used by the US Army's Nuclear Cratering Group (Project Tugboat) to create a small boat harbor north of Pelekane Bay during 1969 to 1970. The blasting deposited extensive coral silt and rubble on the reef and reduced ocean circulation in Pelekane Bay (*Day, 1972*). Several studies described the Pelekane Bay coral reef communities during this time (*Cheney, Hemmes & Nolan, 1977; Tissot, 1998*). The Environmental Protection Agency (EPA) currently lists Pelekane Bay as an "impaired waterbody" due to sedimentation. In addition, the adjacent watershed has been identified by the Hawai'i Coral Reef Strategy (*The Kohala Center, 2011*) as one of the watersheds in most critical need of restoration. Diverse research projects have been conducted in the past decade by numerous organizations in the Pelekane region (e.g., *Hoover & Gold, 2006; Cochran, Gibbs & Logan, 2007; Group 70 International, 2007; Beets, Brown & Friedlander,*

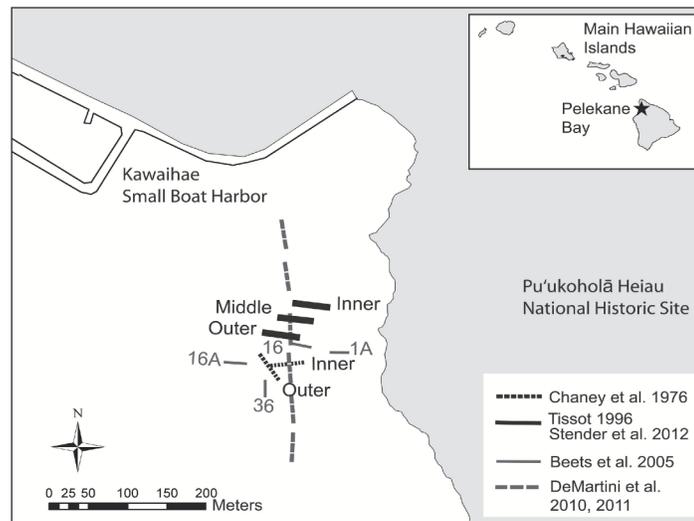


Figure 1 Map of historical and present survey locations. Map of historical and present survey locations, Pelekane Bay, Hawai'i with adjacent Kawaihae harbor and watershed (GIS data source: Hawai'i State GIS).

2010; Thornberry-Ehrlich, 2011; The Kohala Center, 2011; Minton et al., 2011; Storlazzi et al., 2013; DeMartini et al., 2013).

Evaluation of watershed impacts on a coral reef requires quantitative measurement of the biological changes in the area that receives the runoff. A baseline for marine vertebrates and invertebrates (Cheney, Hemmes & Nolan, 1977) and marine algae (Ball, 1977) was established over three decades ago in Pelekane Bay. These surveys allowed Tissot (1998) to describe dramatic declines in biota that occurred between 1976 and 1996. The objective of the present study was to re-survey the fish and benthic communities surveyed by Tissot (1998) in order to document changes in this area. Detection of long term changes is critical for identifying issues and developing solutions (Jokiel et al., 2004).

MATERIALS AND METHODS

Ecological surveys were conducted between 18 and 23 June, 2012. The map of Pelekane Bay in Tissot (1998) was processed in ArcGIS in order to determine exact transect locations. The map was geo-referenced using polynomial coefficients derived from a set of small, well-defined landscape features (Richards & Jia, 2006) with known geographic coordinates on a satellite image. Beginning and ending locations of each transect were established using a Garmin GPSMAP 78sc. Three parallel 50 m transects were reestablished (Fig. 1) following the descriptions and map in Tissot (1998). All three transects (Fig. 1) fall into the coral reef and hard substrate category described by Cochran, Gibbs & Logan (2007) based on the NOAA habitat maps (Fig. 2).

Relative abundance and composition of benthic organisms and substrate were quantified using *in situ* photographs. Approximately 100 high resolution digital images were taken along each of the three 50 m transect lines on 18 June, 2012 using an Olympus 5050 zoom digital camera with an Olympus PT050 underwater housing. An aluminum

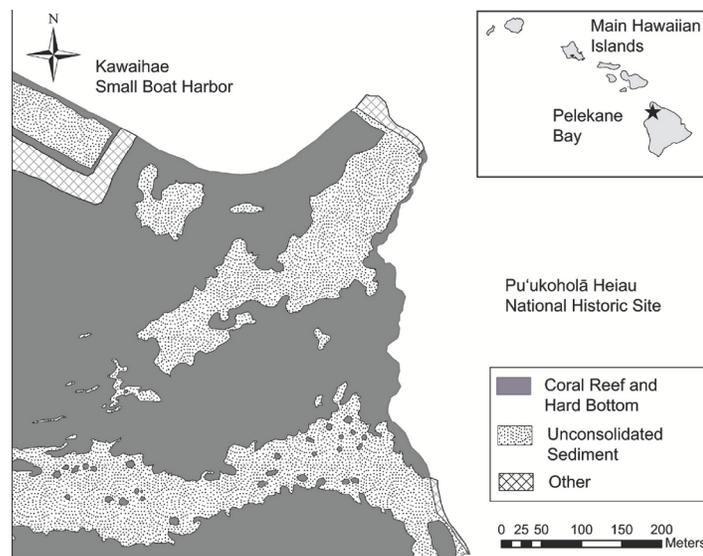


Figure 2 Benthic habitat map of the study area. Map of benthic habitat, Pelekane Bay, Hawaii with adjacent Kawaihae harbor and watershed (GIS data source: [Cochran, Gibbs & Logan, 2007](#), Hawaii State GIS).

monopod frame positioned the camera vertically at 0.7 m above the substrate to provide a standardized 0.35 m² image area. A 6-cm bar on the monopod base served as the reference scale in each image.

The software program PhotoGrid ([Bird, 2001](#)) was used to quantify percent cover of benthic organisms including individual coral species and higher taxonomic algal groups (e.g., coralline algae, turf, macro, etc.) and abiotic substrate. For each 50 m transect, 100 images were selected and 25 random points were displayed onto each image for analyses.

Rugosity measurements of topographical relief were conducted along each transect. A 15 m chain marked at 1 m intervals with 1.3 cm links was draped along the length of each transect following the contours of the benthos. An index of rugosity was calculated using the ratio of the reef contour distance as measured by chain length to the linear horizontal distance ([McCormick, 1994](#)).

Repeated fish surveys were initiated at approximately the same time of day during the survey period to reduce temporal variability. A visual belt transect approach was employed ([Brock, 1954](#)) with numerical abundance, species, and total length of fishes recorded ([Brown et al., 2003](#)). A diver swam along the three 50 m × 4 m transects (200 m²) at >1 h intervals between surveys. Ten replicates of each of the three transects were conducted ($n = 30$) within the six day survey period.

Water quality was measured in order to establish the relative conditions along a gradient from the stream mouth to open waters during the survey period. Data were collected on 23 June 2012, using a multi-parameter water quality meter (YSI 6920 V2 SONDE). Water quality measurements included temperature (°C), pH, salinity (ppt), and turbidity (NTU). Subsequent to the fish survey, a diver swam twice along each transect with the SONDE to

Table 1 Table of descriptive statistics for water quality parameters. Means of temperature, pH, salinity, and turbidity were measured at the inner ($n = 137$), middle ($n = 133$), and outer transects ($n = 165$). Coefficient of Variation is indicated in parentheses.

Variables	Inner	Middle	Outer
Temperature (°C)	27.0 (0.1%)	26.9 (0.2%)	26.4 (0.5%)
pH	8.10 (0.1%)	8.10 (0.0%)	8.13 (0.1%)
Salinity (‰)	34.7 (0.2%)	34.8 (0.2%)	35.1 (0.3%)
Turbidity (NTU)	1.8 (15.7%)	1.5 (18.8%)	0.8 (34.5%)
Rugosity ($n = 5$)	1.54 (9.3%)	1.67 (5.9%)	1.91 (6.8%)

take measurements at five second intervals. Time at the beginning and ending positions of transects was determined using a watch synchronized with the SONDE to verify data corresponding to each transect.

Statistical analysis was conducted using Minitab 15 (Minitab, Inc., 2007) to evaluate differences in abundance of reef fishes among years. Mean density per 100 m² was calculated by species, families, and feeding guilds and $\ln(x + 1)$ transformed to address assumption of normality and homoscedasticity (Zar, 1999). Overall effects of year and transect on variations in fish abundance were appraised for 1996 and 2012 data using two-way analysis of variance (ANOVA) with subsequent Tukey's HSD multiple comparisons. Each species was independently tested using one-way ANOVA and post-hoc multiple comparisons for all years. Similarly, each of the major family groups and feeding guilds were independently tested by year and followed by post-hoc Tukey's HSD comparison for all years. Paired t -tests and percent change were used to compare temporal changes in coral cover and composition between years. The Shannon-Weiner diversity index was used to calculate fish diversity. Standard errors of the means (mean \pm s.e.) were reported with mean density of fish to describe the measure of the uncertainty.

RESULTS

Benthic surveys and environmental conditions

On 23 June 2012, the inner and middle transects were characterized by similar water quality but with slightly higher temperature, lower pH, lower salinity, and greater turbidity than on the outer transect. Turbidity was highest at the inner transect followed by the middle and outer transects as distance from the stream source increased. Conversely, salinity and rugosity were lowest along the inner transect and increasing with distance on the outer transects (Table 1).

There was a substantial drop in overall coral cover between 1976 (44%) and 1996. The change between 1996 (5.5%) and 2012 (6.6%) was not statistically significant (Table 2).

Coral species richness declined from 1976 (9 species) to 1996 (5 species, 44% decline) and subsequently increased in the 2012 surveys (8 species, 60% increase since 1996, Table 3). Species composition also shifted. Five of the species found on transects in 1976 were not present in 1996. Three species recorded in 2012 were not found in 1996 (Table 3). Statistically significant differences were not found in coral species distribution between

Table 2 Table of overall mean coral cover across survey years. Change in total coral cover at Pelekane Bay between 1976 and 2012. One standard errors of the mean are indicated by \pm s.e.

Survey year	Month	Author	Mean cover (%) \pm s.e.
1976	April	Cheney, Hemmes & Nolan (1977)	43.45 \pm 2.45
1996	January–April	Tissot (1998)	5.50 \pm 2.26
2012	June	Stender et al. (2014)	6.58 \pm 2.15

Table 3 Table of coral cover by species across years. Coral cover by species (%). Richness in parentheses.

Species name	1976 (9)	1996 (5)	2012 (8)
<i>Cyphastrea ocellina</i>	0.85	0	0
<i>Leptastrea bottae</i>	0.9	0	0
<i>Montipora patula</i>	3.8	0	0.11
<i>M. capitata (verrucosa)</i>	7.15	0.6	0.44
<i>Pavona varians</i>	0.85	0	0.07
<i>P. duerdeni</i>	0	0	0.12
<i>Pocillopora damicornis</i>	0	0.8	0.12
<i>P. meandrina</i>	3.45	0.7	0.04
<i>Porites compressa</i>	15.9	0.7	2.06
<i>P. lobata</i>	11.05	3.9	3.95
<i>Porites sp.</i>	3.7	0	0

these years due to high variability resulting from patchy distribution. The coral species, *Porites lobata* was dominant in 1996 with 3.9% cover and again in 2012 with 4.0% cover. *Porites compressa* increased substantially since 1996 while other less dominant species remained relatively constant (Table 3). *Montipora capitata* (0.4% cover) showed a marked decline since 1976 (7.2% cover). The inner transect (3.3% cover) had the lowest coral cover followed by the middle (5.8% cover), and the outer transect (10.6% cover). The area covered by silt showed a consistent decline from 1976 (41.0%) to 1996 (30.5%) to 2012 (24.4%).

FISH SURVEYS: SPECIES

A shift in species composition was detected between the three surveys (Table 4). Overall percent similarity in the fish community between 1996 and 2012 was 28.5% compared to 27.6% between 1976 and 2012. Twenty species recorded on transects in 2012 were not noted in 1996 and eighteen species documented in 1996 were not recorded in 2012. In the baseline 1976 surveys there were seven species not common to the subsequent 1996 and 2012 surveys. Statistically significant increases occurred in the abundance of five species between 1976 and 2012. These species included *Acanthurus nigrofuscus* (6.6 fish \cdot 100 m⁻²; $F_{2,5} = 6.31$, $p = 0.043$), *Abudefduf abdominalis* (2.7 fish \cdot 100 m⁻²; $F_{2,5} = 6.58$, $p = 0.040$), *Scarus psittacus* (2.4 fish \cdot 100 m⁻²; $F_{2,5} = 7.21$, $p = 0.034$), Gobiidae spp. (1.2 fish \cdot 100 m⁻²; $F_{2,5} = 16.53$, $p = 0.006$), and *Acanthurus blochii* (0.3 fish \cdot 100 m⁻²;

Table 4 Table of abundant top five species by year. Comparison of most abundant fish species in rank order among surveys.

	1976 (Chaney et al.)	1996 (Tissot)	2012 (Stender et al.)
1	<i>Mulloidichthys samoensis</i> *	Juvenile <i>Scarus</i> spp.	<i>Acanthurus nigrofuscus</i>
2	<i>Chromis ovalis</i>	<i>Ctenochaetus strigosus</i>	<i>Chlorurus spilurus</i>
3	<i>Scarus sordidus</i> **	<i>Gomphosus varius</i>	<i>Thalassoma duperrey</i>
4	<i>Thalassoma duperrey</i>	<i>Thalassoma duperrey</i>	<i>Scarus psittacus</i>
5	<i>Abudefduf abdominalis</i>	<i>Acanthurus triostegus</i>	<i>Abudefduf abdominalis</i>

Notes.* Currently accepted name is *Mulloidichthys flavolineatus*.** Currently accepted name is *Chlorurus spilurus*.

$F_{2,5} = 7.19$, $p = 0.034$), while significant decreases were observed for *Stegastes marginatus* ($0.2 \text{ fish} \cdot 100 \text{ m}^{-2}$; $F_{2,5} = 28.11$, $p = 0.002$) and *Ctenochaetus strigosus* ($0.1 \text{ fish} \cdot 100 \text{ m}^{-2}$; $F_{2,5} = 17.53$, $p = 0.006$). Although the statistical significance of the mean abundance of *Thalassoma duperrey* was marginal ($F_{1,4} = 5.25$, $p = 0.084$), increase in its abundance was substantial from $1.4 \text{ fish} \cdot 100 \text{ m}^{-2}$ in 1996 to $4.8 \text{ fish} \cdot 100 \text{ m}^{-2}$ in 2012, more than the triple abundance of 1996. Similarly an increase in the abundance of *Chlorurus spilurus* was not statistically significant. However, it was numerically more abundant in 2012 ($7.2 \text{ fish} \cdot 100 \text{ m}^{-2}$) than in 1996 ($0 \text{ fish} \cdot 100 \text{ m}^{-2}$) or in 1976 ($2.9 \text{ fish} \cdot 100 \text{ m}^{-2}$). While *Mulloidichthys flavolineatus* ranked as the most abundant fish in 1976, there was no statistical difference among survey years. The significant increase in the abundance of *Chaetodon lunula* reported between 1976 ($0.0 \text{ fish} \cdot 100 \text{ m}^{-2}$) and 1996 ($0.2 \text{ fish} \cdot 100 \text{ m}^{-2}$) did not occur in 2012 ($0.2 \text{ fish} \cdot 100 \text{ m}^{-2}$). Observed declines occurred in juvenile *Scarus* spp. ($4.1 \text{ fish} \cdot 100 \text{ m}^{-2}$; $F_{2,5} = 128.77$, $p < 0.000$), *Acanthurus nigroris* ($0.6 \text{ fish} \cdot 100 \text{ m}^{-2}$; $F_{2,5} = 31.68$, $p = 0.001$), *Porphyreus cyclostomus* ($0.2 \text{ fish} \cdot 100 \text{ m}^{-2}$; $F_{2,5} = 56.16$, $p < 0.001$), and *Chaetodonauriga* ($0.2 \text{ fish} \cdot 100 \text{ m}^{-2}$; $F_{2,5} = 12.87$, $p = 0.011$) since 1996. Numerical declines since 1976 include *Chromis ovalis* ($5.9 \text{ fish} \cdot 100 \text{ m}^{-2}$) and *Scarus dubius* ($0.3 \text{ fish} \cdot 100 \text{ m}^{-2}$). A subset of additional data acquired by Beets et al. during 2005 (Beets, Brown & Friedlander, 2010) was reanalyzed using the four transects (1A, 16A, 16, and 36) in close proximity to the Cheney, Hemmes & Nolan (1977) and Tissot (1998) transects (Fig. 1). Four of the top five species in abundance found in 2005 were also found in the present study (*C. spilurus* $31 \text{ fish} \cdot 100 \text{ m}^{-2}$, *A. nigrofuscus* $7.4 \text{ fish} \cdot 100 \text{ m}^{-2}$, *S. psittacus* $4.0 \text{ fish} \cdot 100 \text{ m}^{-2}$, juvenile Scarids $3.2 \text{ fish} \cdot 100 \text{ m}^{-2}$, and *T. duperrey* $2.0 \text{ fish} \cdot 100 \text{ m}^{-2}$) with slight differences in rank order (Table 4).

The fish community in 2012 shows higher species richness, overall Shannon-Weiner H' diversity, and mean fish density as compared to previous surveys in 1976 and 1996 (Table 5). A marked difference in the mean density of fishes (per 100 m^2) between the inner (0.29), middle (0.77), and outer transects (1.46) was found. Species richness and diversity (H') was highest at the outer transect (35 species, $H' = 2.41$) as compared to the inner (26 species, $H' = 2.29$) and middle (25 species, Diversity = 2.39) transects, while similar evenness was calculated between the inner (0.70), middle (0.73), and outer (0.68) transects. A two-way ANOVA including year, transects, and interaction between

Table 5 Table of overall fish assemblage by years. Comparison of fish assemblage characteristics among surveys.

	1976 (Chaney et al.)	1996 (Tissot)	2012 (Stender et al.)
Mean number of fish · 100 m ⁻²	27.9	18.1	34.5
Species richness	35	39	41
Diversity (Shannon–Weiner)	1.07	1.17	2.46
Evenness	0.69	0.73	0.66

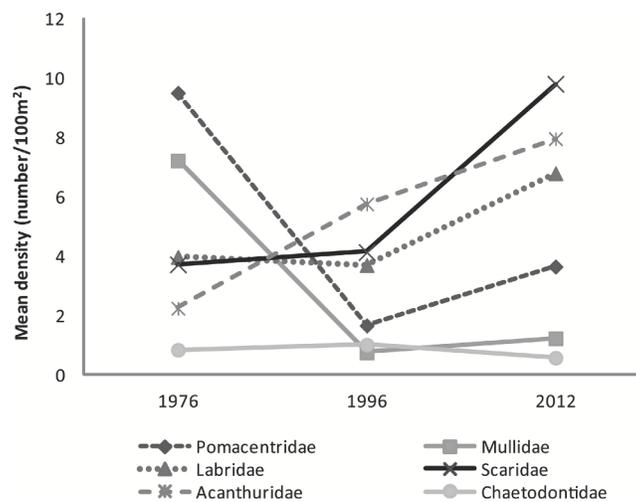


Figure 3 Graph of mean fish density by families across years. Mean abundance of major fish families across survey years.

years 1996 and 2012 with transects as predictors, was highly significant ($R_{adj}^2 = 0.45$, $F_{5,50} = 10.07$, $p < 0.000$). Overall mean abundance in 2012 was statistically higher than in 1996 ($F_{1,50} = 5.41$, $p = 0.024$). It was influenced mainly by the outer transect ($p < 0.000$). There were also statistically significant effects of transect ($F_{1,50} = 11.74$, $p < 0.000$) and interaction between year and transect ($F_{1,50} = 9.55$, $p < 0.000$). Greater fish abundance was influenced mainly by the middle ($t = 2.83$, $p = 0.018$) and outer transects ($t = 4.82$, $p < 0.000$).

FAMILIES

Although substantial percent increases were found in the abundance of major family groups between 1996 and 2012 (Scaridae 137%, Pomacentridae 119%, Labridae 84%, Mullidae 63%, and Acanthuridae 38%) a statistically significant difference was found only in the abundance of Pomacentridae among years ($F_{2,5} = 10.36$, $p = 0.017$) with number of species within this family significantly declining between 1976 (9.5 ± 0.4 fish · 100 m⁻²) and 1996 (1.7 ± 0.3 fish · 100 m⁻²; $t = -4.55$, $p = 0.014$) and increasing in the 2012 study (3.7 ± 1.1 fish · 100 m⁻²) (Fig. 3).

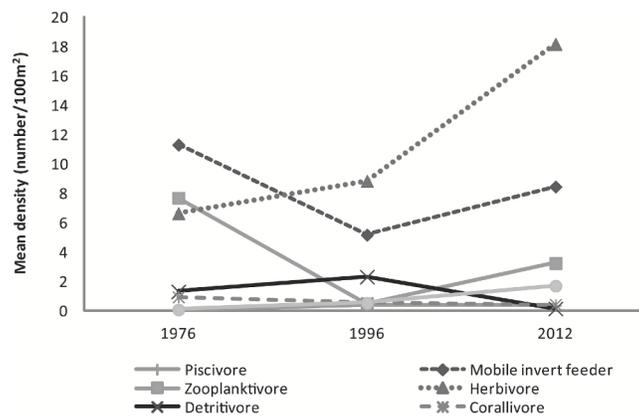


Figure 4 Graph of mean fish density by feeding guilds across years. Mean abundance of feeding guilds across survey years.

FEEDING GUILDS

The mean abundance of herbivorous species has increased from 1976 (6.6 ± 3.4 fish \cdot 100 m^{-2}) to 1996 (8.8 ± 0.5 fish \cdot 100 m^{-2}) to 2012 (18.2 ± 8.2 fish \cdot 100 m^{-2}) a 51% and 174% respective increase between years. Mobile invertebrate feeders ($F_{2,5} = 28.85$, $p = 0.002$), zooplanktivores ($F_{2,5} = 13.16$, $p = 0.01$), and detritivores ($F_{2,5} = 18.87$, $p = 0.005$) greatly varied among years. Sessile invertebrate feeders became significantly more abundant in 2012 (1.7 ± 0.3 fish \cdot 100 m^{-2}) compared to 1976 (0.1 ± 0.03 fish \cdot 100 m^{-2} ; $t = 7.32$, $p = 0.002$) and 1996 (0.5 ± 0.1 fish \cdot 100 m^{-2} ; $t = 5.08$, $p = 0.009$). The decline in zooplanktivores was significant between 1976 (7.7 ± 0.1 fish \cdot 100 m^{-2}) and 1996 (0.5 ± 0.4 fish \cdot 100 m^{-2} ; $t = -5.02$, $p = 0.009$), but marginally increased by 85% in 2012 (3.2 ± 1.1 fish \cdot 100 m^{-2} ; $t = 3.17$, $p = 0.055$). In contrast, detritivores were less abundant in 2012 (0.1 ± 0.1 fish \cdot 100 m^{-2}) than in both 1976 (1.3 ± 0.6 fish \cdot 100 m^{-2} ; $t = -3.45$, $p = 0.041$) and in 1996 (2.3 ± 0.3 fish \cdot 100 m^{-2} ; $t = -6.09$, $p = 0.004$). *Ctenochaetus strigosus* was the only species comprising the detritivore feeding guild which decreased considerably over the 36 year period since the original surveys. Slight decline in corallivore was observed. Piscivores remained low across the surveys (Fig. 4).

DISCUSSION

Fish assemblage abundance, richness, and diversity in Pelekane Bay have improved over the past 16 years following a severe decline between 1976 and 1996. Our data also shows an increased abundance of herbivores. This pattern agrees with results of a 2005 survey by U.S. National Park Service Inventory and Monitoring Program (Beets, Brown & Friedlander, 2010). Species composition has shifted relative to the 1976 survey but remains similar to that observed in 2005. Results of the present survey are in agreement with the findings of DeMartini et al. (2013) who demonstrated a significant positive effect of improved habitat (lower sediment accumulation and greater availability of branching corals) on the density of juvenile parrotfishes. The same pattern of increasing fish abundance along a gradient of improving habitat was shown in our study as well as the study by Beets, Brown & Friedlander (2010).

The 2012 study showed stabilization and perhaps a slight increase in coral cover since 1996 following a substantial reduction between 1976 and 1996. The increase in herbivorous fishes has likely helped the coral population by reducing algal competition in favor of corals. Moreover, recent episodic large wave events demonstrate that natural processes remove accumulated sediment deposits on coral reefs. The November 2010 flash flood introduced a high sediment load into the bay, but the residence time of the sediment was short due to a subsequent large wave event in January which transported the sediment into deep water offshore (*Storlazzi et al., 2013*). This was followed by the March 2011 tsunami that re-suspended and removed a great deal of sediment from the reef (*DeMartini et al., 2013*). Such events may remediate sediment impacts on the benthic community and improve inshore habitat quality over time.

Since 1996 there have been substantial changes at Pelekane Bay that may explain the increases in fish populations. A public county road that formerly ran along the coastline was realigned at a higher elevation in 1996 in order to restore the shoreline to conditions that existed at the time when the historic Pu'ukoholā temple was dedicated. Removal of the road limited shoreline accessibility. New rules restricted camping to Spencer Beach Park at the south end of Pelekane Bay which resulted in lowered fishing pressure in the study area. In addition, a new NPS visitor information center was built in 2007. The visitor center is located close to the bay with an overlook complete with telescopes that allows for constant observation of the reefs by visitors and rangers. Rangers now conduct patrols along the shoreline as part of their duty. Access to Pelekane Bay from the harbor area to the north was further restricted in 2011 due to increased harbor security under the Homeland Security Program at Kawaihae Harbor following the terrorist attack of Sept. 11, 2001.

The establishment of nearby marine protected areas designated by the State of Hawai'i in 1998 may also have contributed to the increase in fish populations. In select regions, the West Hawai'i Fisheries Management Areas (FMAs) and Fisheries Replenishment Areas (FRAs) were designed to limit high take methods of fishing, create fish reserves. Marine protected areas (MPAs) act as fish refuges with research demonstrating an increase in the number and size and connectivity within and between reserves (*Friedlander et al., 2010*). Areas adjacent to reserves benefit as fishes move in and out of the area and "spill-over" into nearby regions (*Birkeland & Friedlander, 2001*). The "spill-over" effect was particularly significant for resource fishes including parrotfishes in Hawai'i (*Stamoulis & Friedlander, 2012*). Although fishing is still permitted by law, Pelekane Bay has developed into a *de facto* marine protected area due to more limited access.

A seasonal effect among the three survey periods is most likely minimal relative to inter-annual differences in the overall fish abundance. For example, inter-annual variability of recruit abundance in Hawai'i is greater than the seasonal variability (*Walsh, 1987*). Lunar differences in recruitment and spawning periodicity have been reported for several species in Hawai'i (*Walsh, 1987*), but the three surveys used in the present analysis were conducted on multiple days with varying moon phases within each year. The potential effect of lunar phase on overall fish abundances were averaged and not biased towards new or full moon when recruitment and spawning are reported to occur for some species.

Results of the extensive studies by *Storlazzi et al. (2013)* and *DeMartini et al. (2013)* indicated that the turbidity, sediment cover and sediment accumulation rate are highest near the sediment source (stream mouth) and decrease on the reef with increasing distance from the stream mouth. Our study is in agreement with these observations. Biotic factors show an inverse relationship to this sediment pattern with the lowest rugosity, coral cover, coral richness, fish abundance, fish diversity, and evenness increasing with distance from the stream mouth.

Pelekane Bay has a long history of chronic land-based influences including sedimentation and resuspension which has affected coral reef recovery. Substantial sediment accumulation between 1928 and 2011 has occurred in Pelekane Bay (*Storlazzi et al., 2013*). Comparison of bathymetry over this time period revealed that 22,489 to 37,483 m⁻³ of sediment was deposited that resulted in a shoaling of 0.41 to 0.61 m during this time interval. Nevertheless natural resilience of reef ecosystems can facilitate recovery (*Nyström & Folke, 2001*). Full recovery to pre-disturbance levels may be an extended process, requiring many more decades. Even though the reefs have been damaged, our data show that further decline can be stopped and recovery can begin once stressors are reduced. Such damaged reefs may be prime candidates for restoration activities because at this point on the degradation curve a slight improvement in the environment may result in a greater improvement in coral and fish assemblages than might be observed from similar restorative effort on a mildly stressed reef. Our conclusion is that watershed restoration projects, reduced fishing pressure, and increases in marine protected areas in adjacent regions have allowed for partial recovery of fish populations since the *Tissot (1998)* surveys.

The community structure of the Pelekane Bay reef over the past two centuries apparently has changed in a manner that results in tolerance resistance to severe impacts including storm events and land-based sedimentation. Results of this survey show that the Pelekane Bay reef has the ability to absorb severe disturbance while continuing to maintain functional capacities. Factors that can affect reef resilience include improved water and substrate quality (*Wolanski, Richmond & McCook, 2004*), herbivore abundance, stable coral cover, and species and habitat diversity (*McClanahan et al., 2012*). These factors have all improved since the previous survey. Recent change in the reef community of Pelekane Bay exemplified the positive effects of an integrated approach of watershed management and acute wave disturbances on mitigating local human impacts.

The long-term data set that now exists for Pelekane Bay will be valuable in the future for continued assessment of reef community response to environmental change and improved management strategies. Continued monitoring and expansion of the original dataset will allow evaluation of relationships between abiotic and biotic factors. These data can be used to examine ecological trends and patterns in response to human and natural impact.

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Competing Interests

All authors declare they have no competing interest in financial, non-financial, professional or personal conflicts of interest.

Author Contributions

- Yuko Stender conceived and designed the experiments, performed the experiments, analyzed the data, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper, presentation.
- Paul L. Jokiel conceived and designed the experiments, performed the experiments, contributed reagents/materials/analysis tools, wrote the paper, reviewed drafts of the paper, grant administration/management.
- Ku'ulei S. Rodgers performed the experiments, analyzed the data, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper, grant administration/management.

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Effects of terrigenous sediment on settlement and survival of the reef coral *Pocillopora damicornis*

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ABSTRACT

Survival and settlement of *Pocillopora damicornis* larvae on hard surfaces covered with fine ($<63 \mu\text{m}$) terrigenous red clay was measured in laboratory Petri dishes. The dishes were prepared with sediment films of various thicknesses covering the bottoms. Coral larvae were incubated in the dishes for two weeks and the percent that settled on the bottom was determined. There was a statistically significant relationship between the amount of sediment and coral recruitment on the bottom, with no recruitment on surfaces having a sediment cover above 0.9 mg cm^{-2} . Experimental conditions for the delicate coral larvae were favorable in these experiments. Total survival over the two week settlement tests expressed as the sum of coral recruits and live larvae at the end of the experiment did not show a significant decline, so the major impact of the sediment was on successful settlement rather than on mortality. Larval substrate selection behavior was the primary factor in the observed result.

Subjects Ecology, Environmental Sciences, Marine Biology

Keywords Sediment, Coral, Larvae, Settlement, Reproduction, Survival

INTRODUCTION

Sedimentation has been identified as a major detrimental factor on coral reefs (*Johannes, 1975; Cortes & Risk, 1985; Rogers, 1990; Grigg & Birkeland, 1997*). *Fabricius (2005)* noted that evaluation of the impact of terrestrial runoff on coral reef ecology is very difficult even though sedimentation has a very high impact relative to other processes. Extreme sedimentation can smother and kill corals (*Edmondson, 1928*). Suspended sediment reduces irradiance, restricts photosynthesis and negatively affects coral growth (*Davies, 1991; Anthony & Connolly, 2004*). An inverse relationship has been established between sediment loading and coral larval survival and development (*Gilmour, 1999*). Research has also identified lethal and sub-lethal effects to corals from substances associated with sediments such as pesticides, fertilizers, and petroleum products (*Glynn et al., 1989; Te, 2001*). Particles can act as substrate for these chemicals and other contaminants. These pollutants carried in sediments can affect settlement, recruitment, and survivorship of coral and their larvae. Even low levels of these toxins have been shown to dramatically affect morphology and physiological processes of corals (*Glynn et al., 1986*).

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Observations indicate that coral planulae do not settle on silt covered surfaces (Harrigan, 1972). Rogers (1990) summarized the existing literature and concluded that 'normal' sedimentation rates for coral reefs appear to be on the order of $10 \text{ mg cm}^{-2} \text{ d}^{-1}$ or less, with typical suspended solids concentrations less than 10 mg l^{-1} . She identified the need to determine the quantity of different types of sediment that will deter coral settlement. Lewis (1974) reported that a sprinkling of fine washed sand in the bottom of test bowls reduced settlement to less than one third of the settlement rate on a clean glass surface. Hodgson (1991) studied coral settlement on a glass surface that was only partially covered with a mixture of sand, silt and clay. In this situation he found that the larvae will still settle on areas that are clear of sediment. Te (1992) cultured larvae of the coral *Pocillopora damicornis* to four concentrations of sediment (0, 10, 100, 1000 mg l^{-1}) for 14 days under two contrasting water agitation levels and found no significant difference in larval settlement on the glass walls of the containers. Presumably the vertical glass walls did not accumulate sediment, so there was no difference in substrate between the treatments. Babcock & Davies (1991) used sediment composed of fine sand and silt of mixed terrigenous and carbonate origin to determine the effect of various rates of sedimentation ($0.5\text{--}325 \text{ mg cm}^{-2} \text{ d}^{-1}$) on settlement rates of *Acropora millepora* in aquaria. Total number of settled larvae was not significantly affected by sedimentary regime, but higher sedimentation rates reduced coral settlement on horizontal surfaces where sediments could accumulate. More data are needed on the effect of sediment thickness on recruitment of corals onto a surface. As pointed out by Fabricius (2005), the mechanisms by which sediment limits coral development are complex and have been difficult to isolate and quantify. It is clear that coral larvae can survive in highly turbid water and can settle in some situations under conditions of high sedimentation rate. Questions remain as to the quantity of sediment on a surface that will prevent settlement and survival of larvae.

In Hawai'i as in other high islands of the Pacific, flood events transport large amounts of red terrigenous soils onto reefs (Field et al., 2008a). The larger particles settle out quickly but the finest fraction ($<63 \mu\text{m}$) disperses throughout the reef system (Fig. 1). These fine red muds adhere to surfaces (Fig. 2) as well as form deposits that are continually remobilized by wave events. There are no data on how these fine coatings influence coral settlement and survival of recruits. The purpose of this study was to establish this value using uniform coatings of fine terrigenous red clay muds on hard substrate.

MATERIALS AND METHODS

Experiments were conducted in Petri dishes in the laboratory at the Hawai'i Institute of Marine Biology located on Moku o Lo'e Island in Kane'ohe Bay, O'ahu. Settlement of planulae larvae of the reef coral *Pocillopora damicornis* on hard surfaces covered with various amounts of fine sediment was measured.

To avoid chemicals and contaminants associated with soil, soil was collected from a steep undisturbed eroding slope in a remote area near the top of Moku o Lo'e. This area has never been planted or used for agriculture and is located at a higher elevation than

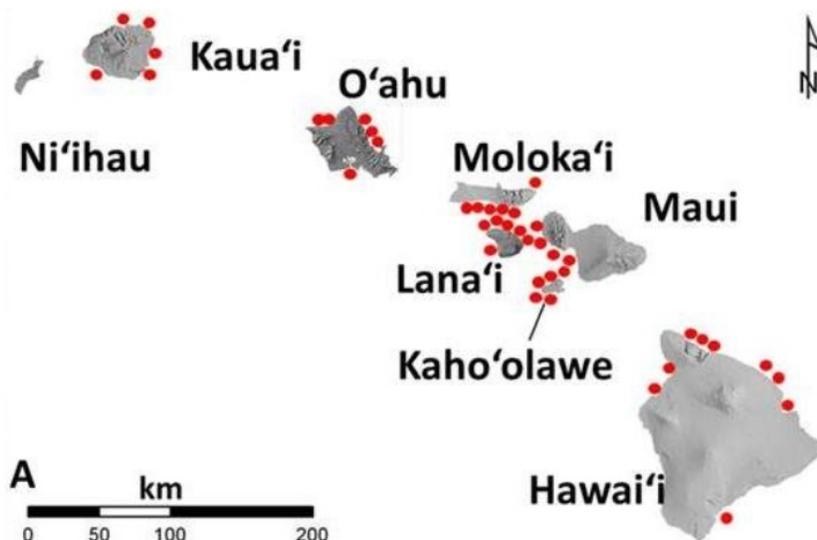


Figure 1 Images of red terrigenous sediment in the Hawaiian islands. (A) Map of the main Hawaiian Islands showing areas with heavy red mud deposits. (B) The Landsat satellite photo taken off south Moloka'i Hawai'i on November 29, 2001 two days after a heavy rainfall showing turbidity plume caused by red muds deposited on the reefs (e.g., *Field et al., 2008b*).

possible sources of anthropogenic contamination. The red subsoil here is typical of the volcanic soils found throughout the high islands of the tropical Pacific region. The soil was thoroughly suspended in seawater using a commercial grout mixer, and screened through a 63 μm sieve. The resulting slurry of fine silt was allowed to settle and the supernatant water siphoned off to produce a dense mud consisting of very fine particles. The stock mud slurry was used throughout the experiments. The wet mud was used to prepare each series of dilutions because drying the mud results in accretions that do not go back into suspension easily. An estimate of the sediment film thickness in the various treatments was obtained. First, the sediment concentration (mg of dry sediment per cm^{-3} of water-sediment film) was measured. A slurry was made from the bulk sediment stirred in a beaker of sea water.

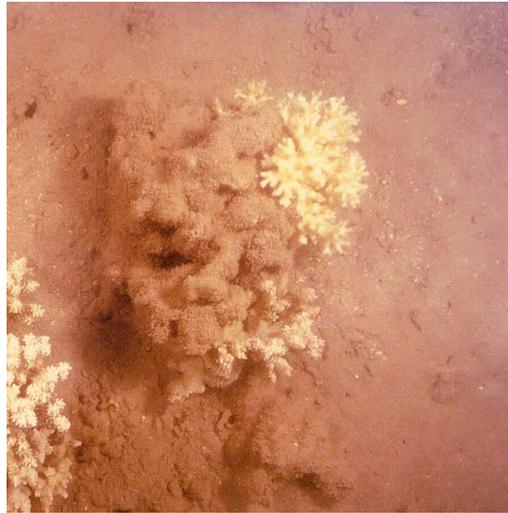


Figure 2 The coral *Pocillopora damicornis* surrounded by hard substrate covered with a film of red mud on turf algae at Moloka'i, Hawaii.

The sediment was allowed to settle and the overlying water decanted. Aliquots of 1 cc were taken from the settled sediment layer using a 1 cc syringe and placed in pre-weighed dishes, dried and re-weighed. The sediment thickness in the treatments was calculated as the ratio of weight of dry sediment (g cm^{-3}) of the settled wet material to the concentration of dry sediment (g cm^{-2}) in the treatment to obtain an estimate of the sediment film thickness (cm). Sediment thickness ranged from 0.008 to 0.08 mm.

Pocillopora damicornis is a branching, reef building coral that is commonly found throughout the Pacific and Indian Oceans (Veron, 1986). This species releases abundant positively buoyant planulae on a lunar cycle throughout the year (Jokiel, 1985). Colonies of *P. damicornis* ($n = 20$) were collected from the shallow reef flats surrounding Moku o Lo'e prior to the full moon and placed in aerated containers. Planulae used in the experiments were collected fresh each morning and transferred to the experimental Petri dishes using a pipette.

The experiments were conducted in 100 mm diameter \times 15 mm deep Petri dishes that were conditioned in sea water for two weeks prior to introduction of sediment and planulae. Conditioning of the surfaces is necessary because the planulae require a thin biofilm layer for settlement (Richmond, 1985; Baker, 1995; Tran & Hadfield, 2012). A volume of 35 ml of seawater was prepared for each dish in a screw top vial. A treatment with no added sediment served as the control. A sediment concentration series was prepared using 1 drop, 2 drops, 3 drops etc. of stock sediment added to the series of vials. The sediment solutions were homogenized by shaking the vials vigorously before pouring the contents into the pre-conditioned Petri dishes. The sediment was then allowed to settle until the water was clear and a uniform film of silt formed on the bottom over the preexisting biofilm layer. Ten planulae were then gently added to each dish (Fig. 3A). Due to low rates of settlement, the number of larvae was increased to 25 planulae in the subsequent trials. The results were expressed as % of original larvae that settled. Petri dish

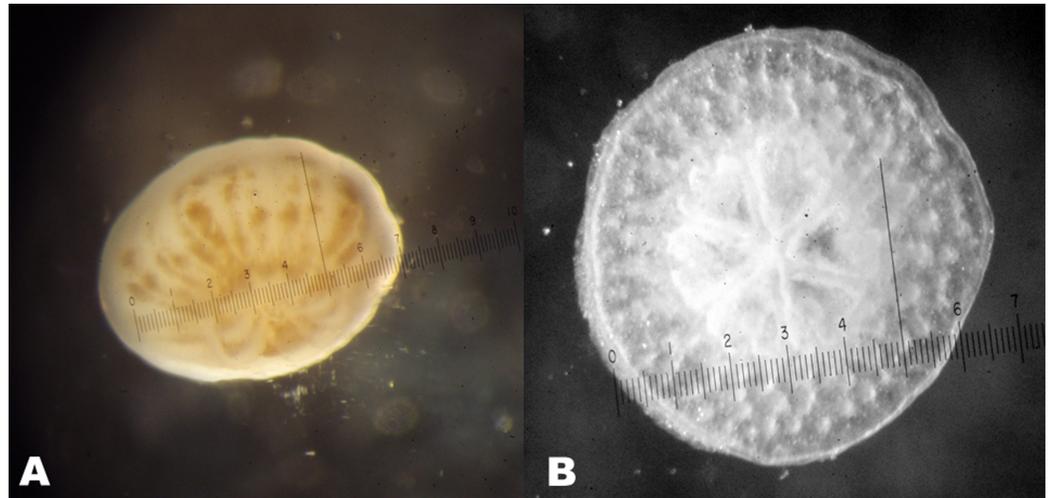


Figure 3 (A) Swimming planula of the coral *P. damicornis*. (B) Settled planula of the coral *P. damicornis*. Scale in μm .

covers prevented evaporation and disturbance by air movement. The dishes were held at ambient outdoor air temperature under shaded natural light in a covered area with good air circulation. Experiments were conducted at the normal salinity of Hawaiian waters of from 35‰ to 36‰. Air temperature and water temperature are very close to each other in Kāneʻohe Bay (*Bathen, 1968*), thus the experiment simulated normal reef temperatures. The temperature during this experiment held between 25 °C to 27 °C. Larvae prefer low light conditions for settlement (*Baker, 1995*) so the experiment was conducted under a shed roof with irradiance of approximately 5% of full sunlight as measured with an integrating quanta meter (LI-COR INC.). Thus conditions of temperature, irradiance and salinity were similar in all cases.

At the end of a two week incubation period the surviving planulae larvae and coral recruits (*Fig. 3B*) were counted. After removing the larvae, the sediment from each Petri dish was washed onto a pre-weighed Whatman GF/F 47 mm glass microfiber filter. The initial dry weight of the filter was subtracted from the weight of the dried filter with sediment and sediment weight normalized to the bottom area of the Petri dish. Larvae percentage survival (total swimming plus total live recruits) and percentage of larvae that settled were calculated. A few of the planulae settled and began to calcify on the surface film of the water as previously reported by *Richmond (1985)* who attributed this behavior to lack of suitable settlement substrate. These coral recruits were not included in the total coral recruits on substrate, but were included in the survivor total. Only planulae that had settled and calcified on the Petri dish bottom or on the sides were used in the analysis of recruitment versus sediment.

The first five runs were made with 11 different sediment levels. During the last two runs the gradient was reduced to seven different levels. Statistical analysis of the coral settlement data was performed using Minitab™ Version 14 statistical software. The percent settlement and percent survival data were transformed using the arcsine square

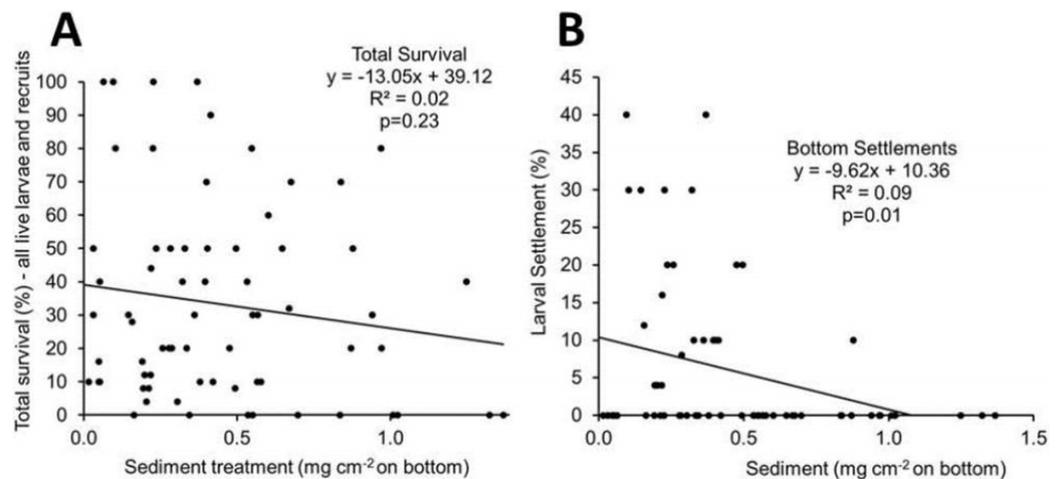


Figure 4 (A) Total larval survival as a function of sediment load (% live larvae and live coral recruits) at the end of each two week incubation. (B) Larval bottom settlement as a function of sediment load (%) at the end of each two week incubation.

root transformation of proportional data in order to meet the requirement for normal distribution in the settlement and survival data.

RESULTS AND DISCUSSION

Percent survival expressed as sum of live coral recruits and live larvae at the end of each two week experiment (Fig. 4A) did not show significant mortality. Figure 4B shows the relationship between the amounts of sediment covering the bottom of the dish in mg cm^{-2} versus percent of larvae that settled on the bottom. The linear regression analysis showed a significant relationship between the amount of sediment and the percent settlement of larvae at $\alpha = 0.5$, however only 9% of the variability was explained due to the large number of recruitment runs with no settlement (Fig. 4B). No recruitment occurred over sediment films that exceeded 0.9 mg cm^{-2} (Fig. 4B).

Some of the larvae settled on the sediment-free walls of the Petri dishes, but there was no significant difference between settlements and sediment treatment. We observed that “tracks” were formed on the sediment film in a number of the dishes (Fig. 5) by larvae seeking suitable substrata at both high and low levels of sediment. Planulae are positively attracted to substrate (Edmondson, 1946; Harrigan, 1972). The planulae move about using cilia to seek out a suitable place to settle based on physical and chemical cues. Where sediment covered the biofilm surface, some planulae apparently resorted to “crawling” along the floor of the Petri dish in search of an exposed area, pushing the fine sediment out of their way. In a few instances larvae subsequently settled on these cleared tracks under conditions that normally would block recruitment.

It is well established that “normal” suspended sediment rates on coral reefs range from $10 \text{ mg cm}^{-2}/\text{day}$ or less (Rogers, 1990). At the upper end of this range, the accumulation of sediment on 1 cm^{-2} of surface would be 10 mg unless it is removed by water motion or other disturbances. However, coral recruitment is blocked on surfaces with only

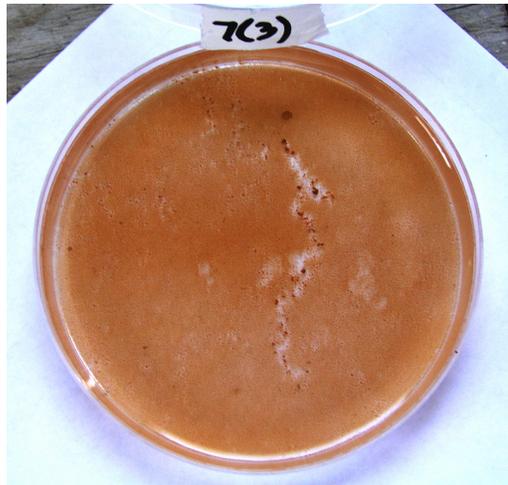


Figure 5 Tracks in the sediment film made by “crawling” planulae larvae. Diameter of Petri dish is 10 cm.

1 mg cm^{-2} of sediment. Corals have been shown to thrive in experiments with very high concentrations of suspended sediment in the lab and the field (Te, 1992; Te, 2001; Hodgson, 1991). In natural environments corals do exist in areas of extremely high sediment (DeMartini et al., 2012; Larcombe, Costen & Woolfe, 2001). Thus, surface sediment seems to be a more critical factor than suspended sediment rates for coral settlement. Other evidence to support this is a unique strategy some corals possess. Under conditions of environmental stress including sedimentation, *P. damicornis* larvae exhibit reverse metamorphosis, a survival mechanism known as “polyp bailout”, where they will release from their calices to resettle onto more suitable substrate. Thus it is possible for this species to settle in highly sedimented environments and still survive where other species may perish.

Sediment resuspension and water motion are critical factors that influence benthic sediment layers. Larcombe et al. (1995) describes the most important factors that control the settlement of suspended sediments as winds and waves. Tidal currents were also found to be important in preventing long-term buildup of sediments. These influences may increase or remove sediment concentrations under which coral larval settlement occurs. Our study shows that when no other factors are involved $<0.9 \text{ mg cm}^{-2}$ of sediment (0.047 mm thick) will block recruitment completely. Sediments exhibit high spatial and temporal variability due to inconsistency in timing and delivery of sediment sources (stream discharge, land-based run-off, landslides, etc.) and events (rainfall, storm surf, etc.) to nearshore reefs (Storlazzi & Jaffe, 2008). Due to these highly variable fluctuations, natural levels of sedimentation are difficult to ascertain, however typical suspended solids concentrations are $<10 \text{ mg l}^{-1}$. In the main Hawaiian Islands, Coral Reef Assessment and Monitoring data from 91 stations show a wide range of fine sediment ($<63 \mu\text{m}$) from 0.1% to 63.1% of the bulk sediment collected (Rodgers, 2005).

Harrington et al. (2004) found that settlement rates of the reef-building corals *Acropora tenuis* and *A. millepora* depended on crustose coralline algae (CCA) species and whether

the CCA was alive or dead. [Tran & Hadfield \(2011\)](#) found “larvae of the scleractinian coral *Pocillopora damicornis* require a natural cue from surface-biofilm bacteria to select a suitable substratum on which to attach, metamorphose, and grow into a benthic polyp”. [Davies et al. \(2014\)](#) examined settlement cues for several coral species originating from different ocean provinces and detected significant differences in cue preferences among coral species, even for corals originating from the same reef. The thin layer of fine sediment that blocked settlement of *Pocillopora damicornis* larvae in this experiment raises the possibility that fine sediment films could block cues and impact coral settlement across a wide range of species.

Our laboratory results should be used with caution in applying the results to field situations. However, the value of this research is we show that an extremely thin film can block recruitment.

In summary, the results of the present investigation support and amplify the findings of previous investigations:

- Although a variety of settling cues have been shown it is possible that a thin film of sediment can override these cues blocking larval settlement.
- Recruitment rate of larvae in sediment experiments is very low ([Fig. 4](#)). [Te \(1992\)](#) recorded 2% to 3% settlement of *Pocillopora damicornis* larvae over a two week period. [Babcock & Davies \(1991\)](#) report a mean of only 15% settlement in a two day experiment using larvae of the coral *Acropora millepora*.
- There is no significant difference in recruitment versus sedimentation on vertical walls that do not accumulate sediment as shown previously ([Te, 1992](#); [Babcock & Davies, 1991](#)).
- Larval behavior is an important factor in determining settling success and survival. Larvae will seek a suitable settlement site ([Harrigan, 1972](#)) and will find areas that are free of sediment. [Hodgson \(1991\)](#) conducted larvae settlement experiments on *P. damicornis* on glass plates with sediment layers of 0 to 500 mg cm⁻², but the sediment covering the glass settling plates was not uniform, having some areas clear of sediment. The corals were able to find and settle in open areas not covered with sediment.
- A relatively thin uniform coating of land-derived sediment can prevent coral recruitment. [Hodgson \(1991\)](#) reports a larval settlement threshold for *P. damicornis* of 536 mg cm⁻² over patchy horizontal surfaces that blocked 95% of coral settlements. Results of the present study refine this cutoff to a lower value of 1 mg cm⁻², for a uniform sediment film of fine muds.

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Competing Interests

None of the authors have financial, non-financial, professional, or personal competing interests.

Author Contributions

- Kaipo Perez III and Ku‘ulei S. Rodgers conceived and designed the experiments, performed the experiments, analyzed the data, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.
- Paul L. Jokiel conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.
- Claire V. Lager performed the experiments, analyzed the data, prepared figures and/or tables, reviewed drafts of the paper.
- Daniel J. Lager performed the experiments, analyzed the data.

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Response of reef corals on a fringing reef flat to elevated suspended-sediment concentrations: Moloka'i, Hawai'i

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ABSTRACT

A long-term (10 month exposure) experiment on effects of suspended sediment on the mortality, growth, and recruitment of the reef corals *Montipora capitata* and *Porites compressa* was conducted on the shallow reef flat off south Moloka'i, Hawai'i. Corals were grown on wire platforms with attached coral recruitment tiles along a suspended solid concentration (SSC) gradient that ranged from 37 mg l⁻¹ (inshore) to 3 mg l⁻¹ (offshore). Natural coral reef development on the reef flat is limited to areas with SSCs less than 10 mg l⁻¹ as previously suggested in the scientific literature. However, the experimental corals held at much higher levels of turbidity showed surprisingly good survivorship and growth. High SSCs encountered on the reef flat reduced coral recruitment by one to three orders of magnitude compared to other sites throughout Hawai'i. There was a significant correlation between the biomass of macroalgae attached to the wire growth platforms at the end of the experiment and percentage of the corals showing mortality. We conclude that lack of suitable hard substrate, macroalgal competition, and blockage of recruitment on available substratum are major factors accounting for the low natural coral coverage in areas of high turbidity. The direct impact of high turbidity on growth and mortality is of lesser importance.

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INTRODUCTION

Sedimentation is a major detrimental factor on coral reefs (*Johannes, 1975; Cortes & Risk, 1985; Grigg & Birkeland, 1997*). Extreme sedimentation can smother and kill corals (*Edmondson, 1928*), whereas suspended sediment reduces irradiance, restricts photosynthesis, reduces coral growth (*Davies, 1991; Anthony & Connolly, 2004*), and impedes coral larval survival and development (*Gilmour, 1999*). Pollutants that accompany land-derived sediment can further affect settlement, recruitment, and survivorship of coral and larvae (*Glynn et al., 1986*).

The classic work of *Rogers (1983)* and *Rogers (1990)* concludes that mean suspended-particulate matter for reefs that are not impacted directly by human activities generally is less than 10 mg l⁻¹. Concentrations above this value result in fewer coral species, less

live coral, lower coral growth rates, greater abundance of branching forms, reduced coral recruitment, decreased calcification, decreased net productivity of corals, and slower rates of reef accretion. *Erfemeijer et al. (2012)* found that reported tolerance limits of coral reef systems for chronic suspended sediment concentrations range from $<10 \text{ mg l}^{-1}$ in pristine offshore reef areas to $>100 \text{ mg l}^{-1}$ in marginal near shore reefs. Some coral species can tolerate short-term exposure (days) to suspended sediment concentrations as high as $1,000 \text{ mg l}^{-1}$ while others show mortality after exposure (weeks) to concentrations as low as 30 mg l^{-1} .

Quantifying the mechanisms responsible for coral reef decline in high sediment areas has been more challenging. As pointed out by *Fabricius (2005)*, the mechanisms by which sediment limits coral development are complex and are difficult to isolate and quantify. *Erfemeijer et al. (2012)* showed a significant relationship of coral sensitivity to turbidity and sedimentation with growth form and note that some of the variation in sensitivities reported in the literature may have been caused by differences in the type and particle size of sediments involved.

Weber, Lott & Fabricius (2006) conducted short term (12–60 h) coral exposures to ten different sediment types at environmentally relevant concentrations ($33\text{--}160 \text{ mg dry weight cm}^{-2}$) in laboratory and field experiments. Changes in the photosynthetic yield of the coral *Montipora peltiformis* was measured by pulse–amplitude modulated chlorophyll fluorometry (PAM) as proxy for photophysiological stress from exposure, and to determine rates of recovery. Different sediments exerted greatly contrasting levels of stress in the corals. Grain size and organic and nutrient-related sediment properties were key factors determining sedimentation stress in corals after short-term exposure. Photophysiological stress was measurable after 36 h of exposure to most of the silt-sized sediments, and coral recovery was incomplete after 48–96 h recovery time. The four sandy sediment types caused no measurable stress at the same concentration for the same exposure time. Stress levels were strongly related to the values of organic and nutrient-related parameters in the sediment, weakly related to the physical parameters, and unrelated to the geochemical parameters measured. *M. peltiformis* removed the sandy grain size classes more easily than the silt, and nutrient-poor sediments were removed more easily than nutrient rich sediments. They found that silt-sized and nutrient-rich sediments can stress corals after short exposure, while sandy sediments or nutrient-poor silts affect corals to a lesser extent.

These results were followed up by *Weber et al. (2012)* who postulated that the coral death was microbially mediated. Microsensor measurements were conducted in mesocosm experiments and in naturally accumulated sediment on corals. Organic-rich sediments caused tissue degradation within 1 d, whereas organic-poor sediments had no effect after 6 d. In the harmful organic-rich sediment, hydrogen sulfide concentrations were low initially but increased progressively because of the degradation of coral mucus and dead tissue. Dark incubations of corals showed that separate exposures to darkness, anoxia, and low pH did not cause mortality within 4 d. However, the combination of anoxia and low pH led to colony death within 24 h. Their data suggest that sedimentation kills corals

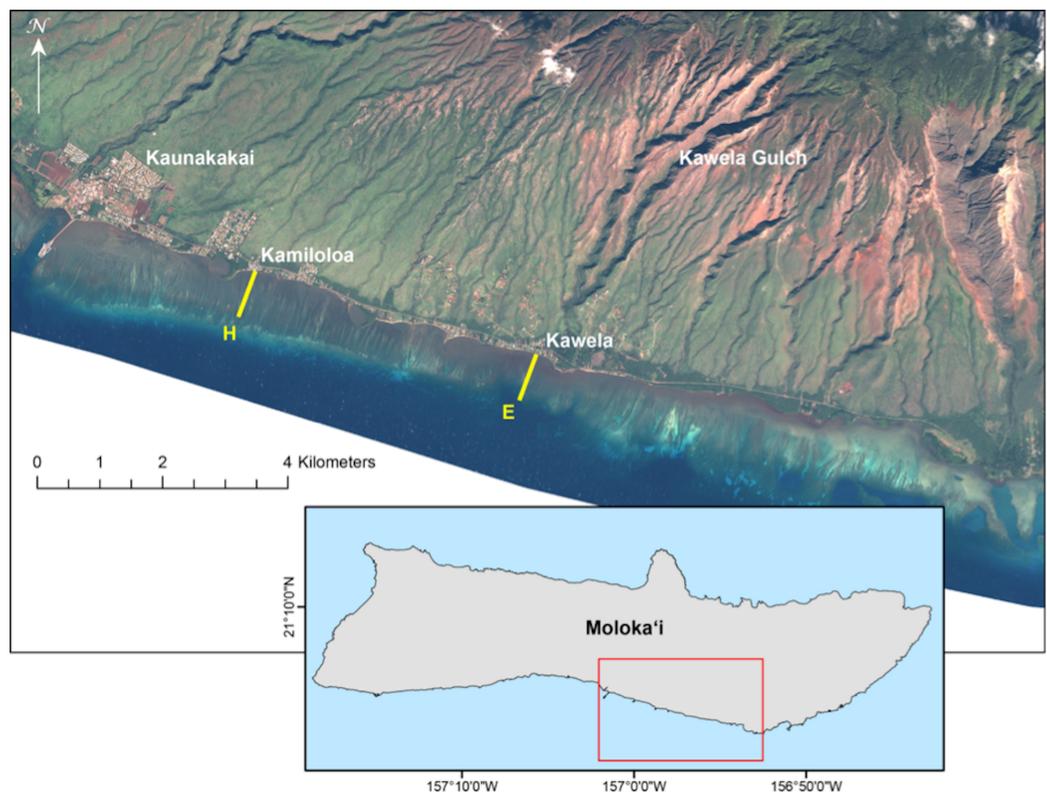


Figure 1 Landsat satellite image of study site on the south shore of Moloka'i, Hawai'i. Landsat satellite image showing locations of U.S. Geological Survey water-quality transects on south Moloka'i reef flat (transect E at Kawela, and transect H at Kamiloloa) where coral growth platforms were established for this study. Note the strong turbidity gradient along the coast that is clearly visible from the air.

through microbial processes triggered by the organic matter in the sediments, and that the organic enrichment of coastal sediments is a key process in the degradation of coral reefs exposed to terrestrial runoff.

Results of short-term exposure of corals to sedimentation are useful in identifying acute effects. However, from a demographic point of view it is critical that we gain a better understanding of coral population dynamics in relation to impacts from sediment on reef ecosystems. Therefore, we undertook a study to measure the impact of suspended particulate matter on coral recruitment, growth, and mortality for the two locally dominant reef flat coral species along a gradient of terrigenous sediment impact (Fig. 1).

MATERIALS AND METHODS

Site description

An ideal site to study the effects of sediment on corals is located on the south coast of Moloka'i in the Hawaiian Islands (Fig. 1). This is an extensive shallow reef flat with depths of approximately 0.5 m to 1.0 m from inshore to offshore locations. Extensive geological, oceanographic, sedimentological, and biological data are available from this area (see synthesis by *Field et al., 2008a*, and references therein), and provide a solid basis for the

design of this biological study. A strong inshore to offshore turbidity gradient occurs at all points along this coast due to extensive terrigenous sediment discharge from multiple drainage basins (Field *et al.*, 2008b), of which Kawela is the most significant (Fig. 1). The USGS program established nine transects with six water-sampling stations (50 m, 100 m, 250 m, 400 m, 550 m, 700 m from shore) along each cross-shore transect on the Moloka'i reef flat in 2004 to describe the physical and sedimentological conditions.

Methods

At the USGS stations during 7–9 April 2007, water samples were collected daily using a Niskin water sampler just above the seabed along two shore-normal transects (E and H) at a series of six fixed stations along each transect and located 50 m (sites E-50 and H-50), 100 m (sites E-100 and H-100), 250 m (sites E-250 and H-250), 400 m (sites E-400 and H-400), 550 m (sites E-550 and H-550) and 700 m (sites E-700 and H-700) from shore on the reef flat (Fig. 1). These data were used to evaluate the spatial and temporal variability in suspended-sediment concentration (SSC) in mg l^{-1} as defined and measured by Presto *et al.* (2006). The SSC measurement was used in this study because it is an established USGS protocol for collection of sediment and for analysis of suspended sediment samples (Edwards & Glysson, 1999). The water samples were processed following methodology described in Poppe *et al.* (2000). This SSC data was used in site selection of two transects that showed a distinct sediment gradient increasing with distance from shore. Transect E, offshore Kawela, is directly impacted from sediment emanating from Kawela Gulch. Transect H, off Kamiloloa, is to the west and downcoast from the large sediment inputs farther east (Fig. 1), but is still subject to elevated SSCs. Biological survey data collected at each site (Rodgers *et al.*, 2005) were used as criteria in site selection to determine abundance and distribution of corals along a sediment gradient. In addition, biological and physical survey data were collected at each site including benthic cover, coral diversity and richness, and sediment composition and grain-size. A total of 40 digital photos were taken within the 7 m radius at each of the 54 stations (Rodgers *et al.*, 2005). Our operating hypothesis was that a gradient in coral mortality, growth, and recruitment would be detected along the turbidity gradient.

A coral experimental setup consisting of a coral growth wire platform and two standard coral recruitment arrays (Brown, 2004) were established at 10 of the 12 USGS water sampling stations along Transects E and H (Fig. 2) at five stations: 100 m, 250 m, 400 m, 550 m, and 700 m from shore. The USGS station at 50 m from shore was not selected due to the shallow depth at low tide and lack of coral growth.

Two species of corals (*Montipora capitata* and *Porites compressa*) dominate the south Moloka'i reef flat and thus were chosen for the study. Small colonies approximately 10 cm in diameter were collected in the area and labeled with embossed plastic tags attached to the coral with vinyl-coated wire. The initial skeletal weight of each colony was measured using the buoyant weighing technique (Jokiel, Maragos & Franzisket, 1978). Changes in coral growth were determined by subtracting the final buoyant weights of each coral from its initial weight in grams. Twenty corals of each species were randomly assigned to the

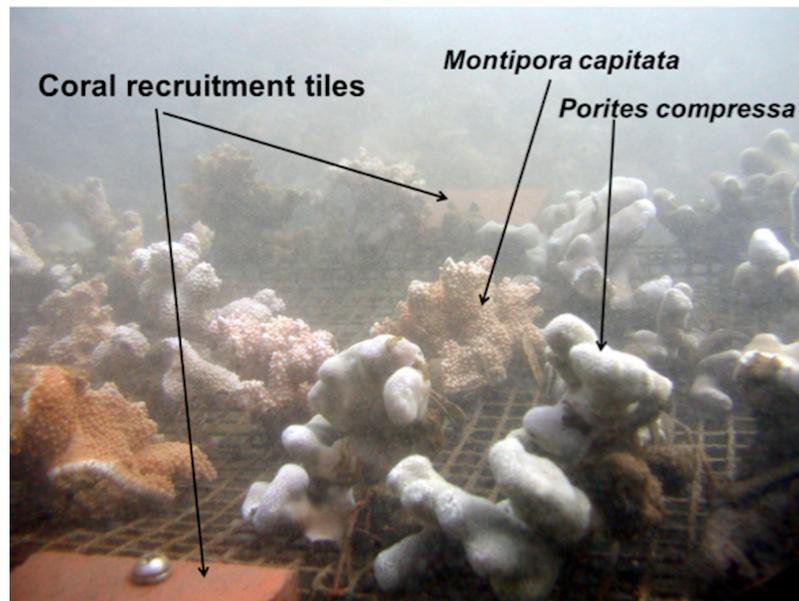


Figure 2 Photograph of coral growth wire platform with corals ($n = 40$) and coral recruitment tiles ($n = 4$).

various positions on each platform placed at the ten stations ($n = 400$). Each platform held 20 *P. compressa* and 20 *M. capitata* colonies. The corals were attached to the vinyl-coated wire-mesh coral growth platform with fine vinyl coated wire. Each platform was anchored to the bottom with steel rods to prevent movement and maintain the corals slightly above the reef substratum. In some of the shoreward locations, corals would sink into soft mud if placed directly on the bottom. Each frame held two pairs of standard coral recruitment tiles extensively used as a preferred substrate for scleractinian recruitment for a number of studies around the world: Australia ([Harriott & Fisk, 1987](#); [Mundy, 2000](#)), French Polynesia ([Adjeroūd, Penin & Carroll, 2007](#)), the Caribbean ([Kuffner et al., 2006](#)), the Red Sea ([Abelson, Olinky & Gaines, 2005](#)), and here in Hawai'i ([Friedlander & Brown, 2005](#)). A set of two unglazed terracotta tiles (10 cm \times 10 cm surface area of 0.023 m) was assembled with a plexiglass spacer to create a gap between the two tiles. This gap was created to inhibit grazing by invertebrates and fishes on the underside of tiles where most coral recruitment occurs ([Birkeland, Rowley & Randall, 1981](#); [Adjeroūd, Penin & Carroll, 2007](#); [Cox & Ward, 2003](#); [Arnold & Steneck, 2011](#)). One set was placed at either end of the growth platform ([Fig. 2](#)). Retrieved tiles were properly labeled with site, location, plate number, and orientation (top or bottom). Tiles were then rinsed and dried. Recruits were counted using a Wild Heerbrugg M5 zoom stereo dissecting microscope. All surfaces of each tile were scanned (top, bottom, and sides). Coral recruits were circled with a fine-tipped permanent marker and initial taxonomic assignment made and recorded in a spreadsheet. Coral recruits were identified using descriptions and photographs provided by Dr. Eric Brown of the National Park Service. Since juvenile corals have few useful taxonomic characters ([Babcock et al., 2003](#)), coral recruits were identified to genus according to differences in

morphology. The experiment was set out on 2 February 2007 and on 24 October 2007 the corals were brought back into the laboratory. Mortality, partial mortality, and changes in skeletal weight were determined for each coral and the number of coral recruits on the coral recruitment tiles was recorded. Mortality and partial mortality were recorded in three categories: live (complete living tissue), partial (fractional living tissue), and mortality (no living tissue). All macroalgae was removed from each platform, rinsed, dried and an ash-free dry weight was determined.

General linear models (GLM) were selected through backward elimination using $\alpha = 0.05$ in R (*R Development Core Team, 2008*). GLMs were conducted using growth and mortality/partial mortality as dependent variables regressed against the predictors: species, turbidity, distance from shore, and macroalgae to explore the variation in coral growth and mortality.

RESULTS AND DISCUSSION

The full GLM models included growth and mortality as the response variables, and the main effects of coral species, site, distance from shore, turbidity, and benthic cover of macroalgae. The best model in explaining coral growth included species, distance from shore, and benthic cover of macroalgae ($R^2 = 66.91\%$, p -value = 0.0001). The model that best explains mortality/partial mortality includes species, distance, macroalgae, turbidity, and the interaction between species and distance and the interaction between species and turbidity ($R^2 = 60.39\%$, p -value = 0.0038).

Suspended-sediment concentration (SSC) gradients

USGS data (*Field et al., 2008b*) showed that the suspended sediment off south-central Moloka'i along the transects E (Kawela) and H (Kamiloloa) ranged from coarse sand to coarse silt that was moderately to very poorly sorted. The sediment varied in composition from approximately 25–90% carbonate, and thus 10–75% terrigenous volcanics, by mass, with the fine-grain silts and clays being predominantly terrigenous in origin. The percentage of terrigenous sediment decreased with distance from shore while the percentage carbonate material increased with distance from shore. The percentage organic carbon in the samples averaged $8.1 \pm 2.6\%$ by mass, suggesting that the SSC values presented here may be on the order of 5–12% less than a comparative measure of TSS presented in mass per volume. Turbidity data ($n = 6,657$) decreased by 76% between the landward E-100 and seaward E-400 sites, showing a similar pattern to the decrease in SSCs (81%) between the same sites. *Marquis (2005)* points out that turbidity and suspended sediment are not the same. Suspended sediment refers to particulate matter moved by water and is typically measured in milligrams of particulate matter to liters of water. Particles greater than $50 \mu\text{m}$ (i.e., sand) will fall out of the water column in seconds once the water is calmed. Silt-sized particles ($50\text{--}2 \mu\text{m}$) can remain in suspension for minutes in still water, while clay-sized particles ($<2 \mu\text{m}$) can remain in suspension indefinitely. Turbidity is a measure of the cloudiness of water and is usually quantified in nephelometric turbidity units (NTUs). Either organic matter, such as algae, or inorganic particles, like silt, can cause turbidity. Turbidity measurements in the field can be taken rapidly. At a given site there is a

Table 1 Suspended sediment concentration (SSC) values taken at the 12 experimental sites.

Transect	Distance mark (m)	Mean mg l ⁻¹	SE
E	50	37.2	8.6
E	100	36.8	6.0
E	250	23.1	4.7
E	400	7.9	2.1
E	550	3.2	0.7
E	700	4.5	1.8
H	50	31.1	7.2
H	100	24.1	9.8
H	250	10.2	2.8
H	400	6.0	1.4
H	550	6.1	1.5
H	700	3.1	0.4

strong relationship between turbidity and suspended sediment (*Marquis, 2005*). Therefore, turbidity measurements along the south Moloka'i coast show the same patterns as the SSC data and reinforce our observations of a strong sediment gradient. Suspended sediment concentrations at the experimental sites are presented in [Table 1](#).

Transects E (Kawela) and H (Kamiloloa) display the typical pattern along this coast with elevated SSCs inshore that decrease with distance from shore, with SSCs decreasing almost an order of magnitude between the stations 50 m from shore to those 700 m from shore; in general, the transect E stations directly off Kawela Gulch had higher SSCs than those farther west as one moves downcoast along the shore to transect H. These trends are the result of wind-driven waves and currents that continually re-suspend the seabed sediment, causing elevated turbidity and reduced photosynthetically-available radiation as previously reported (*Ogston et al., 2004; Presto et al., 2006; Piniak & Storlazzi, 2008*). The red dashed line in [Fig. 3](#) shows the 10 mg l⁻¹ cutoff, which is the upper SSC boundary for living coral reefs as originally proposed by *Rogers (1990)*. Coral coverage data shown in [Fig. 4](#) supports this generalization, with no coral found at stations that experience SSCs greater than 10 mg l⁻¹.

Mortality

The percent coral mortality recorded at the end of the 10-month experiment is shown in black with percent partial mortality shown in grey ([Fig. 5](#)). Considering the constant level of high turbidity and sedimentation, as described by *Field et al. (2008b)*, coral mortality was remarkably low except at the stations nearer to shore on transect E (E-100, E-250) which is the area closest to a major sediment source at Kawela Gulch. The overall model ($R^2 = 60.39\%$, p -value = 0.003) shows that coral mortality/partial mortality decrease with distance from shore, increases with increasing macroalgae and turbidity, and the species *Montipora capitata* had a higher mean mortality/partial mortality than *Porites compressa*. *M. capitata* also showed higher mortality with increasing distance from shore ($p = 0.05$) and with increasing turbidity ($p = 0.02$) than *P. compressa* ([Figs. 5A and 5C](#)).

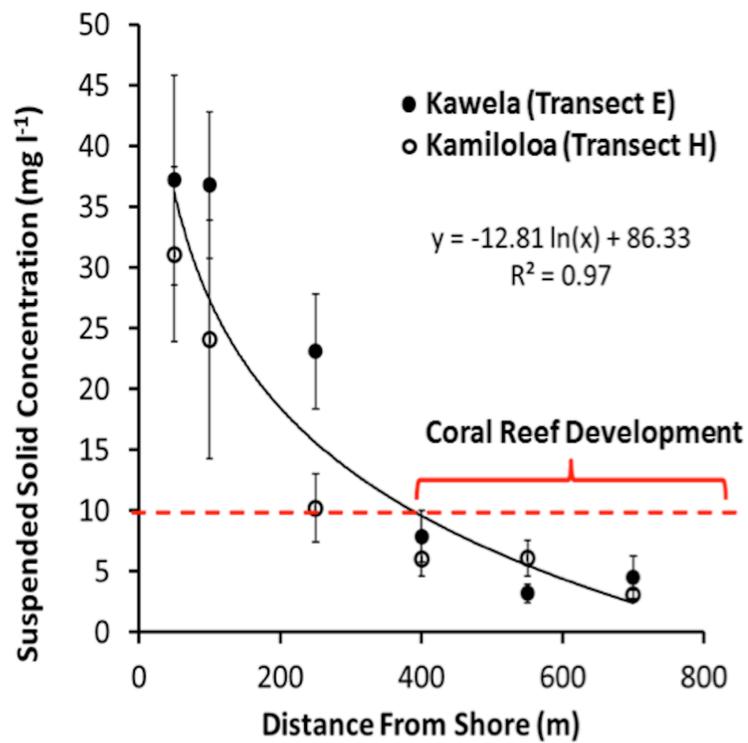


Figure 3 Suspended-sediment concentration (SSC) \pm SE along Kawela (E) and Kamiloloa (H) transects.

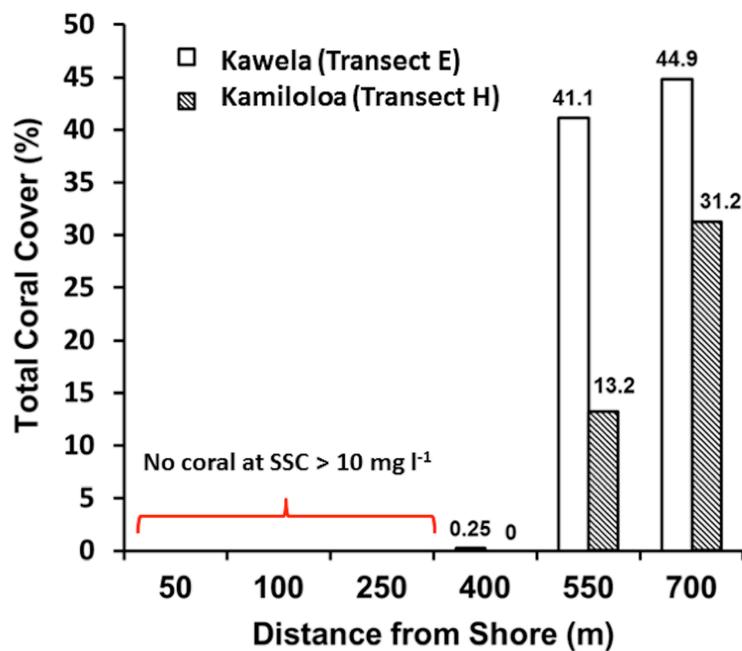


Figure 4 Total coral cover along Kawela (E) and Kamiloloa (H) transects (data from *Rodgers et al., 2005*).

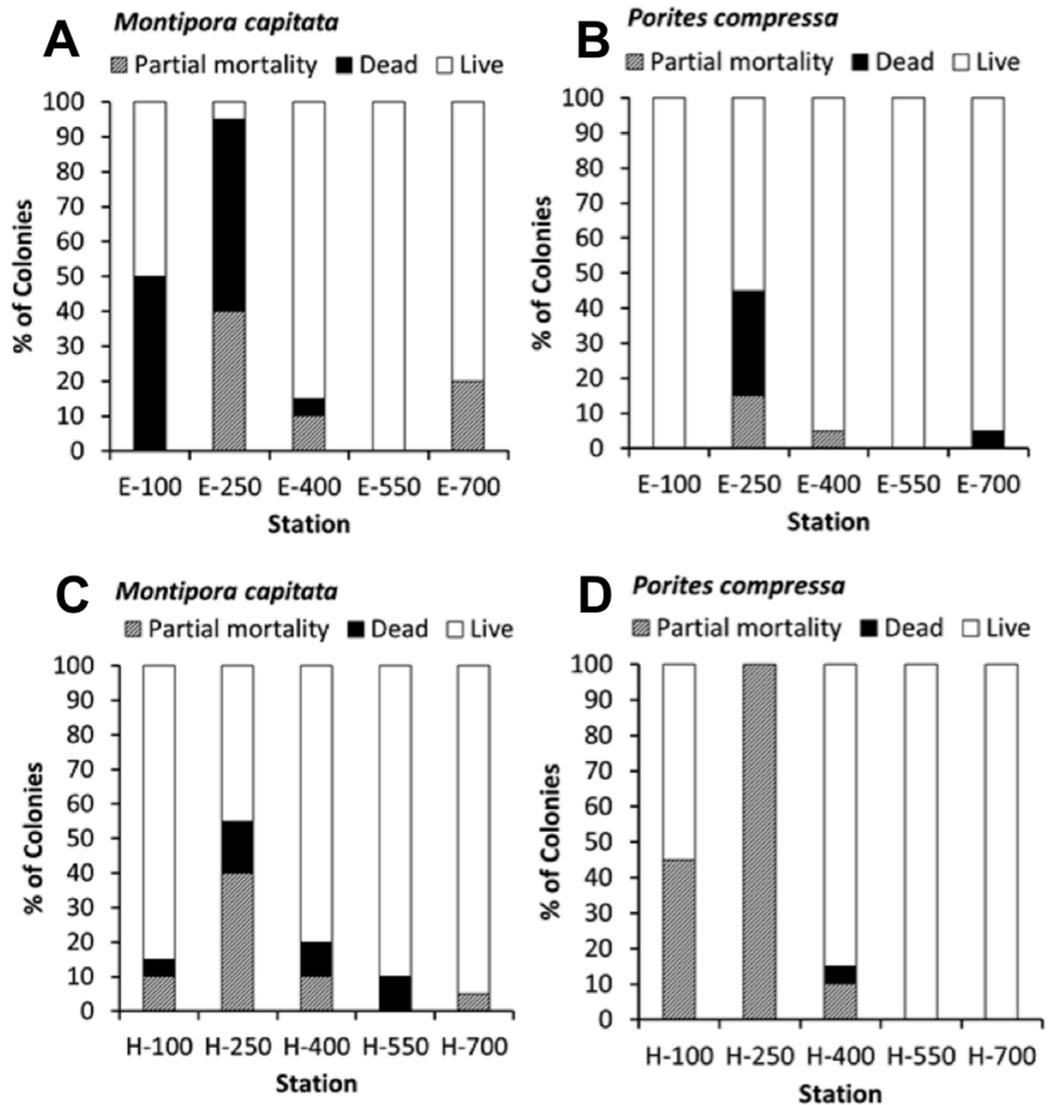


Figure 5 Percent partial mortality and mortality for *Montipora capitata* (A, C) and *Porites compressa* (B, D) ($n = 400$) at all stations along transects E (Kawela) (A, B), and H (Kamiloloa) (C, D).

Growth

Coral growth was quite good in spite of high SSCs. Coral growth was higher at the offshore sites compared to the inshore sites. The best GLM model using growth as the response variable included species, distance from shore, and benthic cover of macroalgae ($R^2 = 66.91\%$, p -value = 0.0001). No difference was found in growth between the two sites. Growth was found to significantly increase with distance from shore (Fig. 6) and decrease with increasing macroalgae. A difference in growth between species was found. *Montipora capitata* shows statistically higher mean growth than *Porites compressa* (p -value = 0.001).

Although an overall relationship was found between growth and distance from shore, coral skeletal growth at transect H (Kamiloloa) shown in Fig. 6A shows a strong

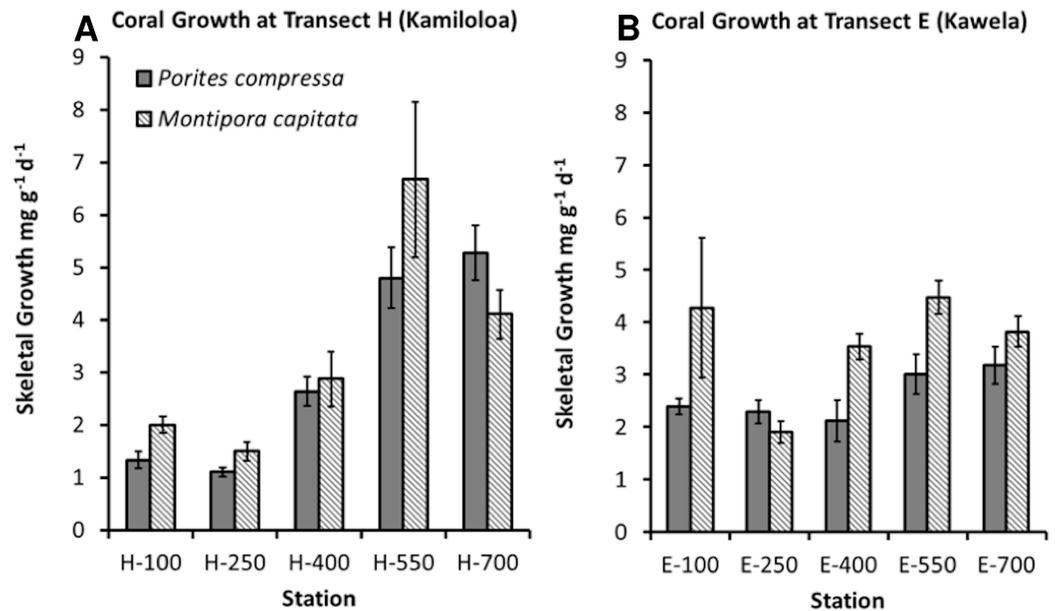


Figure 6 Coral skeletal growth (mg g⁻¹ d⁻¹) ±SE for corals at all stations along transects H (Kamiloloa) and E (Kawela).

relationship with increasing distance from shore, whereas coral skeletal growth along transect E (Kawela) shown on Fig. 6B does not show a strong trend. Development of coral reefs at high turbidity levels has previously been reported by *Larcombe, Costen & Woolfe (2001)*, who found that coral assemblages on some inner-shelf habitats on the Great Barrier Reef shelf reach greater than 50% coral cover under extremely high turbidity generated by wave-driven resuspension of sediment. Likewise, *Roy & Smith (1971)* reported well developed reefs in Fanning Atoll Lagoon in an area where visibility in the water was about 2 m, and suspended load was about 100 times that of the open ocean. The bottom was covered with calcium carbonate mud, where depositional rates appeared to exceed 1 mm/year, and where about 30% of the bottom was covered with live coral. Though there was a decrease in abundance of coral knolls from the clear water areas to the turbid water areas of the lagoon, both areas had lush reef development.

Impact of macroalgae on coral growth and mortality

At the end of the 10-month growth period, it was apparent that the growth platforms had recruited different amounts of macroalgae. In general linear models, growth and mortality/partial mortality was best explained by macroalgal dry weights. Coral growth was found to decrease with increasing macroalgae dry weights (p -value = 0.001) but did not vary with coral species. A statistically significant relationship was also found between coral mortality/partial mortality and macroalgae dry weights (p -value = 0.002) where mortality/partial mortality increases with increasing macroalgae and macroalgae increases with distance from shore. Further, there may be a feedback relationship between macroalgae and high SSC. Macroalgae have been shown to have an impact on nearby corals through a variety of mechanisms or combination of mechanisms. These modifications

Table 2 Coral settlements at each site ranked in relation to suspended solid concentration (SSC). Only five settlements of three genera were found, with none occurring above 6.1 mg l⁻¹ SSC.

Station	SSC (mg l ⁻¹) ± SE	Total coral settlements	<i>Montipora</i>	<i>Porites</i>	<i>Pocillopora</i>
H-700	3.1 ± 0.4	2		1	1
E-700	3.1 ± 0.4	0			
E-550	3.2 ± 0.7	1	1		
H-400	6.0 ± 1.4	0			
H-550	6.1 ± 1.5	2	1	1	
E-400	7.9 ± 2.1	0			
H-250	10.2 ± 2.8	0			
E-250	23.1 ± 4.7	0			
H-100	24.1 ± 9.8	0			
E-100	36.8 ± 6.0	0			

include changes in physical processes of sediment accumulation attenuation of irradiance and marked variation in diurnal dissolved oxygen and pH cycles (Stamski & Field, 2006; Martinez, Smith & Richmond, 2012). On the south Moloka'i reef flat, sediment trapping by macroalgae has been measured (Stamski & Field, 2006). Macroalgae trapped a mean of 1.26 (±0.91 SD) grams of sediment per gram of dry weight biomass and that sediment was dominantly terrigenous mud (59% by weight). Over 300 metric tons of sediment were estimated to be retained by macroalgae across 5.75 km² of reef flat (54 gm²). Macroalgae mats can reduce irradiance by 99% and double sediment accumulation (Martinez, Smith & Richmond, 2012). Algal mats can produce hypoxia and hyperoxia in the extreme diurnal minima and maxima and can significantly acidify the water under the algal mat by decreasing pH and thereby impact corals.

Recruitment

Extremely low levels of coral recruitment occurred in this experiment (Table 2). Recruitment was from one to three orders of magnitude lower than other reefs measured with the same technique throughout the Hawaiian Islands (Table 3). The few recruits occurred on the seaward coral recruitment tiles, with none in the more turbid areas. No recruitment was found at the three stations nearest to shore at either site. Only one recruit was recorded from Transect E (Kawela) at 550 m from shore and four recruits from transect H (Kamiloloa) at 550 m and 700 m from shore (Table 2).

These results are in accord with past coral settlement experiments that have shown a wide variation in coral settlement rates under different conditions. Lewis (1974) reported that a sprinkling of fine washed sand in the bottom of test bowls reduced settlement rate by two thirds. Hodgson (1991) studied coral settlement on a glass surface that was only partially covered with a mixture of sand, silt, and clay. In this situation he found that the larvae will still settle on areas that are clear of sediment. Te (1992) cultured larvae of the coral *Pocillopora damicornis* to four concentrations of sediment (0, 10, 100, 1,000 mg l⁻¹) for 14 days under two contrasting water agitation levels and found no significant

Table 3 Comparison of mean coral recruitment rates (number of recruits $\text{m}^{-2} \text{year}^{-1}$) from the main Hawaiian Islands measured on standard terracotta coral recruitment tiles.

Site	Mean recruits (recruits $\text{m}^{-2} \text{yr}^{-1}$)	Range	Reference
Hanalei Bay, Kaua'i	7,924	403–15,386	<i>Friedlander & Brown (2005)</i>
Puamana, Maui	415	8–1,792	<i>Brown (2004)</i>
Olowalu, Maui	122	95–233	<i>Brown (2004)</i>
Honolua Bay, Maui	41	7–92	<i>Brown (2004)</i>
West Hawai'i	24	0–411	<i>Martin & Walsh (2014)</i>
N. Puako, Hawai'i	167	0–26	Y Stender, pers. com., 2014
Pelekane, Hawai'i	138	0–29	Y Stender, pers. com., 2014
Kawaihae, Hawai'i	304	5–45	Y Stender, pers. com., 2014
Kaunaoa, Hawai'i	282	0–37	Y Stender, pers. com., 2014
South Moloka'i	5.1	0–2	This study

difference in larval settlement on the glass walls of the containers. Presumably the vertical glass walls did not accumulate sediment, so there was no difference in substrate between the treatments. *Babcock & Davies (1991)* used a mixture of fine sand and silt of mixed terrigenous and carbonate origin to determine the effect of various rates of sedimentation ($0.5\text{--}325 \text{ mg cm}^{-2} \text{ d}^{-1}$) on settlement rates of *Acropora millepora* in aquaria. Total number of settled larvae was not significantly affected by sedimentary regime, but higher sedimentation rates reduced coral settlement on horizontal surfaces where sediment could accumulate. The experiments most relevant to the results in [Table 2](#) were conducted by *Perez et al. (2014)*. They measured survival and settlement of *Pocillopora damicornis* larvae on hard surfaces covered with fine-grain ($<63 \mu\text{m}$) terrestrial silts and clays. Coral larvae were incubated in Petri dishes with different amounts of sediment for two weeks and the percent that settled on the bottom was determined. There was a statistically significant relationship between the amount of sediment and coral recruitment on the bottom, with no recruitment on surfaces having a sediment cover above 0.9 mg cm^{-2} , which represents a thickness of 0.05 mm ($5 \mu\text{m}$). Total survival over the two week settlement tests did not show a significant decline, so the major impact of the sediment was on successful settlement rather than on mortality. The larvae simply would not settle on substrate covered with a thin film of fine-grain terrestrial sediment. The reef flat off south Moloka'i in the area of the survey is constantly covered with this fine-grain material on all surfaces due to continual re-suspension of seabed sediment. The resuspension creates the elevated SSC conditions. The sediment settles out when insolation-driven winds ("sea breeze") diminish at night (*Field et al., 2008a*, and references therein).

CONCLUSIONS

- Corals on the Moloka'i reef flat can survive and grow in extremely turbid environments ([Figs. 5 and 6](#)). Coral growth was negatively correlated with SSC levels, although some growth was documented at SSC levels even in excess of 35 mg l^{-1} .

- Coral recruitment was very low (Table 3) in comparison to other areas. Recruitment decreased with increasing SSC and distance from shore (Table 2). No new recruits occurred above a SSC of 6.1 mg l^{-1} . We believe that thin coatings of fine-grain terrestrial silts and clays observed on the reef flat effectively blocked new coral recruitment (Perez *et al.*, 2014).
- Presence of macroalgae mats is a major factor controlling coral mortality and growth on the Moloka'i reef flat.

ADDITIONAL INFORMATION AND DECLARATIONS

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Competing Interests

The authors declare there are no competing interests.

Author Contributions

- Paul L. Jokiel and Ku'u'lei S. Rodgers conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.
- Curt D. Storlazzi and Michael E. Field conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, wrote the paper, reviewed drafts of the paper.
- Claire V. Lager performed the experiments, prepared figures and/or tables, reviewed drafts of the paper.
- Dan Lager performed the experiments, prepared figures and/or tables.

Field Study Permissions

The following information was supplied relating to field study approvals (i.e., approving body and any reference numbers):

The collection permit was obtained through the Hawaii Department of Land and Natural Resources: Permit SAP 2007.

Supplemental Information

Supplemental information for this article can be found online at <http://dx.doi.org/10.7717/peerj.699#supplemental-information>.

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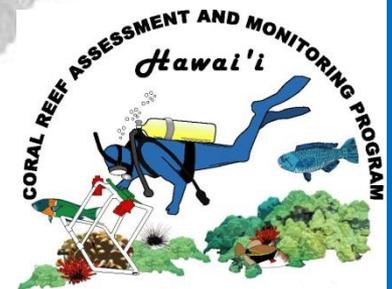
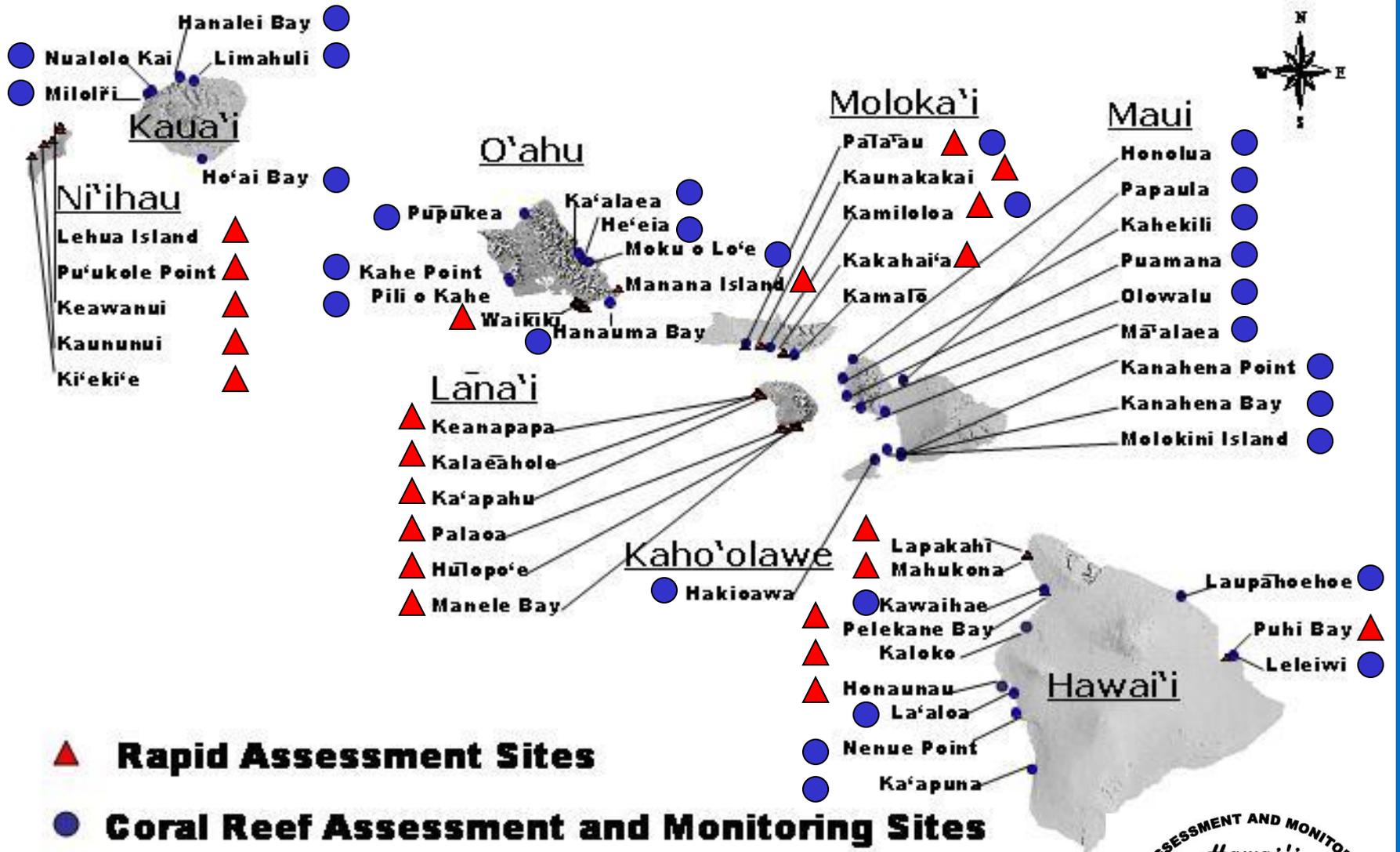
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Use of Integrated Landscape Indicators and development of Biocriteria to Evaluate the Health of Linked Watersheds and Coral Reef Environments in the Hawaiian Islands

Ku‘ulei S. Rodgers, Michael H. Kido, Paul L. Jokiel, Jason S. Rodgers





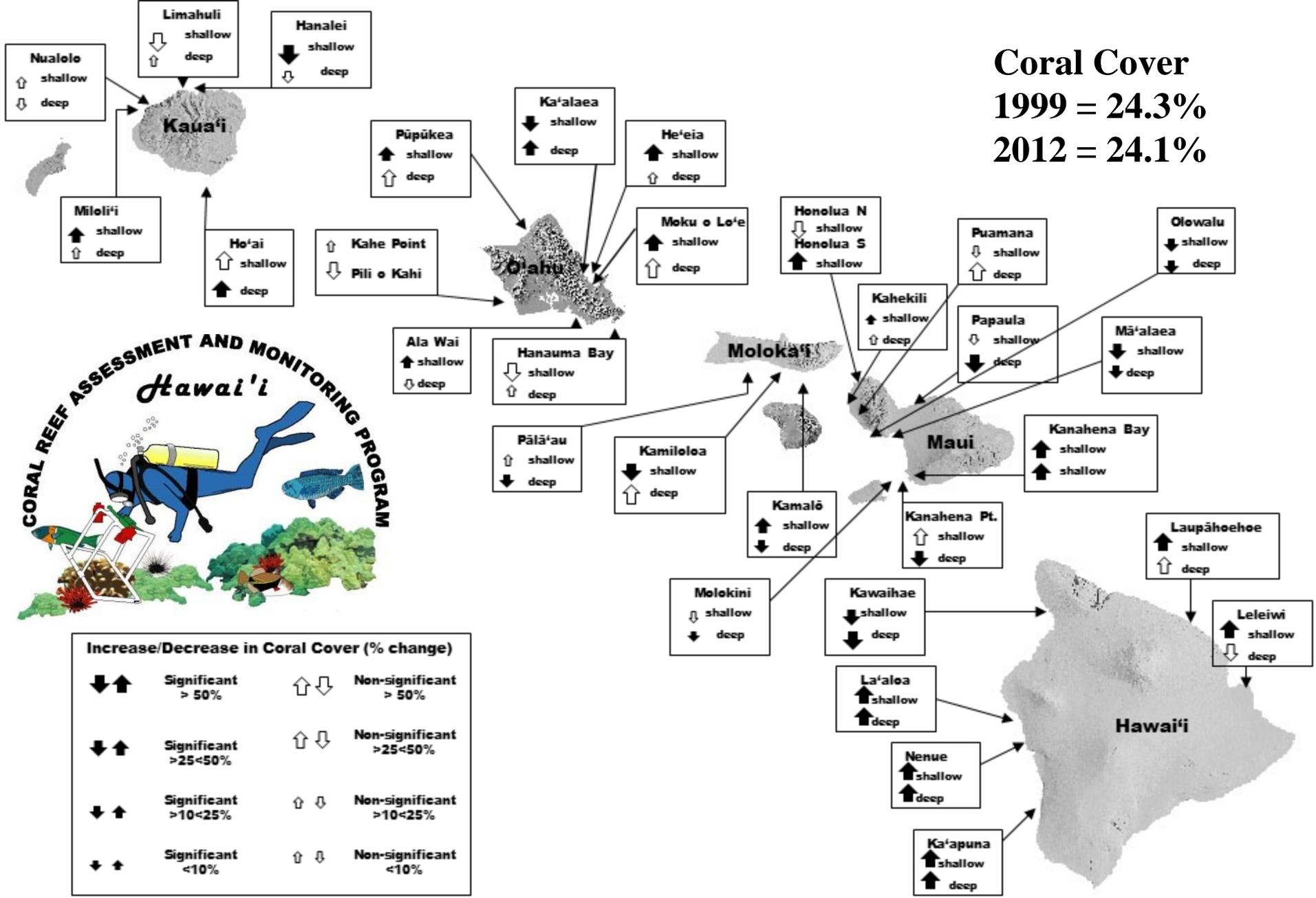
Coral Cover
1999 = 24.3%
2012 = 24.1%



Increase/Decrease in Coral Cover (% change)

↓↑	Significant > 50%	↑↓	Non-significant > 50%
↓↑	Significant > 25 < 50%	↑↓	Non-significant > 25 < 50%
↓↑	Significant > 10 < 25%	↑↓	Non-significant > 10 < 25%
↓↑	Significant < 10%	↑↓	Non-significant < 10%

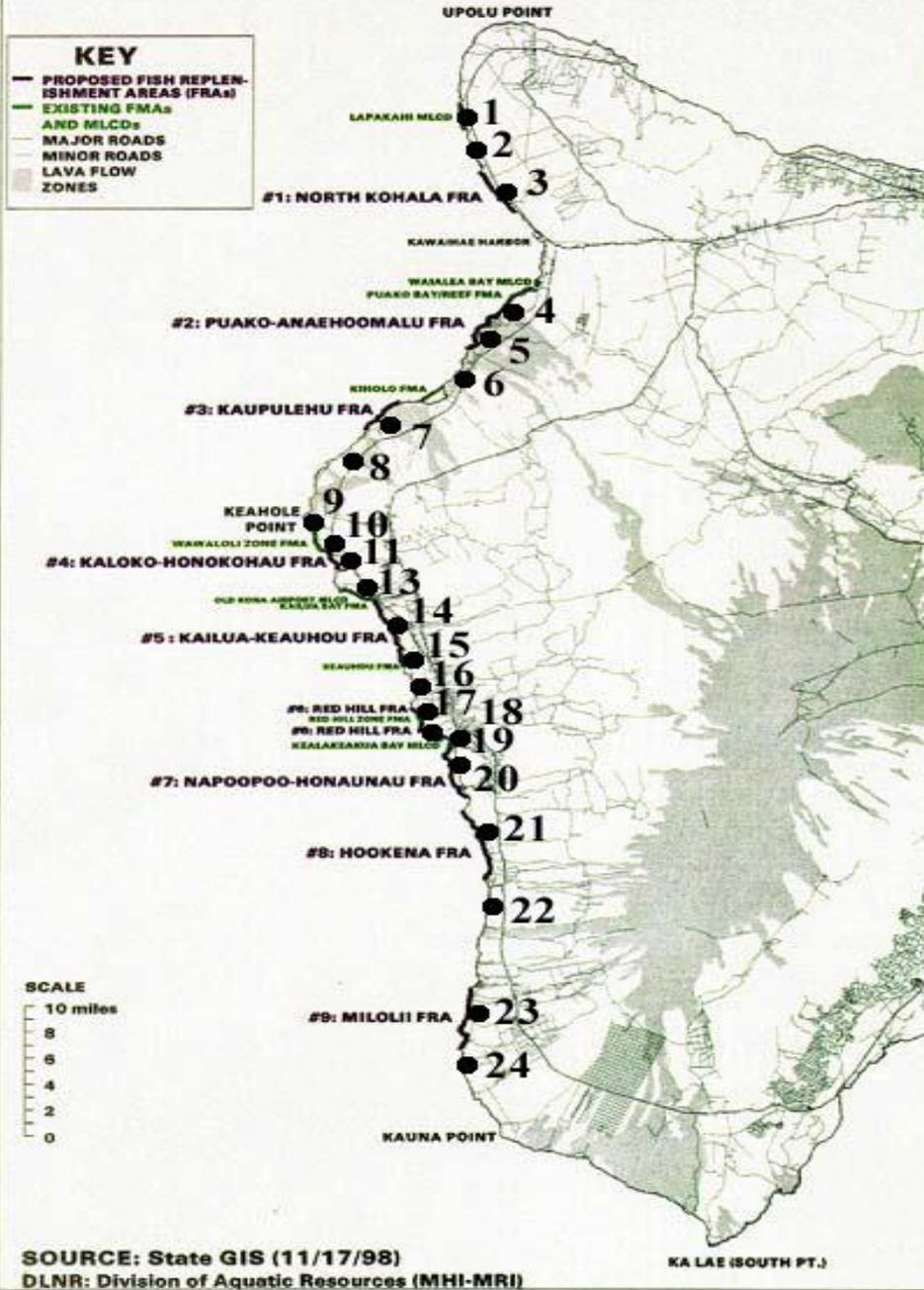
0 50 100 200 300 Kilometers



WEST HAWAII PROPOSED FRAs

KEY

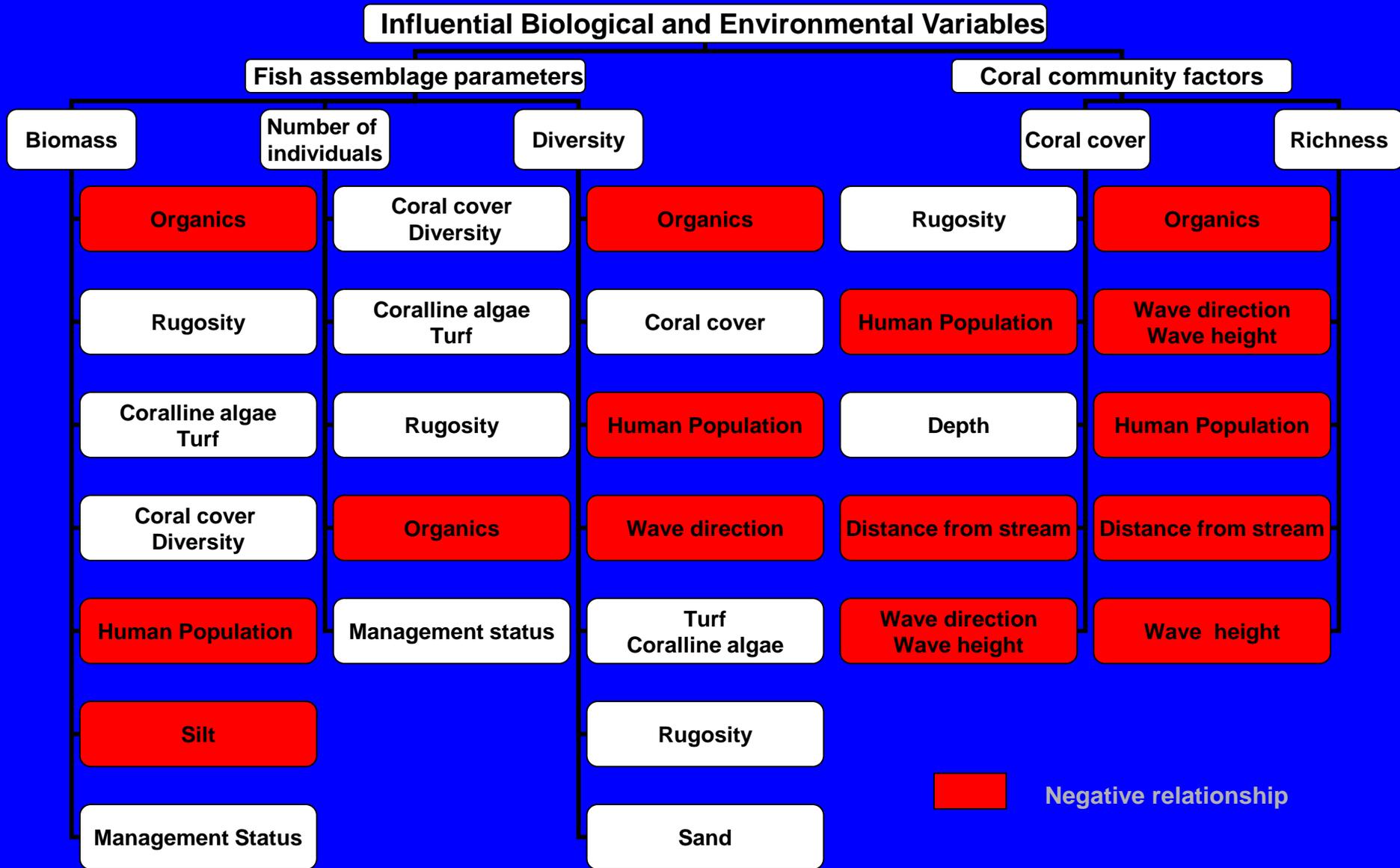
- PROPOSED FISH REPLENISHMENT AREAS (FRAs)
- EXISTING FMA's AND MLCDS
- MAJOR ROADS
- MINOR ROADS
- LAVA FLOW ZONES



Site (N to S)	2003	2007	Δ	P=
Lapakahi	19.50% Decline	11.40%	-8.10%	0.004
Kamilo	49.50% Decline	38.20%	-11.30%	0.020
Waiaka'ilio Bay	54.40% Decline	42.50%	-11.90%	0.047
Puakō	49.90% No Change	47.80%	-2.10%	0.604
'Anaeho'omalu	41.20% Decline	31.50%	-9.70%	0.038
Keawaiki	29.90% Decline	16.70%	-13.20%	0.006
Ka'upulehu	40.90% Decline	31.20%	-9.70%	0.033
Makalawena	45.20% No Change	47.60%	2.40%	0.553
Wawaloli Beach	33.32% Increase	42.25%	8.93%	0.015
Wawaloli	37.21% No Change	37.51%	0.31%	0.859
Honokōhau	48.29% No Change	48.74%	0.45%	0.894
Papawai	32.21% Increase	38.31%	6.10%	0.044
S. Oneo Bay	56.09% Increase	61.86%	5.77%	0.025
N. Keauhou	31.92% No Change	31.10%	-0.81%	0.356
Kualani	52.81% No Change	59.78%	6.97%	0.124
Red Hill	30.68% No Change	33.22%	2.54%	0.511
Keopuka	15.98% No Change	15.59%	-0.39%	0.602
Kealakekua Bay	27.10% No Change	28.64%	1.54%	0.595
Ke'ei	31.20% No Change	28.67%	-2.54%	0.424
Ho'okena (Kalahiki)	36.53% No Change	39.62%	3.09%	0.263
Ho'okena (Auau)	28.18% No Change	28.44%	0.26%	0.925
Miloli'i (Omaka'a)	29.76% No Change	27.08%	-2.68%	0.491
Miloli'i (Manukā)	30.35% No Change	33.17%	2.82%	0.488
Lapakahi	19.50% Decline	11.40%	-8.10%	0.004
Kamilo	49.50% Decline	38.20%	-11.30%	0.020



Influential Indicators of Biological Communities



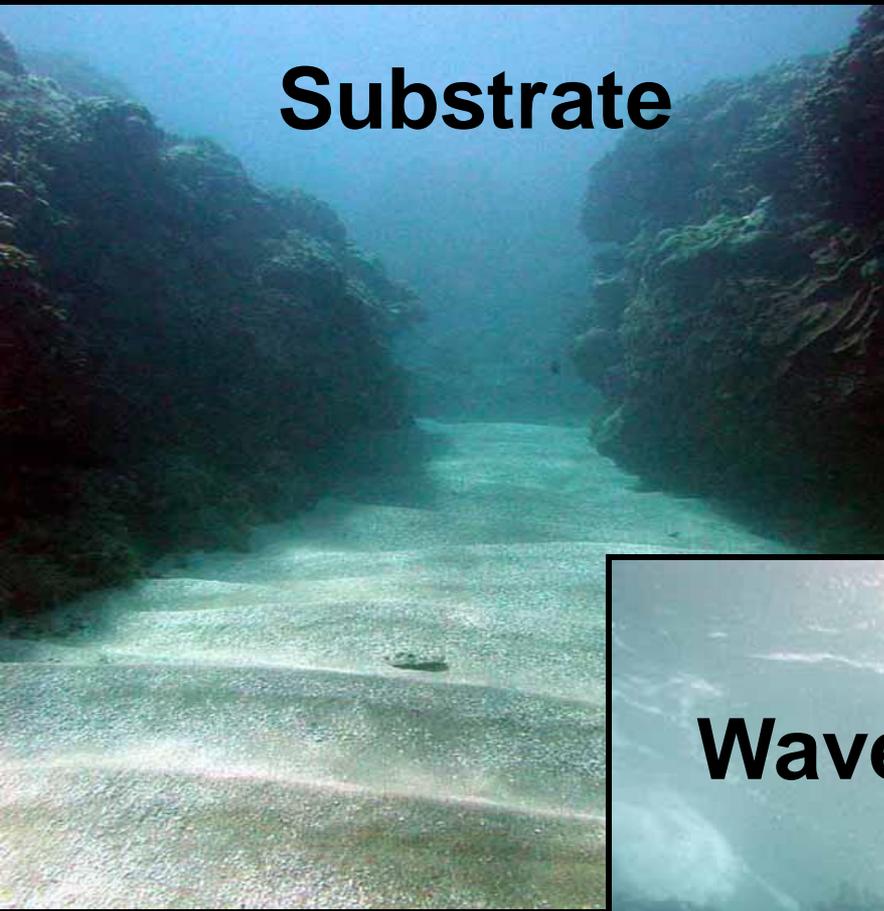
1	A	B	C	D	E	F	G	H	I	J	K	
2		1) Input depth of station in meters	5					Run Default Query	Modify Query	View Data Map	View Querried Data	Site Map
3		2) Select wave exposure	South									
4		3) Input Northing Data In UTM	621672	http://www.dmap.co.uk/ll2tm.htm								
5		4) Input Easting Data in UTM	2351876									
6		5) Input Site Name	Evaluation Site					Unweighted IBI Chart	Cramp Weighted IBI Chart	Custom Weighted IBI Chart		
7		6) Input values for parameters of interest under assessment data below										
8												
9												

	Parameters	Assessment data	RANK	IBI	Cramp Weighted IBI	User Weights	User Weighted IBI	Parameter Impact
11	Organics (LOI)	3.35	0.49	4.89	4.89	0.00	0.00	-
12	CaCO ₃	94.58	0.91	9.11	6.38	0.00	0.00	+
13	medium sand	87.61	0.80	8.00	5.60	0.00	0.00	+
14	fine sand	7.16	0.09	0.88	0.35	0.00	0.00	+
15	very fine sand	4.75	0.44	4.44	3.55	0.00	0.00	+
16	silt	0.47	0.93	9.34	7.47	0.00	0.00	-
17	Montipora flabellata	0	0.00	0.00	0.00	0.00	0.00	+
18	Montipora patula	0	0.00	0.00	0.00	0.00	0.00	+
19	Montipora capitata	0	0.00	0.00	0.00	0.00	0.00	+
20	Pocillopora meandrina	1	0.44	4.44	1.33	0.00	0.00	+
21	Porites compressa	0	0.00	0.00	0.00	0.00	0.00	+
22	Porites lobata	0	0.00	0.00	0.00	0.00	0.00	+
23	Total Coral	1	0.02	0.22	0.20	10.00	0.22	+
24	Coral Species Richness	1	0.00	0.00	0.00	10.00	0.00	+
25	Coral Diversity (H')	0	0.00	0.00	0.00	10.00	0.00	+
26	sand cvr	29.8	0.02	0.23	0.14	0.00	0.00	-
27	calcareous algae	0	0.00	0.00	0.00	10.00	0.00	+
28	macroalgae	25.4	0.05	0.45	0.27	10.00	0.45	-
29	substrate (turf)	43.8	0.78	7.78	4.67	10.00	7.78	-
30	Rugosity	1.31	0.18	1.77	1.77	0.00	0.00	+
31	Wave Height (mean)	4.2	0.27	2.67	2.40	0.00	0.00	-
32	Wave direction (mean)	184.3	0.29	2.89	1.73	0.00	0.00	-
33	population within 5 km	151265	0.02	0.23	0.21	0.00	0.00	-
34	population within 10 km	268400	0.02	0.23	0.14	0.00	0.00	-
35	population within watershed	105365	0.02	0.23	0.14	0.00	0.00	-
36	Stream (distance) m	2671	0.71	7.12	4.27	0.00	0.00	-
37	rain mm	600	0.78	7.77	3.89	0.00	0.00	+
38	fish<5cm (%)	75	0.96	9.55	5.73	0.00	0.00	+
39	5-15cm (%)	8	0.09	0.88	0.53	0.00	0.00	+
40	>15cm(%)	17	0.58	5.77	3.46	0.00	0.00	+
41	Total number of fish	12	0.00	0.00	0.00	0.00	0.00	+
42	Biomass	300.16	0.00	0.00	0.00	0.00	0.00	+
43	Number of fish (hax1000)	0.96	0.00	0.00	0.00	0.00	0.00	+
44	Biomass (tons per hectare)	0.02	0.00	0.00	0.00	10.00	0.00	+
45	Fish diversity (H')	0.98	0.00	0.00	0.00	10.00	0.00	+
46	Fish evenness	0.71	0.24	2.44	1.22	10.00	2.44	+
47	Endemic %	75	0.98	9.77	3.91	10.00	9.77	+
48	Indigenous %	25	0.00	0.00	0.00	10.00	0.00	+
49	Introduced %	0	1.00	10.00	4.00	10.00	10.00	-
50	Corallivores %	0	0.00	0.00	0.00	0.00	0.00	+
51	Detritivores %	0	0.00	0.00	0.00	0.00	0.00	+
52	Herbivores %	0	0.00	0.00	0.00	0.00	0.00	+
53	Mobile Invertebrate feeders %	100	0.98	9.77	3.91	0.00	0.00	+
54	Piscivores%	0	0.00	0.00	0.00	0.00	0.00	+
55	Sessile Invertebrate feeders %	0	0.00	0.00	0.00	0.00	0.00	+
56	Zooplanktivores %	0	0.00	0.00	0.00	0.00	0.00	+

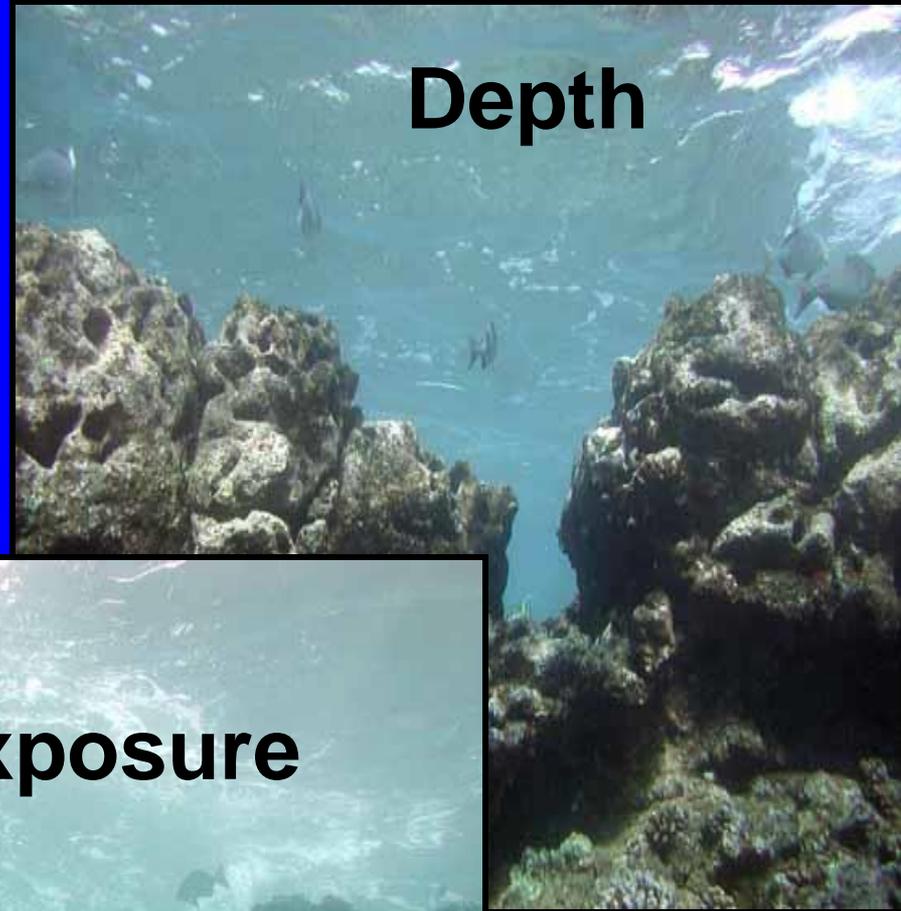
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Classification

Substrate



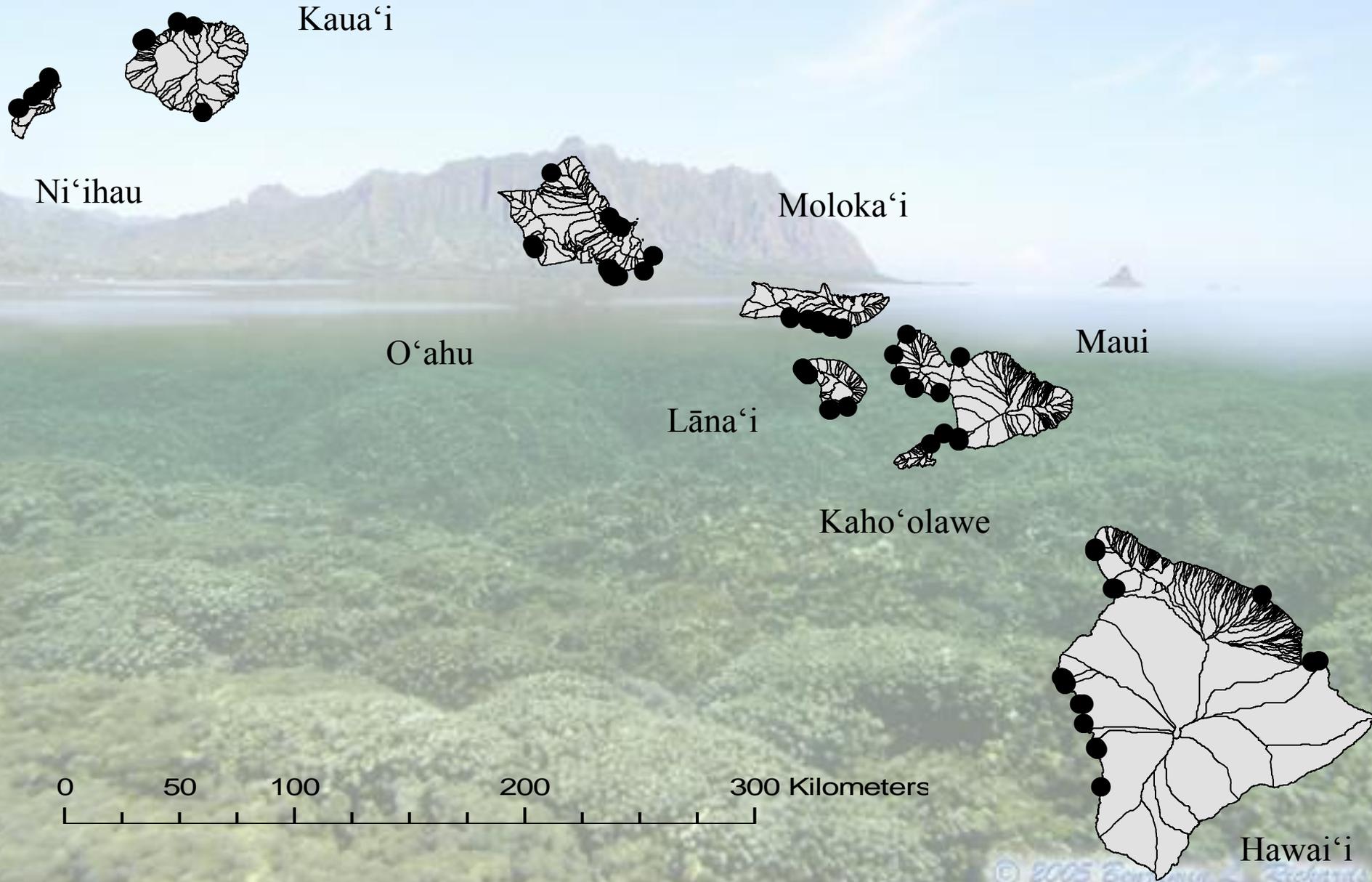
Depth

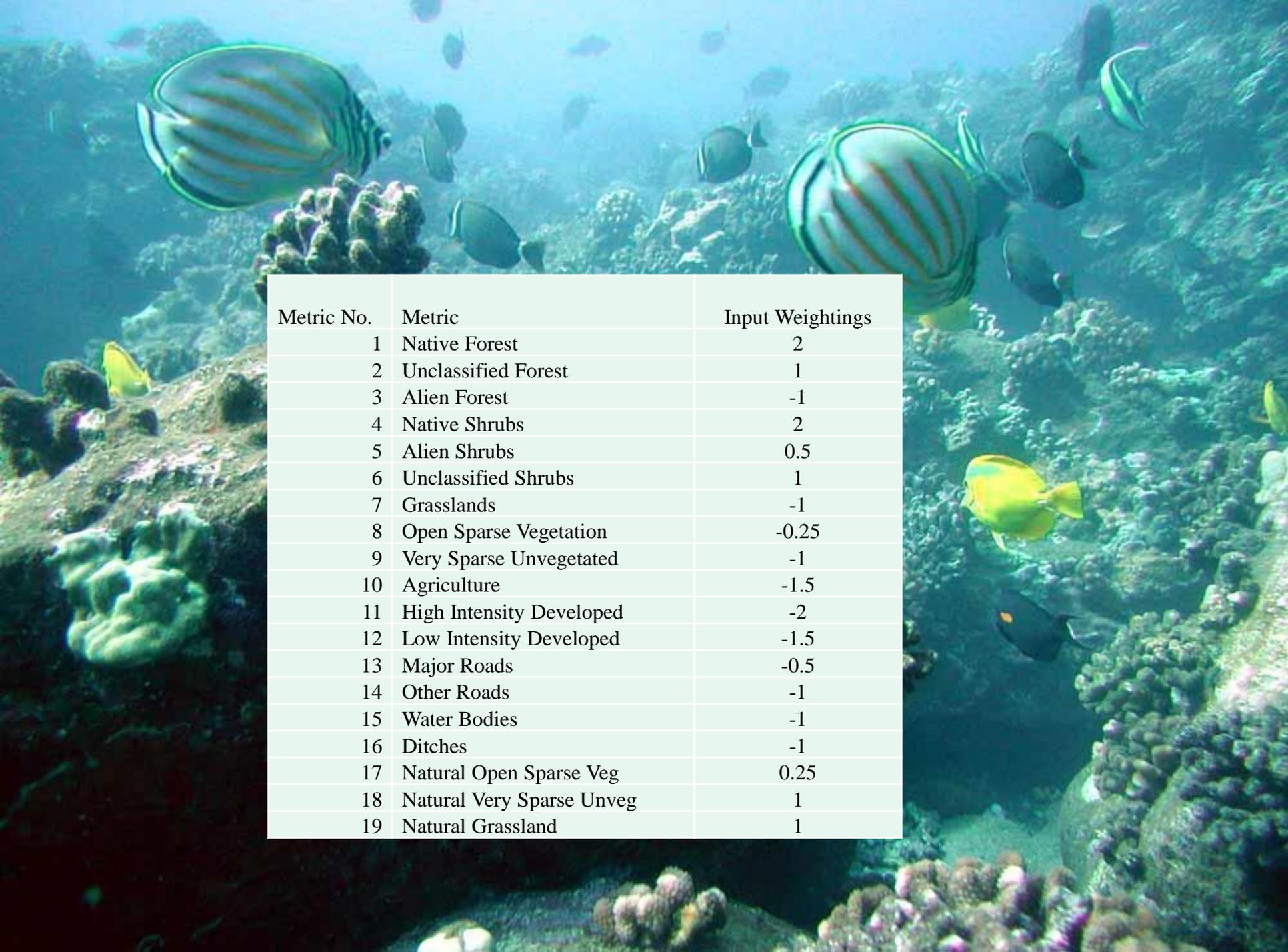


Wave Exposure



Main Hawaiian Islands watersheds and CRAMP sites



An underwater photograph of a vibrant coral reef. The scene is filled with diverse marine life, including several large, colorful striped surgeonfish in the foreground, smaller black and yellow fish, and various types of coral and sea anemones. The water is clear and blue, with sunlight filtering through from above, creating a bright and lively atmosphere.

Metric No.	Metric	Input Weightings
1	Native Forest	2
2	Unclassified Forest	1
3	Alien Forest	-1
4	Native Shrubs	2
5	Alien Shrubs	0.5
6	Unclassified Shrubs	1
7	Grasslands	-1
8	Open Sparse Vegetation	-0.25
9	Very Sparse Unvegetated	-1
10	Agriculture	-1.5
11	High Intensity Developed	-2
12	Low Intensity Developed	-1.5
13	Major Roads	-0.5
14	Other Roads	-1
15	Water Bodies	-1
16	Ditches	-1
17	Natural Open Sparse Veg	0.25
18	Natural Very Sparse Unveg	1
19	Natural Grassland	1

**Shallow south facing sites
positive partial correlation
0.95 ($p < 0.001$)**



**North facing sites
no statistically significant correlation**





Areas restoration efforts are most effective

Evaluate reefs

Predict reef health from watershed health

Coordinate conservation management of the entire ahupua‘a

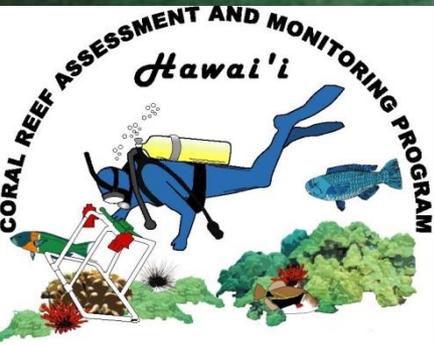
Develop water quality standards for reefs

Response of reef corals to extreme turbidity on the south Moloka'i reef flat.

Ku'ulei Rodgers and Paul L. Jokiel

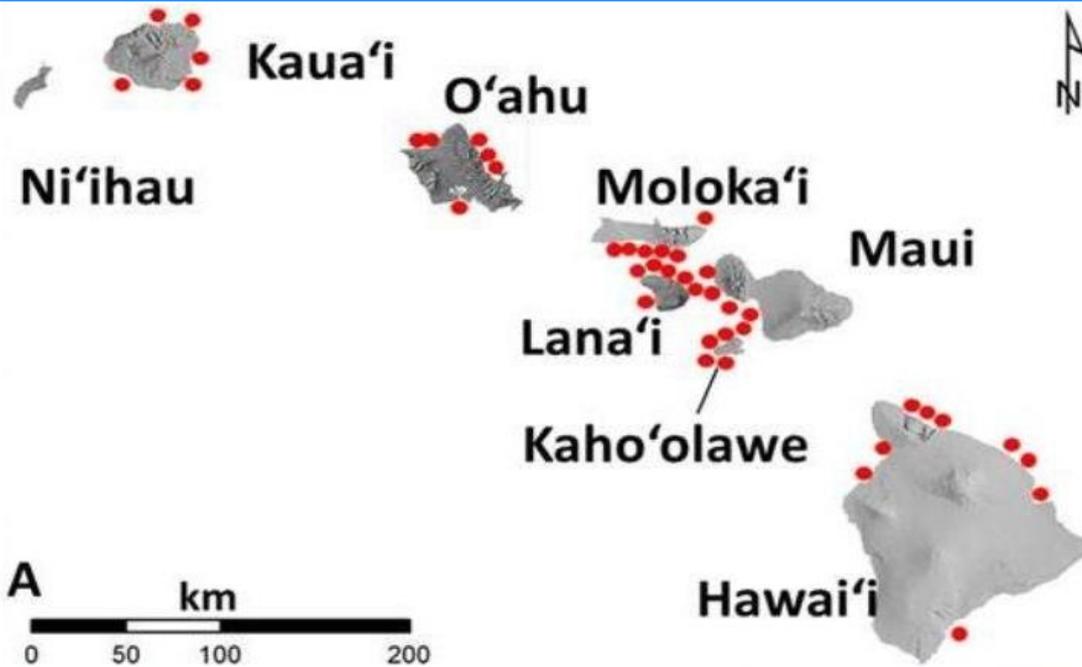
Hawai'i Coral Reef Assessment and Monitoring Program (CRAMP)

<http://cramp.wcc.hawaii.edu>

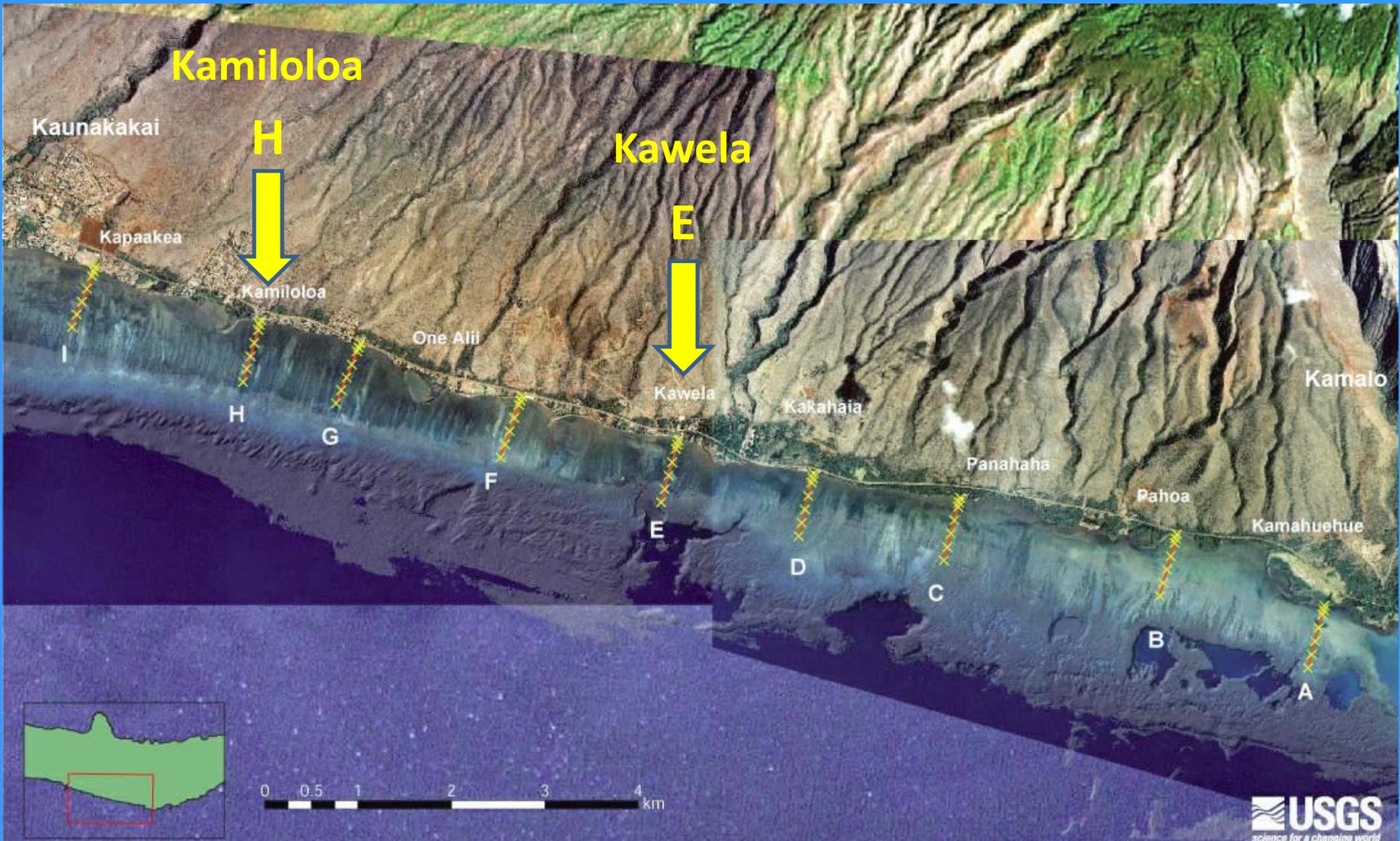


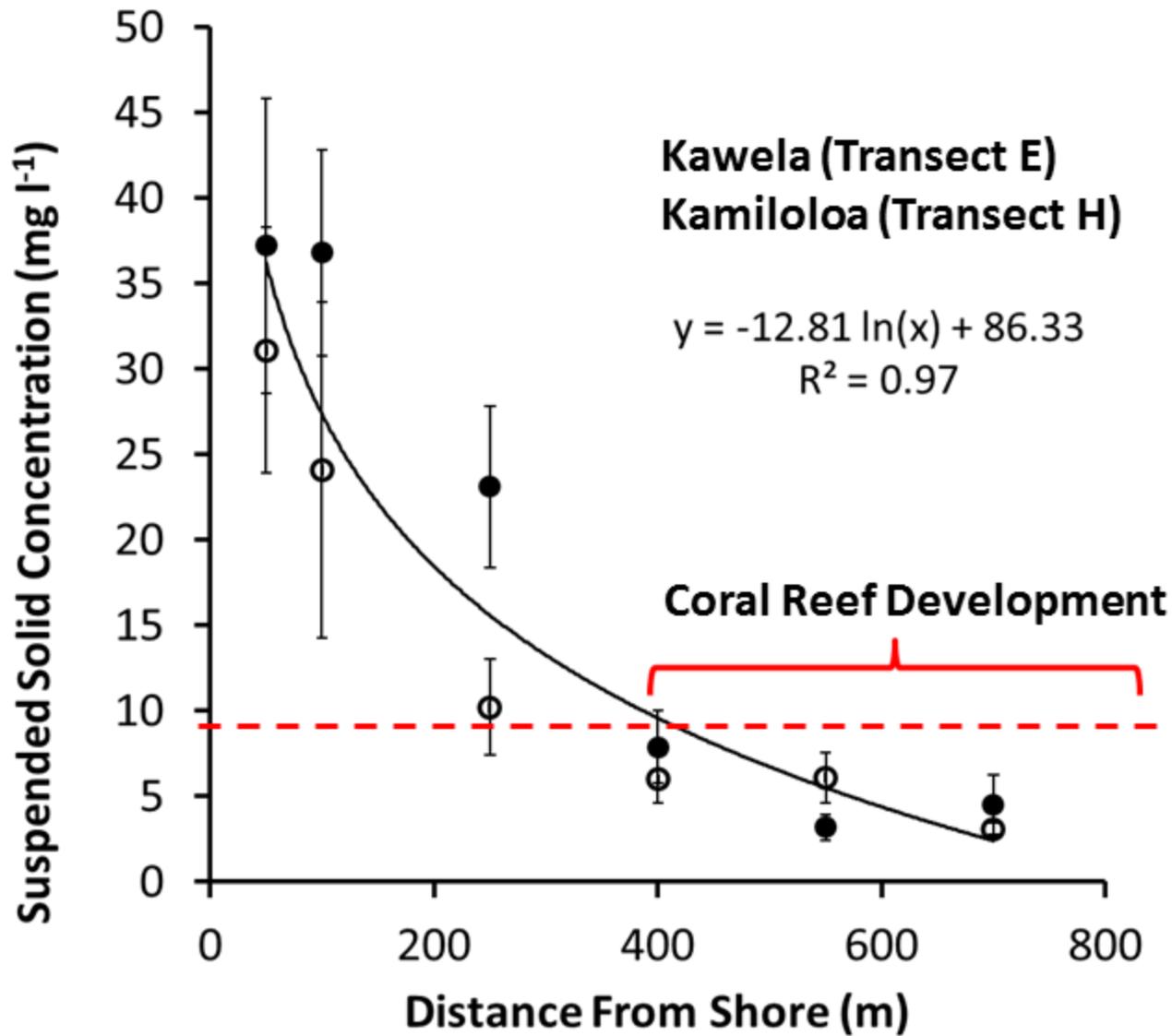
Coral demographics:

1. Recruitment
2. Growth
3. Mortality

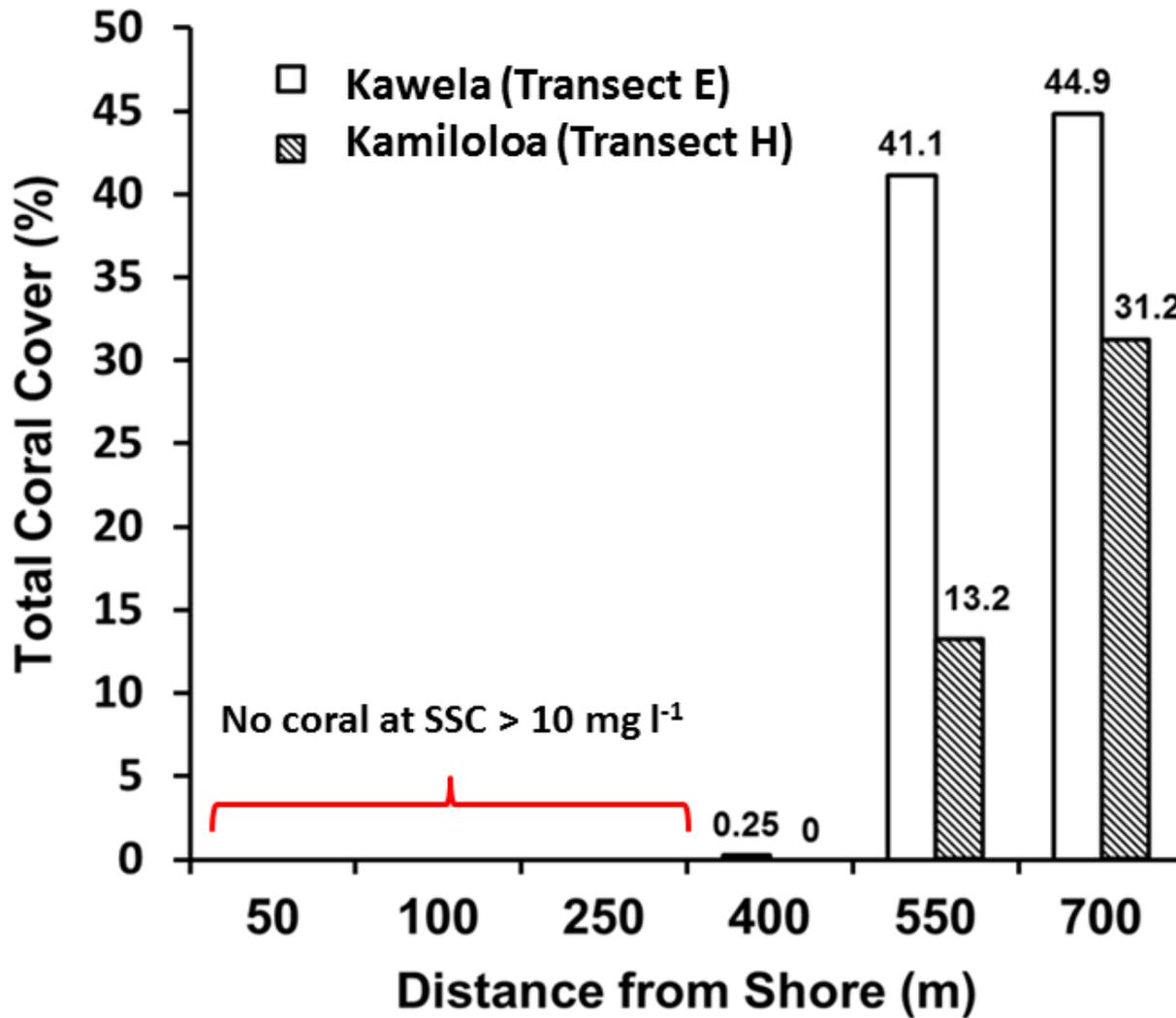


USGS Moloka'i reef flat study





Environment –Coral Coverage

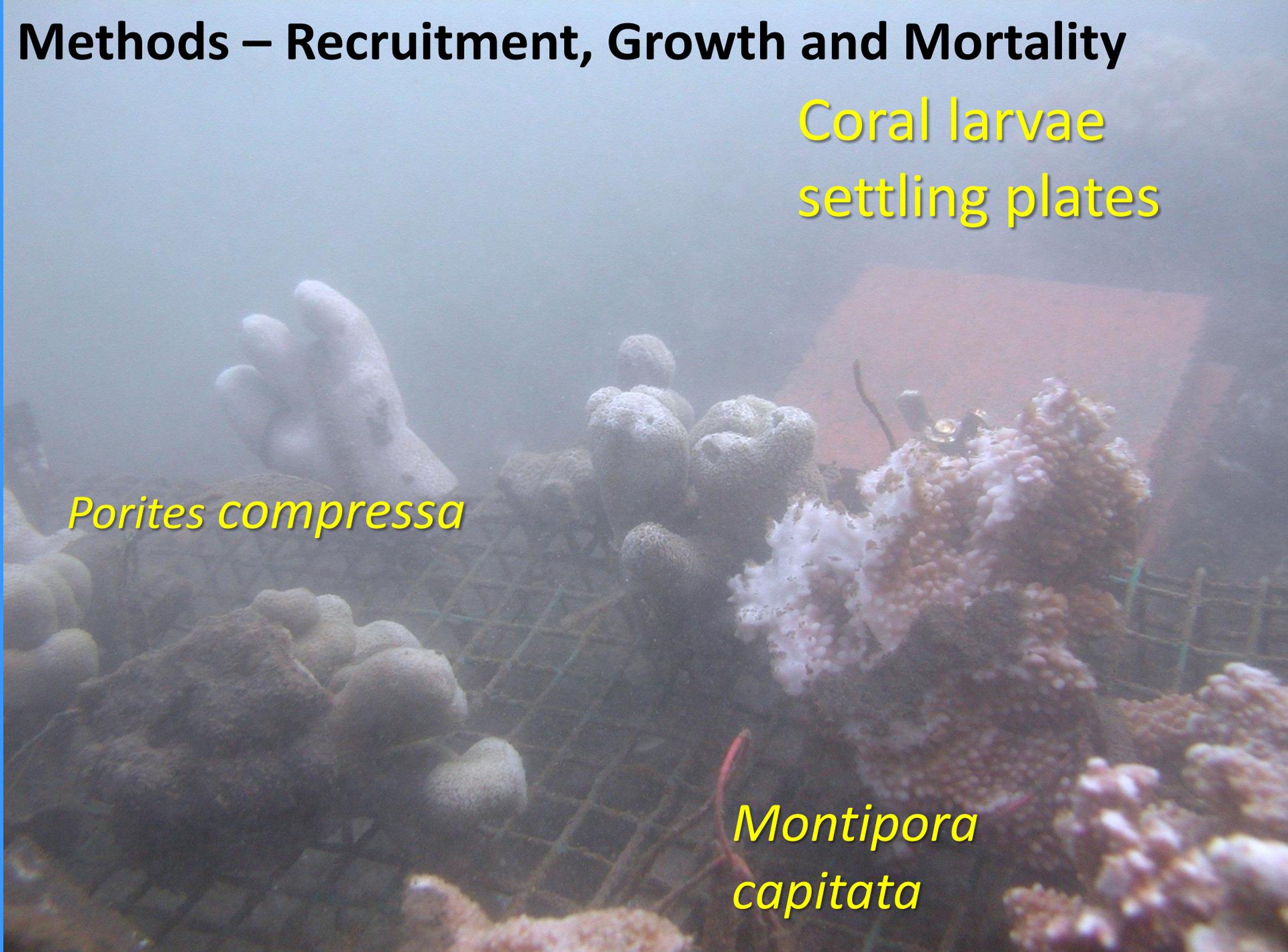


Methods – Recruitment, Growth and Mortality

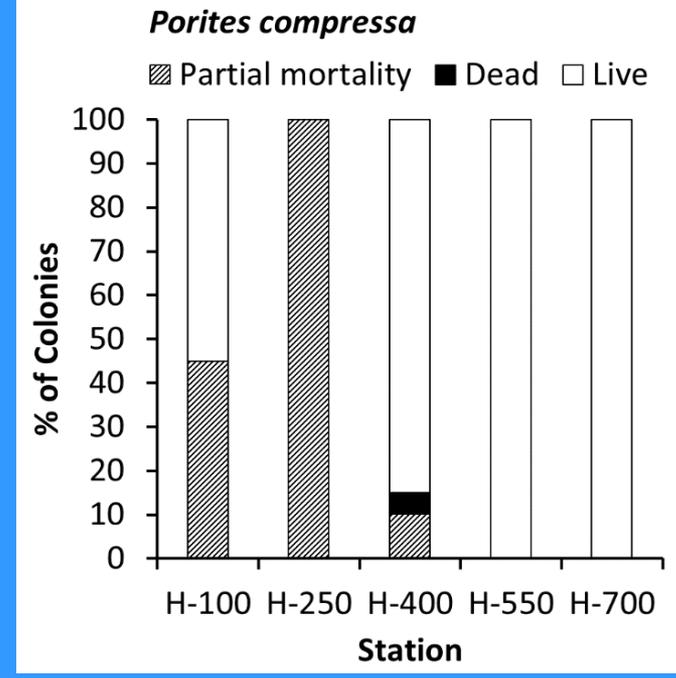
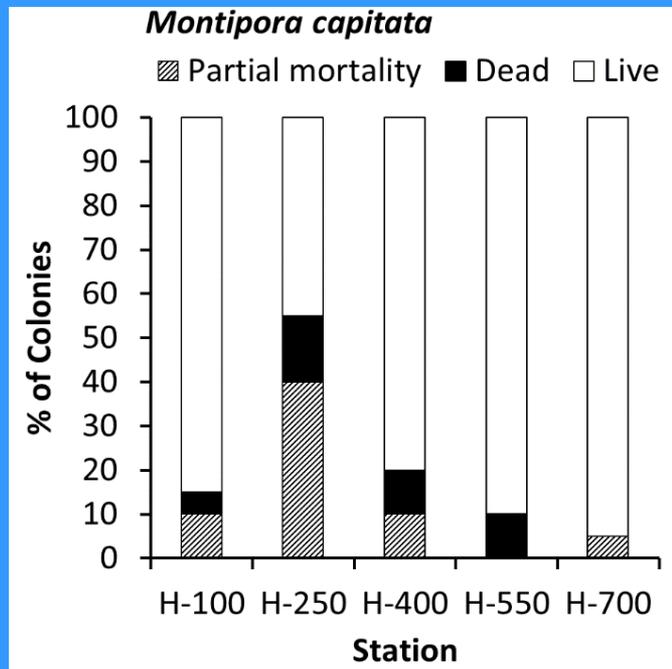
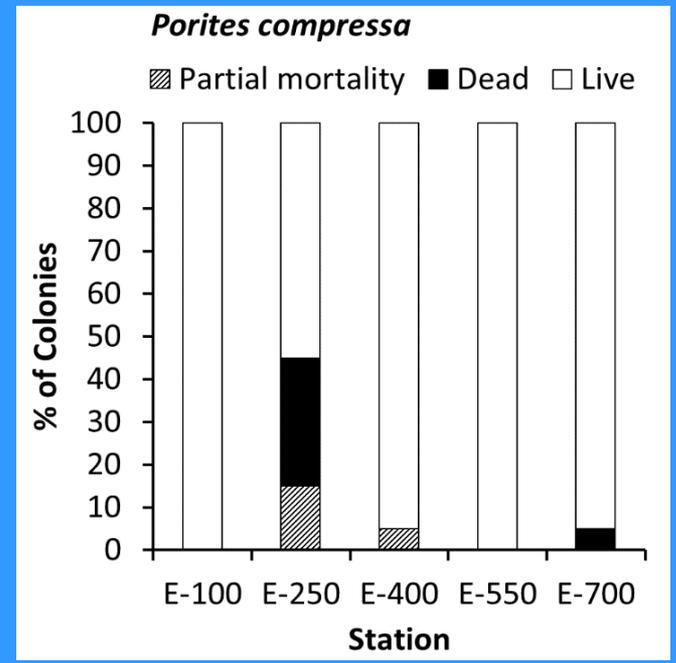
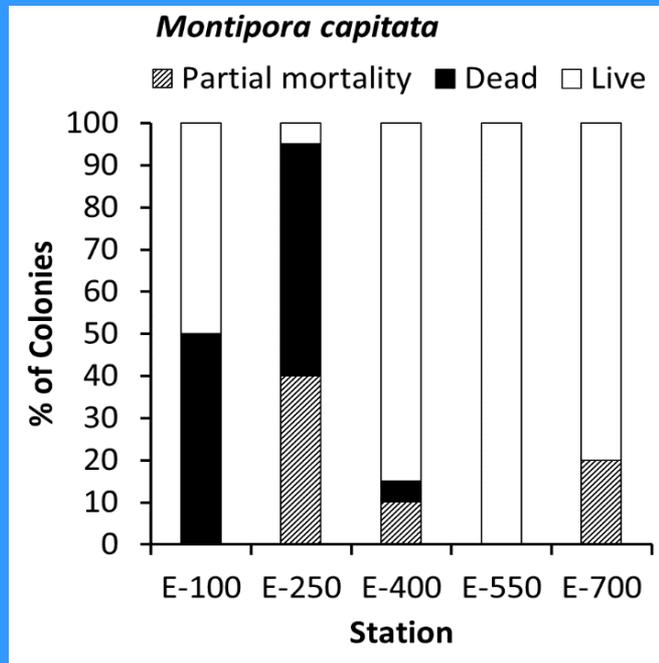
Coral larvae
settling plates

Porites compressa

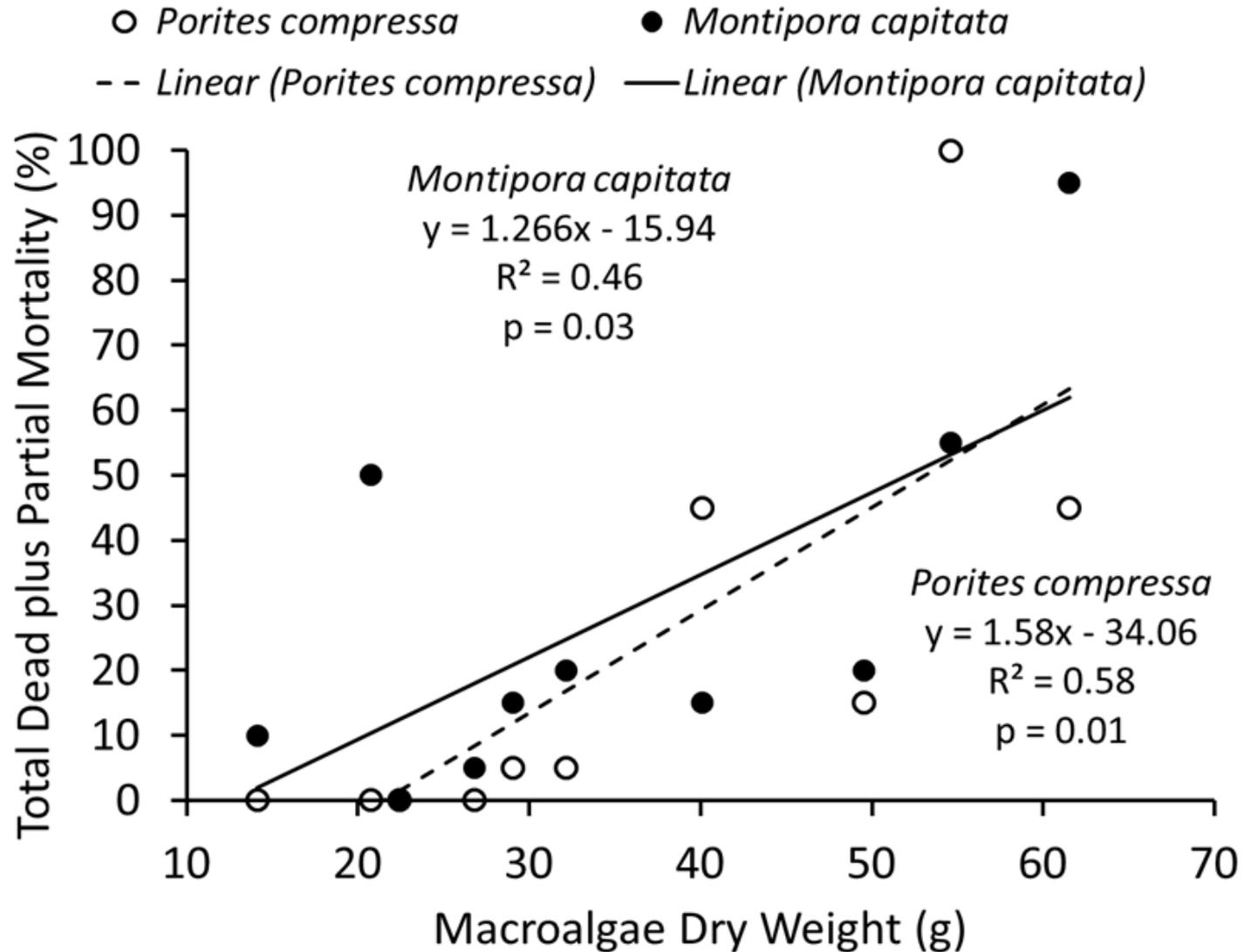
*Montipora
capitata*



Mortality

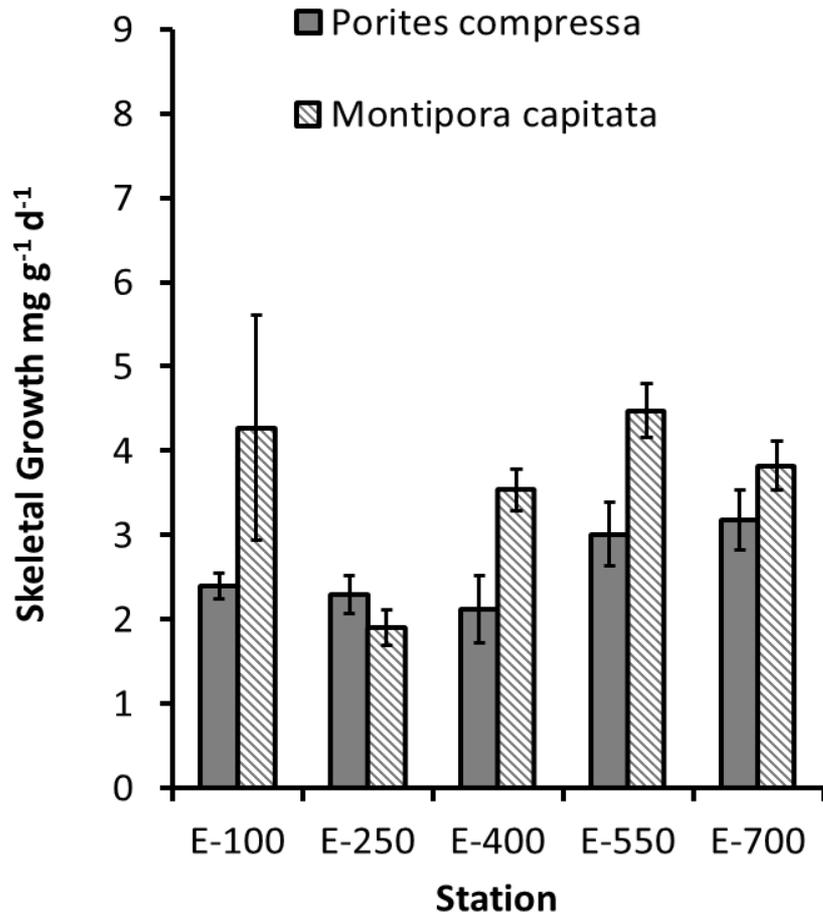


Mortality

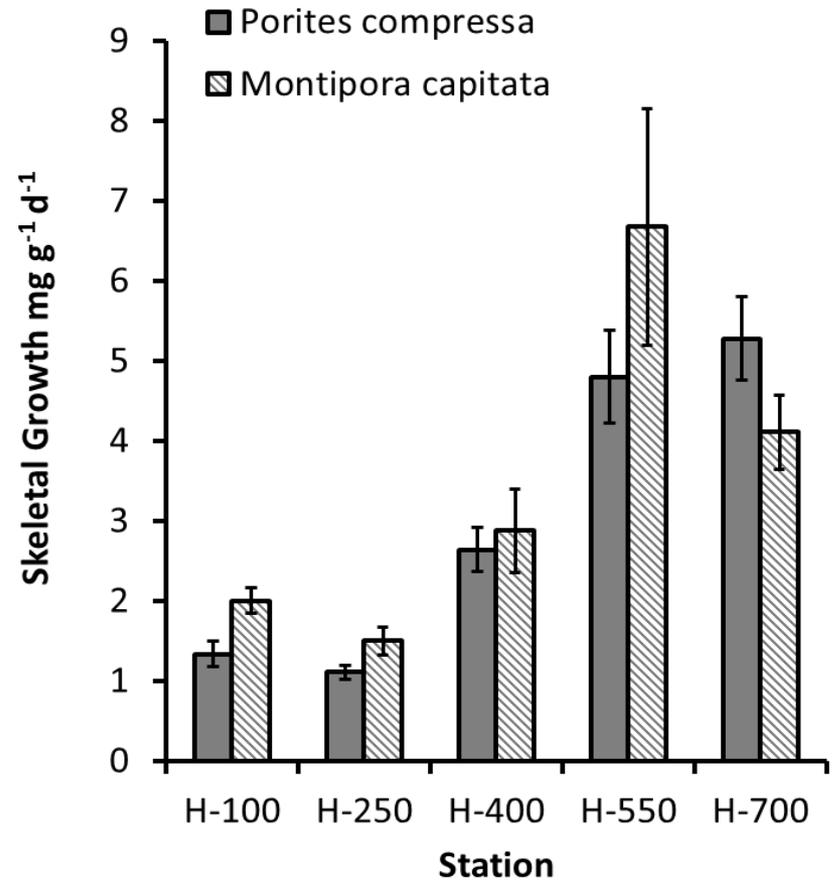


Growth

Coral Growth at Transect E (Kawela)



Coral Growth at Transect H (Kamiloloa)



Recruitment

Table: Comparison of mean coral recruitment rates (number of recruits $\text{m}^{-2} \text{ year}^{-1}$) from the main Hawaiian Islands measured on terracotta recruitment plates.

Site	Mean Recruits (recruits $\text{m}^{-2} \text{ yr}^{-1}$)	Range	Reference
Hanalei Bay, Kaua'i	7,924	403-15,386	Friedlander and Brown (2006)
Puamana, Maui	415	8-1,792	Brown (2004)
Olowalu, Maui	122	95-233	Brown (2004)
Honolua Bay, Maui	41	7-92	Brown (2004)
West Hawai'i	24	0-411	Martin and Walsh (2014)
N. Puako, Hawai'i	42	2-31	Y.Stender pers. com. (2014)
Pelekane, Hawai'i	35	6-96	Y.Stender pers. com. (2014)
Kawaihae, Hawai'i	76	0-132	Y.Stender pers. com. (2014)
Kaunaoa, Hawai'i	70	0-49	Y.Stender pers. com. (2014)
South Moloka'i	4.2	0-2	This study

*All arrays were *in situ* over summer months. 80-90% of all recruitment occurs in the summer months (Brown 2004)

Conclusions:

Corals on the Molokai reef flat:

- **Survive and grow in turbid environments where sediment is resuspended and settles out frequently if they can avoid burial by living on outcrops or vertical walls.**
- **Thin coatings of fine-grain terrestrial silts and clays effectively blocked coral recruitment.**
- **Macroalgal competition inflicted mortality and partial mortality on the corals.**
- **Therefore, recruitment, availability of suitable hard substratum and macroalgal competition rather than growth and mortality limit coral reef development on the Moloka'i reef flat.**

Acknowledgements

Fred Farrell
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Dan Lager
Claire Lager



Assessment of Coral Settlement Distribution and Environmental Condition in Pelekane Bay, Hawai'i

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¹Department of Geography, University of Hawai'i at Mānoa, Honolulu, Hawai'i

²Hawai'i Institute of Marine Biology, University of Hawai'i, Kāne'ohe, Hawai'i

Several coral reef studies have been conducted in Pelekane Bay and the larger Kawaihae area during the last few years to better understand the response of the reef community to cumulative human impacts and effectiveness of management measures, and recovery potential. Key biological and ecological processes, including coral growth, partial-mortality, benthic community structure, habitat utilization by fish recruits, and coral settlement have been examined through collaborative efforts providing insights into impacts of land-based sedimentation and environmental quality on reef communities. The assessment of coral settlement was conducted over the summer of 2014 to build upon these collaborative studies and continue monitoring efforts to describe settlement patterns in the Pelekane Bay and Kawaihae area. Settlement arrays were deployed at 37 sites along an environmental gradient established in 2010 and 2011 to replicate prior data collection and analyses. This presentation aims to discuss the outcome of the latest investigation on coral settlement in reference to other reef studies conducted in recent years, and provide updated information on the overall distribution patterns of coral settlers in Pelekane Bay.

Impacts of Sedimentation on the Coral Reef Community in Pelekane Bay, Hawai'i

Yuko Stender^{1,2}, Paul Jokiel², Ku'ulei Rodgers²

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Outline

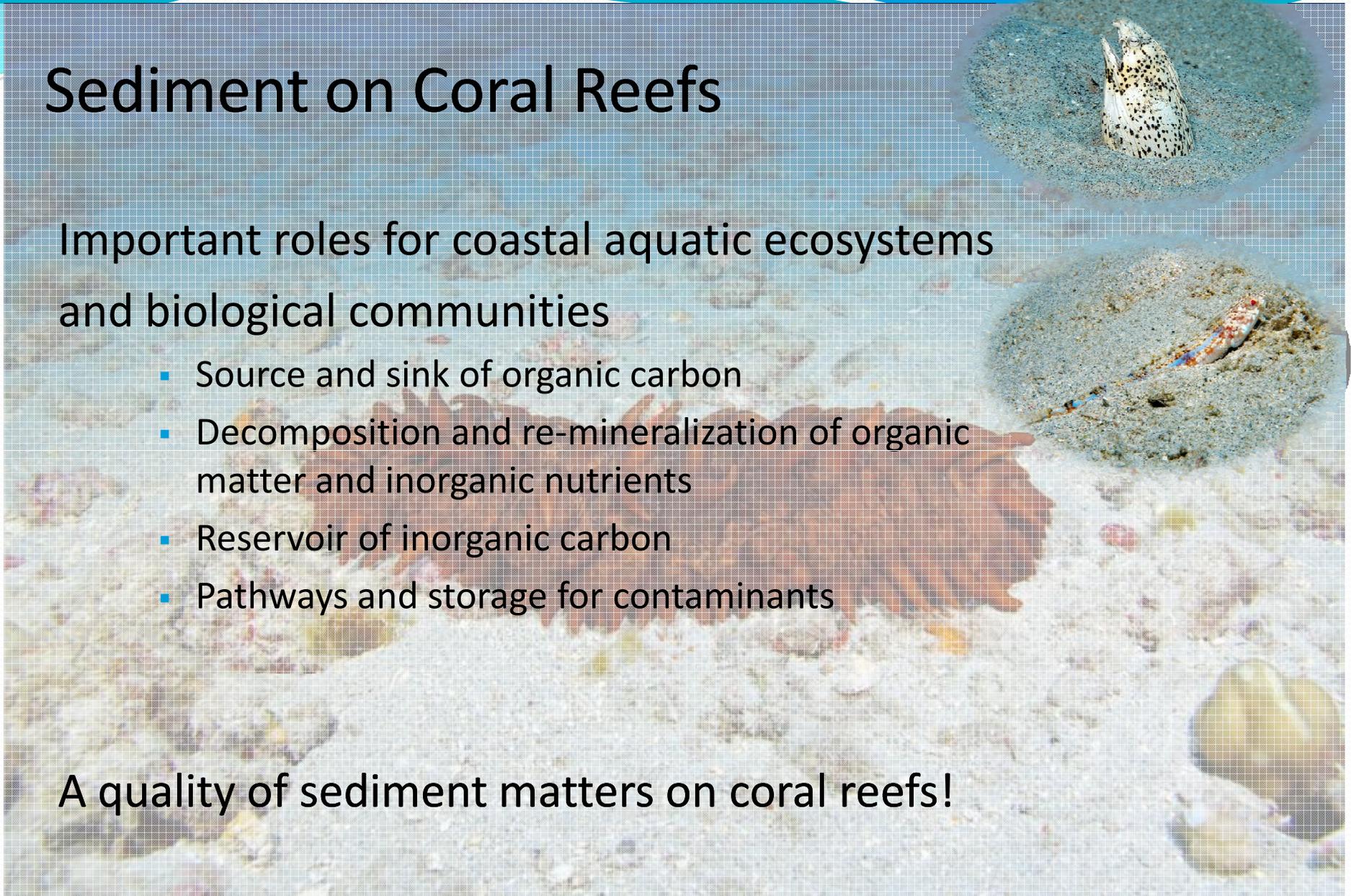
- Sediment and sedimentation process
 - Important role of sediment on coral reefs
 - Land-based sedimentation process
 - Sediment quality and distribution on reefs
 - Land-based impacts in Pelekane
- Collaborative interdisciplinary reef studies in Pelekane

Sediment on Coral Reefs

Important roles for coastal aquatic ecosystems and biological communities

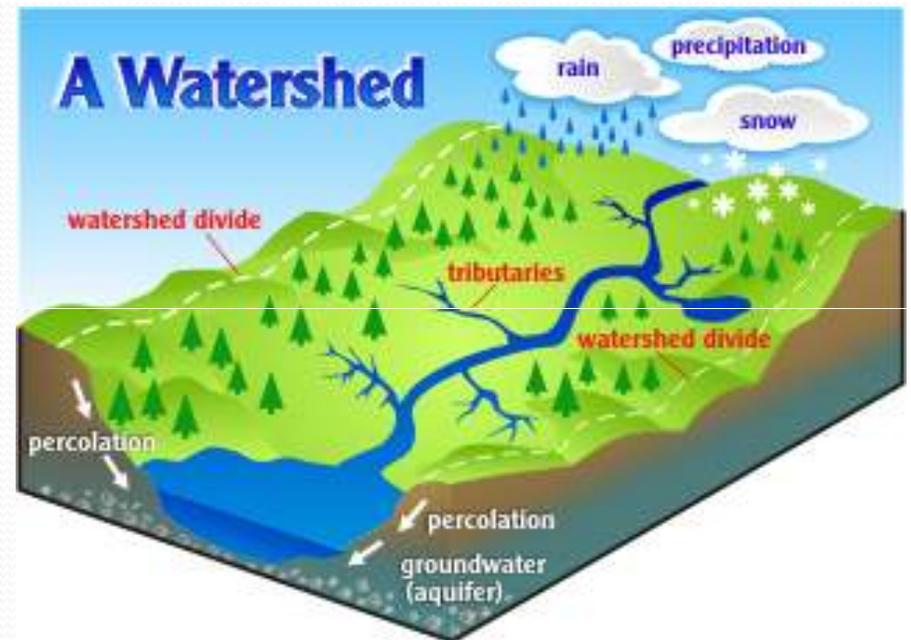
- Source and sink of organic carbon
- Decomposition and re-mineralization of organic matter and inorganic nutrients
- Reservoir of inorganic carbon
- Pathways and storage for contaminants

A quality of sediment matters on coral reefs!



Sedimentation Process

- Landscape characteristics
- Erosion
- Transport
- Storage
- Yield: reaching the outlet of drainage basin



Source: Hawai'i Association of Watershed Partnerships

Quality and Quantity of Sediment on Reefs

- Types: Carbonate-dominant vs. Terrigenous
- Grain size: Course sand vs. Silt/clay
- Sediment Yield
- Residence time :
oceanographic conditions
(waves, long-shore currents,
near-bed shear stress)
shoreline characteristics,
benthic topography



Main Hawaiian Islands:

High mountains and fringing reefs

- Landscape characteristics
 - Soil, geologic materials
 - Climate/weathering
 - Topography
 - Stream characteristics & positions
 - Vegetation
 - Land use





Impacts of historical land use



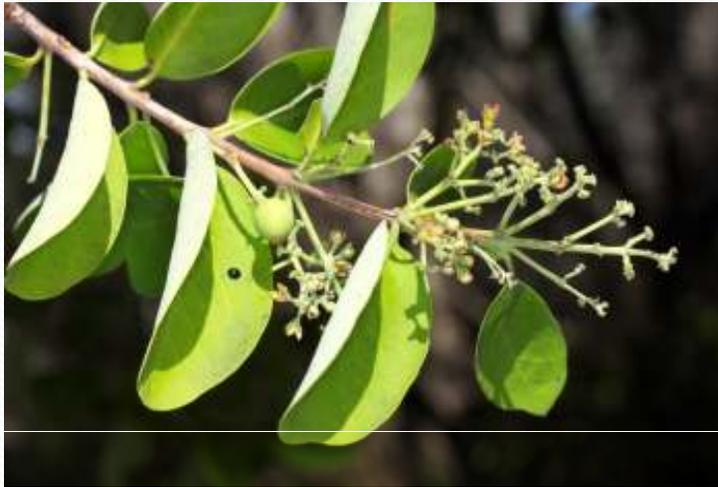
Agricultural land use, Pālā'au, South Molokai

Increasing human activity and coastal development

Effect of climate change (intensified patterns of droughts, storms, sea level rise).



Land Use History in Kawaihae and Pelekane

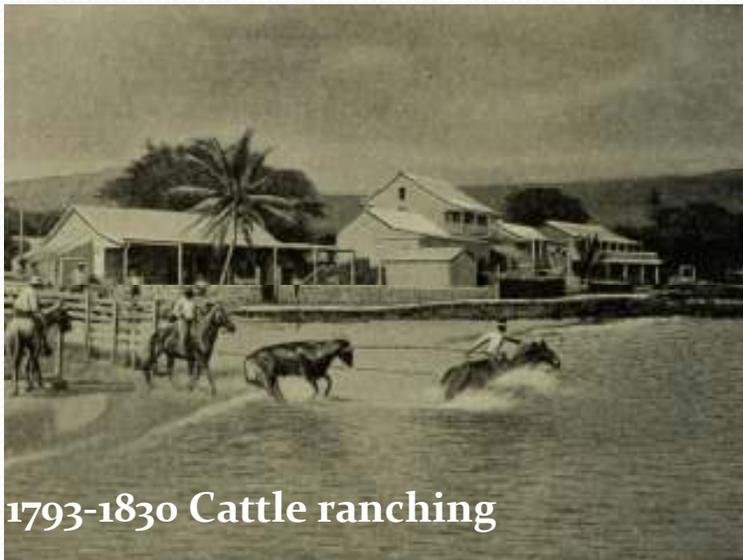


1790-1830 Sandalwood trade



Looking northwest towards the summit of Kohala volcano, Big Island, Hawaii. Photo: Chris Rowan, 2012.

<http://all-geo.org/highlyallochthonous/2012/03/scenic-saturday-from-desert-to-verdant-grassland-in-10-miles-and-1000-m/>

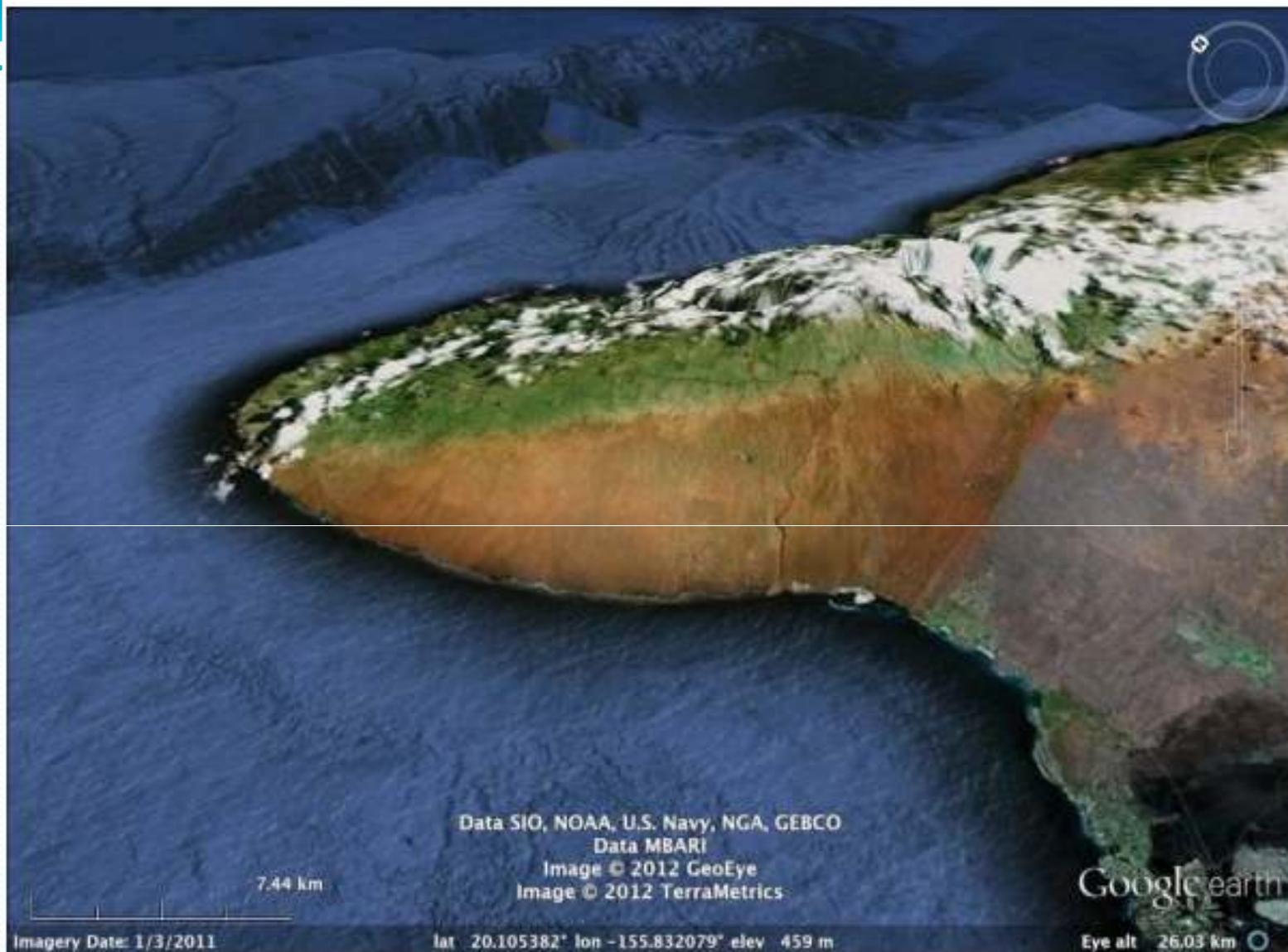


1793-1830 Cattle ranching



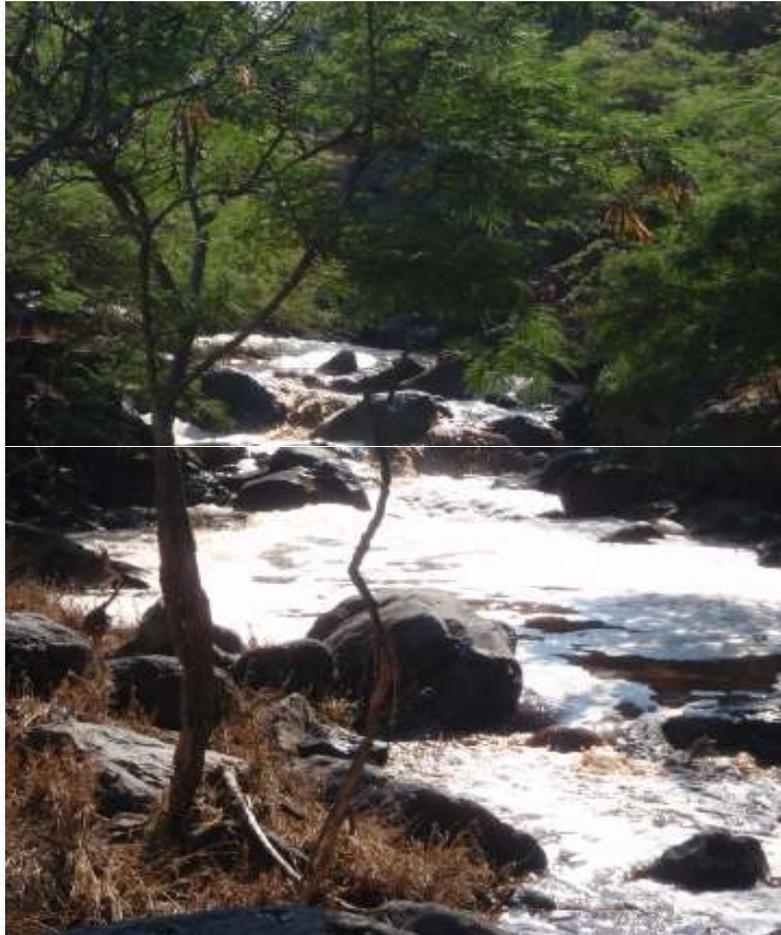
Kawaihae Soils, Hawaii

Hue et al.



Kohala viewed from the southwest in Google Earth. Note the sharp change in colour/vegetation.

<http://all-geo.org/highlyallochthonous/2012/03/scenic-saturday-from-desert-to-verdant-grassland-in-10-miles-and-1000-m/>



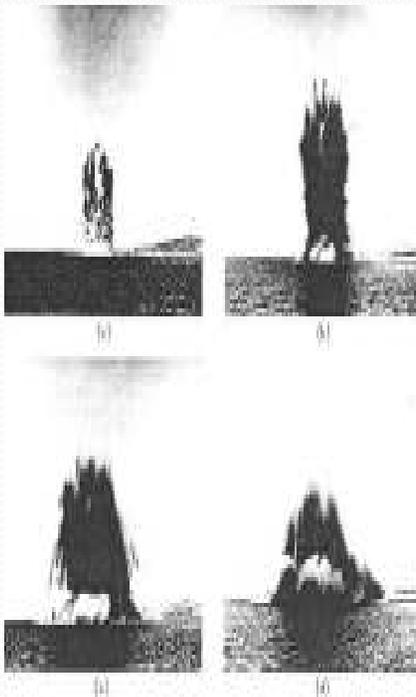
Sediment transport and discharge to the coast
Photo: Pu'ukoholā NPS

18 Nov 2010



1959-60 Kawaihae Harbor dredging
1969-70 Explosive testing (Project Tugboat)

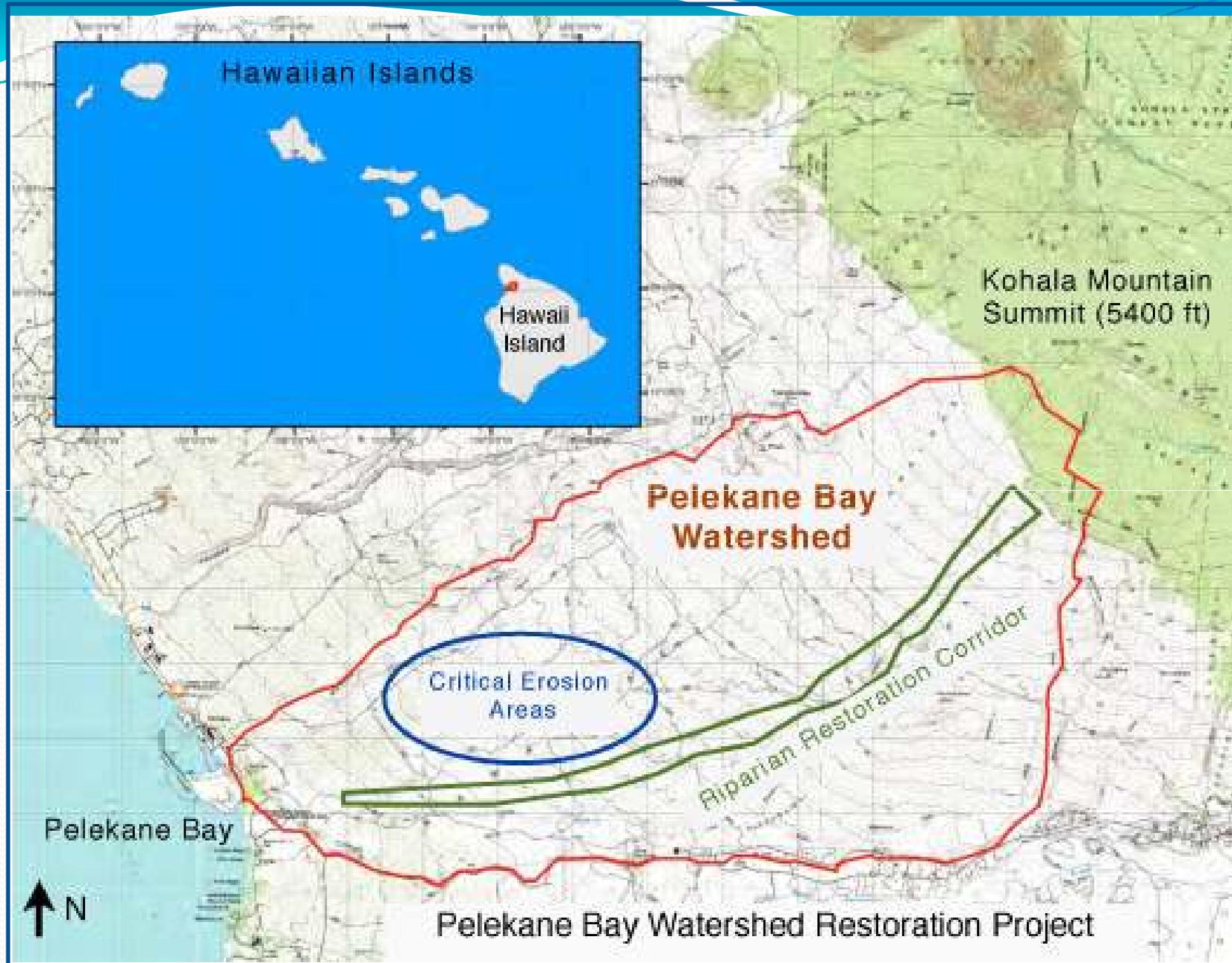
Limited water circulation



Watershed improvement

- Pelekane listed as an impaired body of water by EPA
- One of the state's two priority watersheds for restoration
- Terrestrial and marine investigations
- Restoration efforts by the Kohala Watershed Partnership ~2010 and ongoing





Kohala Watershed Partnership (2011)

Impacts of Land-based Sedimentation on Corals and Reef Communities

Increased loading
Reduced light
Associated pollutants
High levels of organic matter

- Direct:
 - Smothering
 - Blocking larval settlement
 - Habitat characteristics
- Indirect:
 - Reduced photosynthesis
 - High energetic costs and physiological exhaustion
 - Reduced immunity
 - Microbial activity
 - Changes in reef communities



Historical marine projects

- 1969-70 Kanayama and Kawamoto (1970)
- 1976 Chaney et al. (1977)
- 1994-95 Jokiel et al. (1999)
- 1996 Tissot (1998)
- 2000-12 HIMB-CRAMP (Kawaihae)
- 2002 HIMB-CRAMP (Pelekane)
- 2004 USGS (2007), habitat mapping
- 2005 Beets et al. (2010), fish
- 2006 Hoover and Gold (2006)
- 2010-11 **DeMartini et al. (2013), USGS (2013)**
TNC (2011)
- 2011 **HIMB-CRAMP, coral settlement**
- 2012 **Stender et al. (2014)**
- 2014 **HIMB-CRAMP, coral settlement**



Overall Aims

1. To understand the response of the reef community to sedimentation impacts
2. To understand the potential of reef recovery
3. To evaluate habitat quality in relation to reef recovery
4. To evaluate the potential threat that existing mud deposits pose to adjacent, relatively pristine coral reefs



Terrigenous sediment impact on coral recruitment and growth affects the use of coral habitat by recruit parrotfishes (F. Scaridae)

E. DeMartini · E. Jokiel · J. Beets · Y. Stender · C. Storlazzi · D. Minton · E. Conklin

Received: 5 April 2012 / Revised: 25 February 2013 / Accepted: 26 February 2013
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Abstract Some major anthropogenic stressors have impacts that occur at infrequent, unpredictable intervals; their effects are difficult to evaluate in a timely manner unless space is substituted for time. In this paper we substitute space for time along an environmental gradient that allows a predicted temporal response to habitat restoration. We herein describe a 3-year study that combined field experiments and descriptive

Electronic supplementary material The online version of this article (doi:10.1007/s11852-013-0247-2) contains supplementary material, which is available to authorized users.

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Published online: 30 April 2013



Integrated study of sediment impacts on coral reefs

- Sediment quality and accumulation
- Habitat characterization
- Corals
- Fish

surveys of a fringing reef at Pelekane Bay, west Hawaii, along a sedimentation gradient from an intermittent stream that episodically discharges from the Kohala Watershed. This degraded watershed is now being restored by gully excision, habitat engineering, and replanting of native flora. Sediment traps, arrays of settling plates, marked branches of endemic finger coral *Favites compressa*, together with surveys of benthic composition, densities of recruits of economically important parrotfishes, and the relative use of corals by fish recruits, were evaluated during the summers of 2010–2012. As expected, sediment accumulation rate decreased while all coral metrics and the densities, use, and preference of corals by recruit fishes generally increased with distance from the point of sediment discharge. Proportionate abundances of recruit through large adult-sized parrotfishes, overlaid on distributions (mapped by separate study) of sediment impact, allowed us to estimate, as an example, the amount and value of parrotfish resources that are being unrealized because of sediment impacts on recruit parrotfish. Our Pelekane Bay case study thus illustrates how “space-for-time” substitution can be efficiently applied in an evaluation of potential watershed reclamation of reef resources—at a time considerably prior to likely temporal responses of the reef and its resources to watershed restoration.

Keywords Watershed reclamation · Reef sedimentation · *Favites compressa* · *Chlorurus spilatus (parvidens)* · *Scarus pritticus* · Juvenile nursery habitat · Ridge-to-reef · Space-for-time substitution

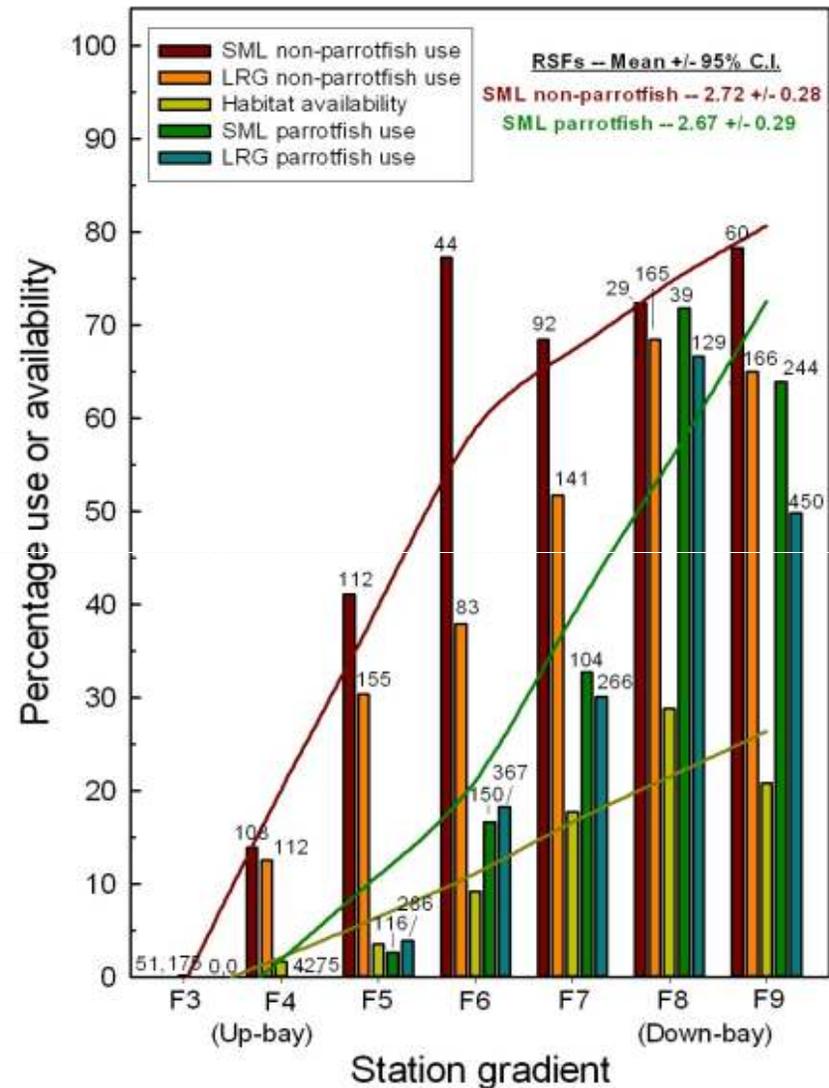
Introduction

Anthropogenic impacts that bridge the land and nearshore marine waters are now recognized among the major stressors of tropical coastal coral reef ecosystems in human-

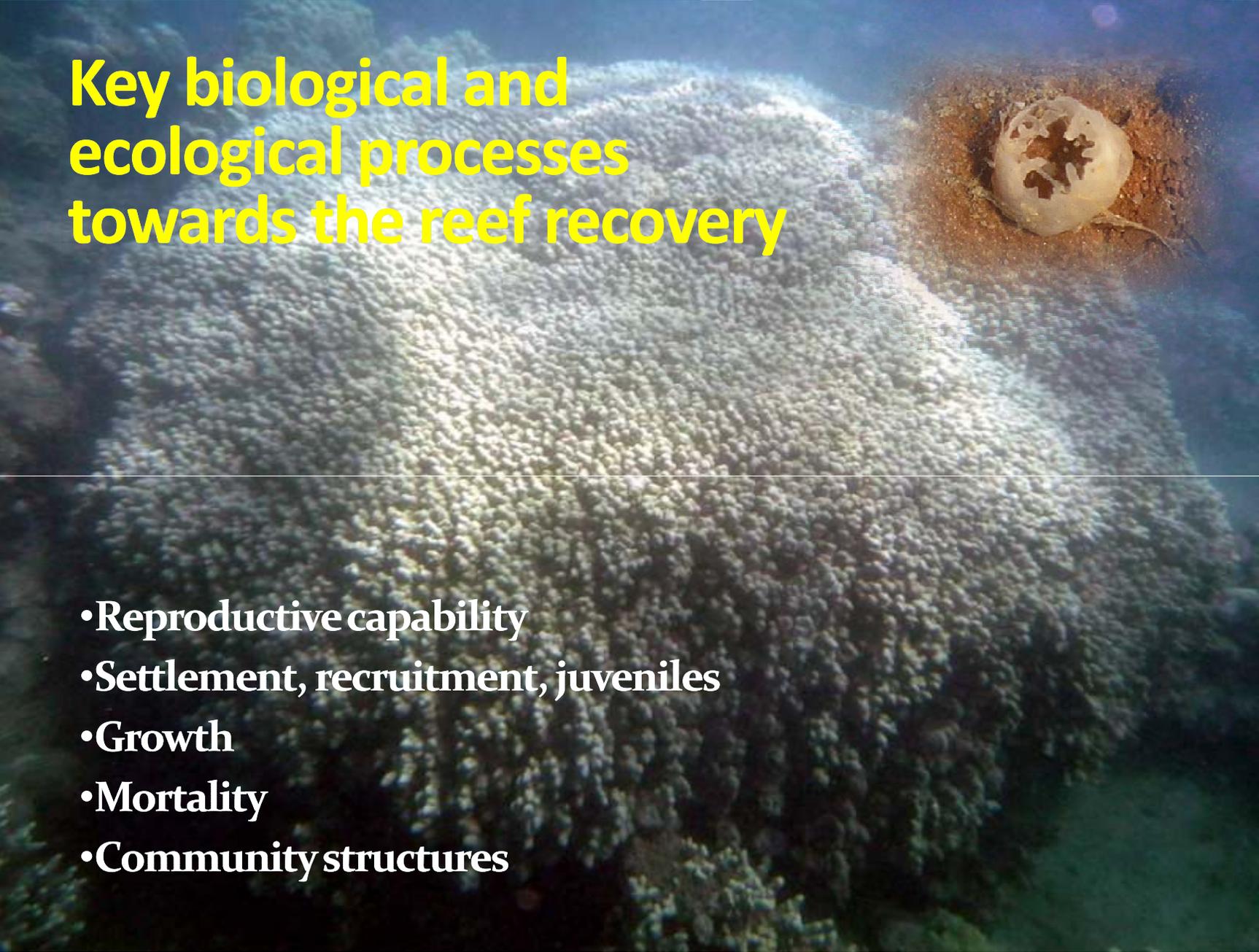
Impact of Sedimentation: Habitat availability and use by reef fish recruits



Recruits of Parrotfish

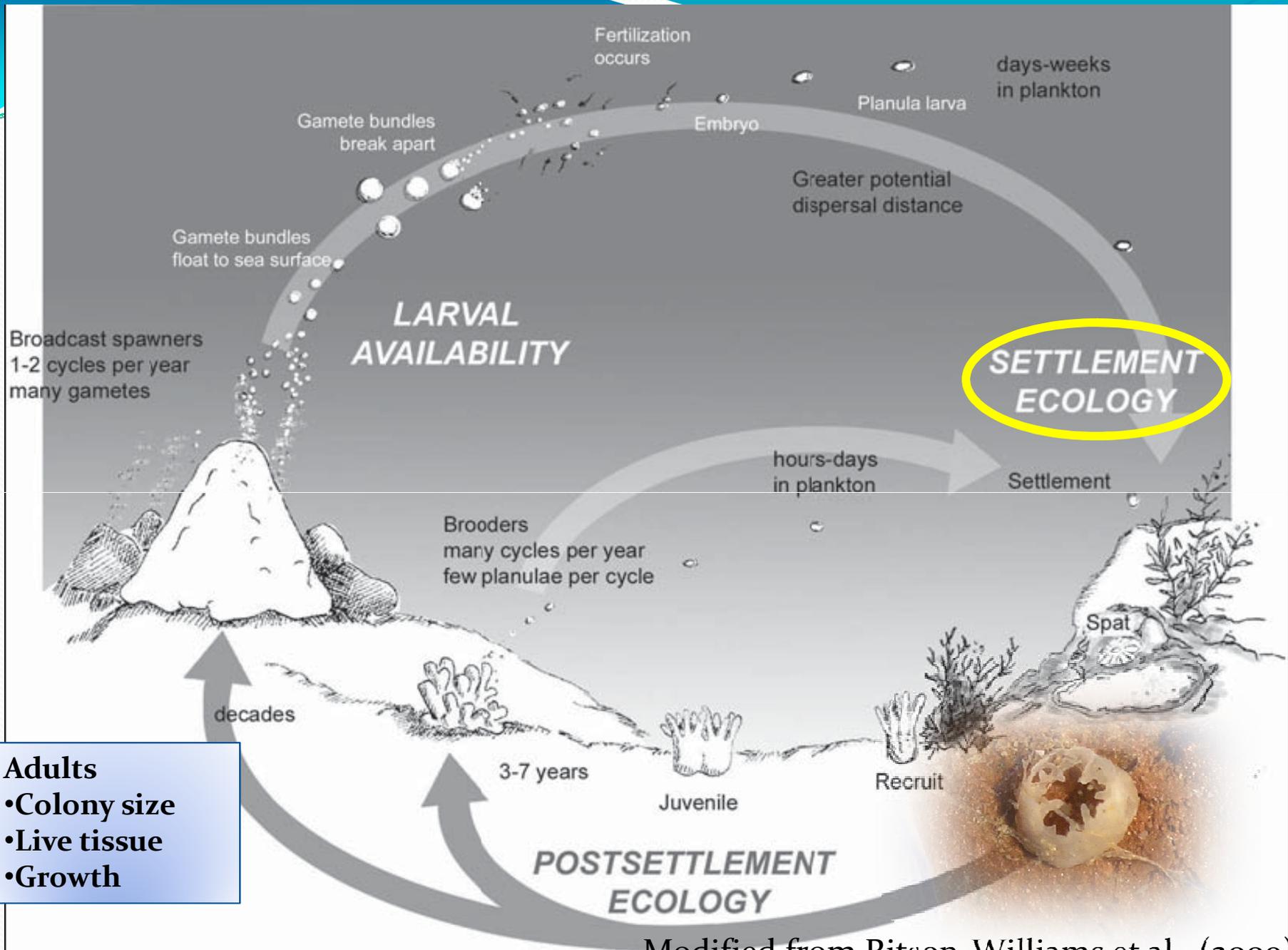


DeMartini E, P. Jokiel, J. Beets, Y. Stender, D. Minton, E. Conklin, C. Storlazzi (2013). Terrigenous sediment impact on coral recruitment and growth affects the use of coral habitat by recruit parrotfishes (F. Scaridae). J Coastal Cons 17:417-429

The image is a composite of two underwater photographs. The top half shows a wide view of a coral reef with a prominent white, bleached area. The bottom half is a close-up of a single coral polyp, which is a small, cylindrical organism with a central opening and several smaller openings around it, embedded in a porous, brownish substrate.

Key biological and ecological processes towards the reef recovery

- Reproductive capability
- Settlement, recruitment, juveniles
- Growth
- Mortality
- Community structures



Modified from Ritson-Williams et al. (2009).

Coral Reproduction

Broadcast Spawners: external fertilization, common, seasonal



Brooders: internal fertilization, less common, year-around

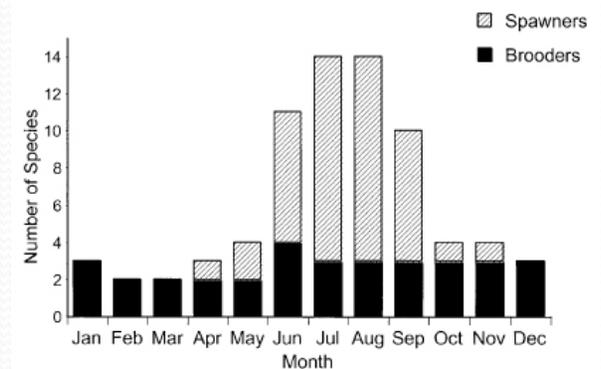
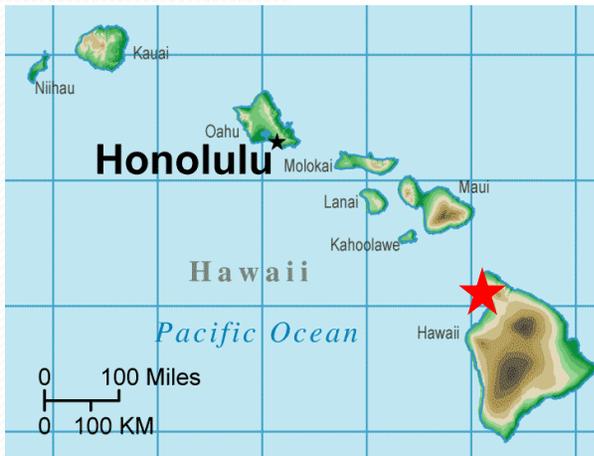
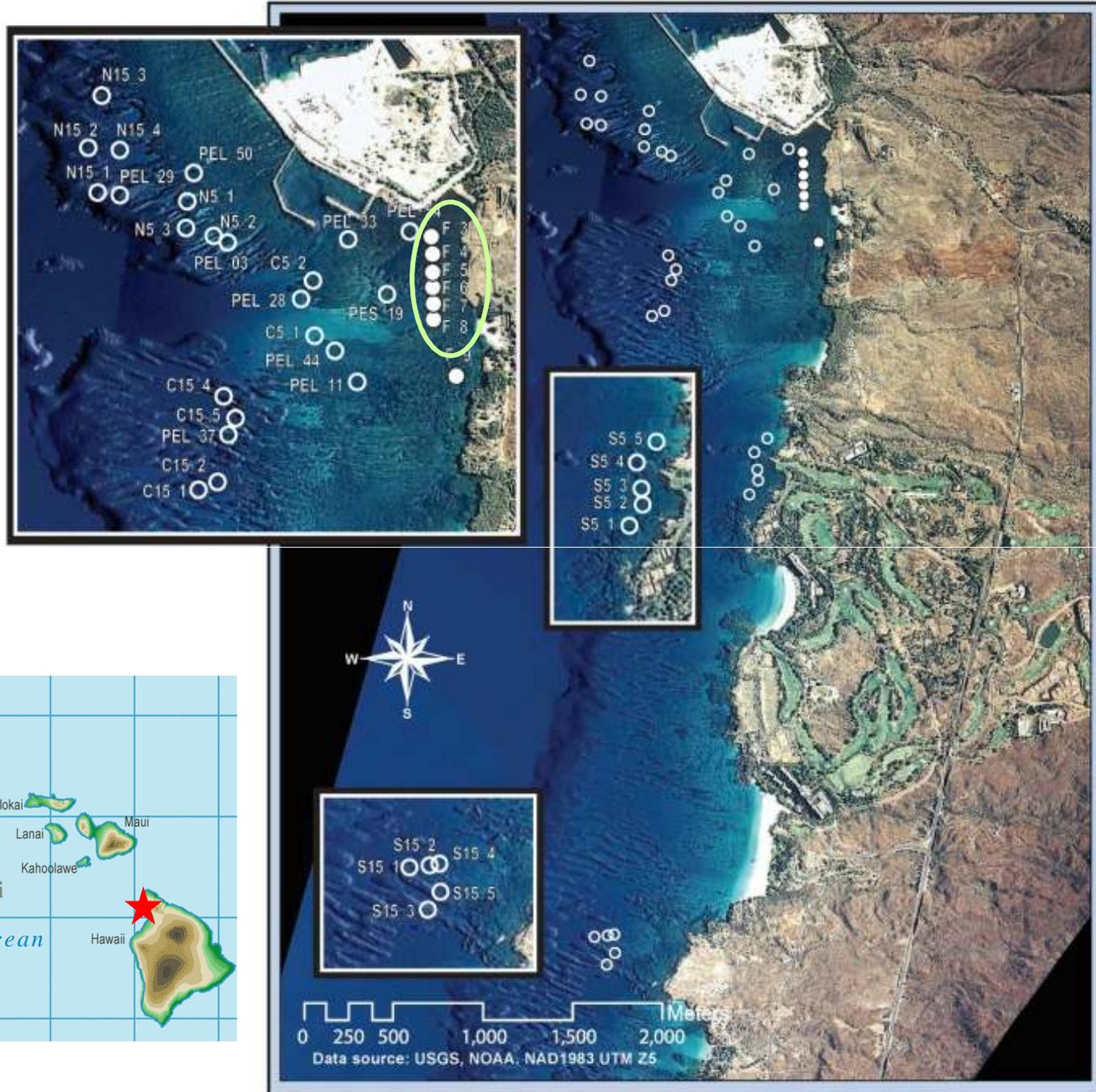
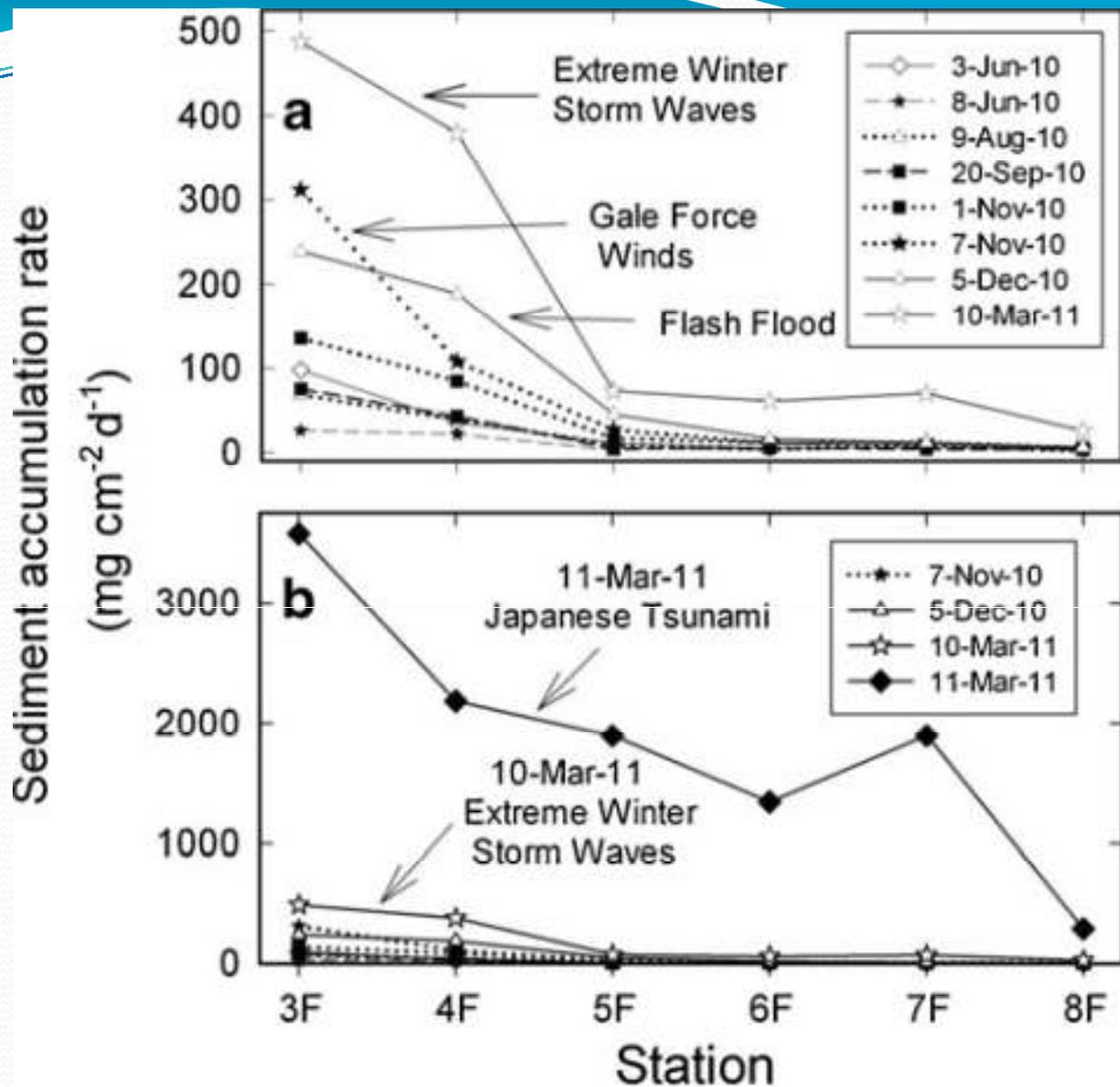


FIGURE 1. Known number of scleractinian coral species planulating and spawning each month in Hawaiian waters.

Kolinski and Cox (2003)

Study sites





DeMartini E, P. Jokiel, J. Beets, Y. Stender, D. Minton, E. Conklin, C. Storlazzi (2013). Terrigenous sediment impact on coral recruitment and growth affects the use of coral habitat by recruit parrotfishes (*F. Scaridae*). *J Coastal Cons* 17:417-429

January 2011 Storm Waves

Station F4, January 21, 2011



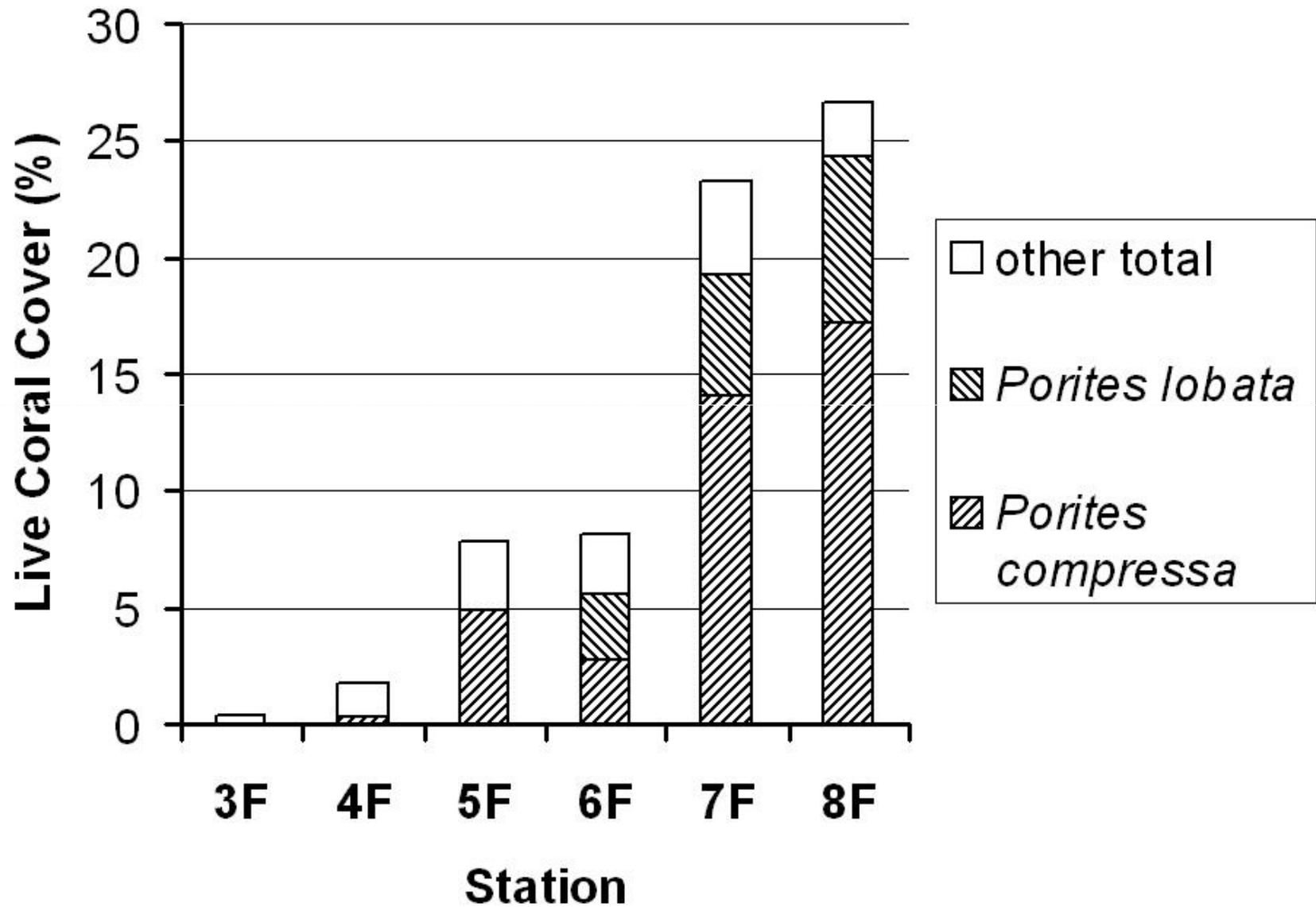
Station F8

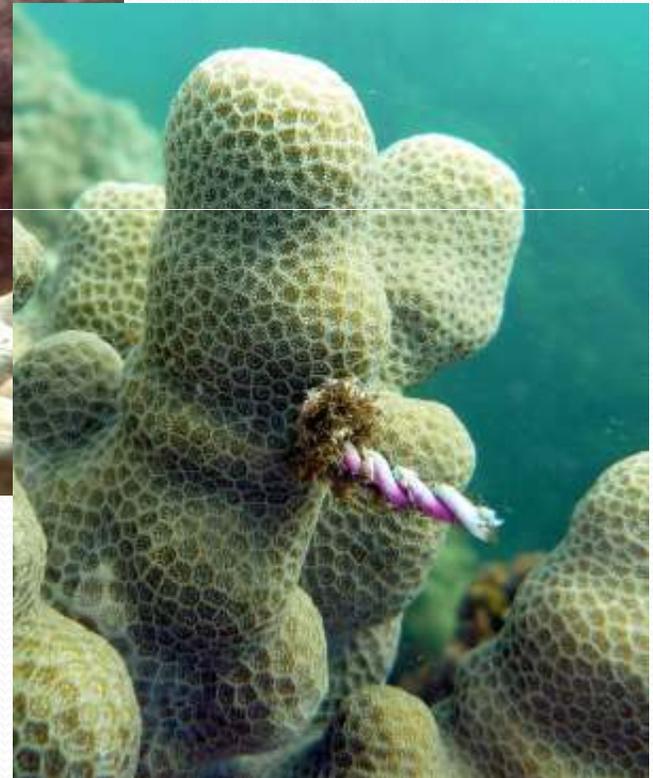


Tsunami surge headed up-river
(March 11, 2011)

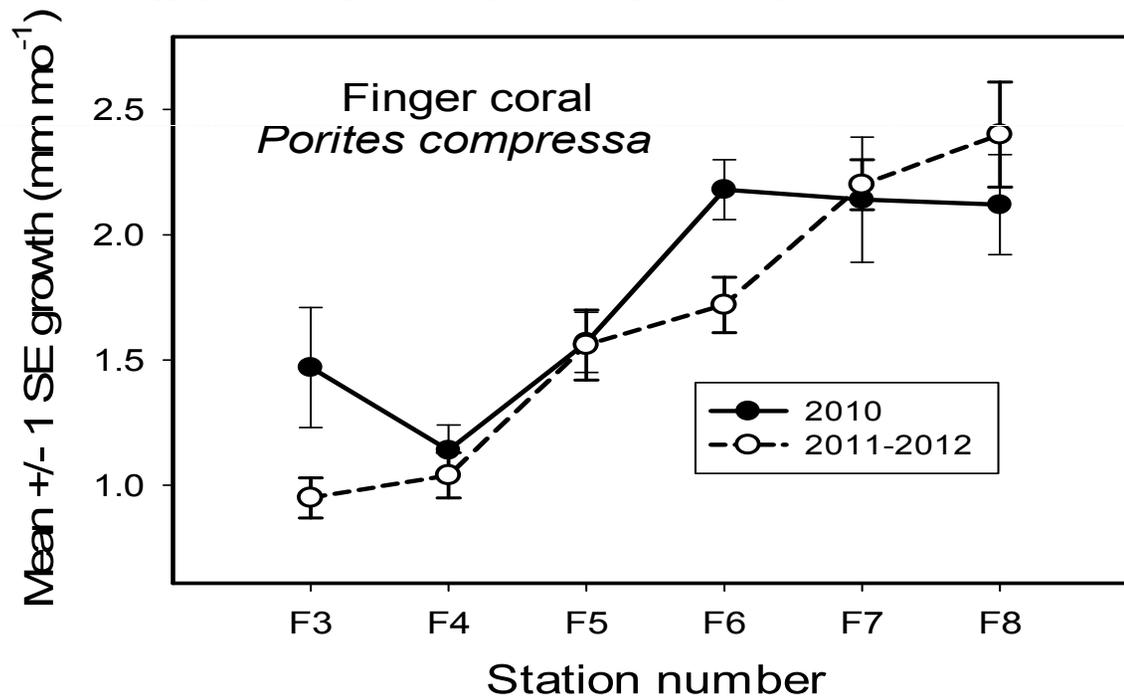
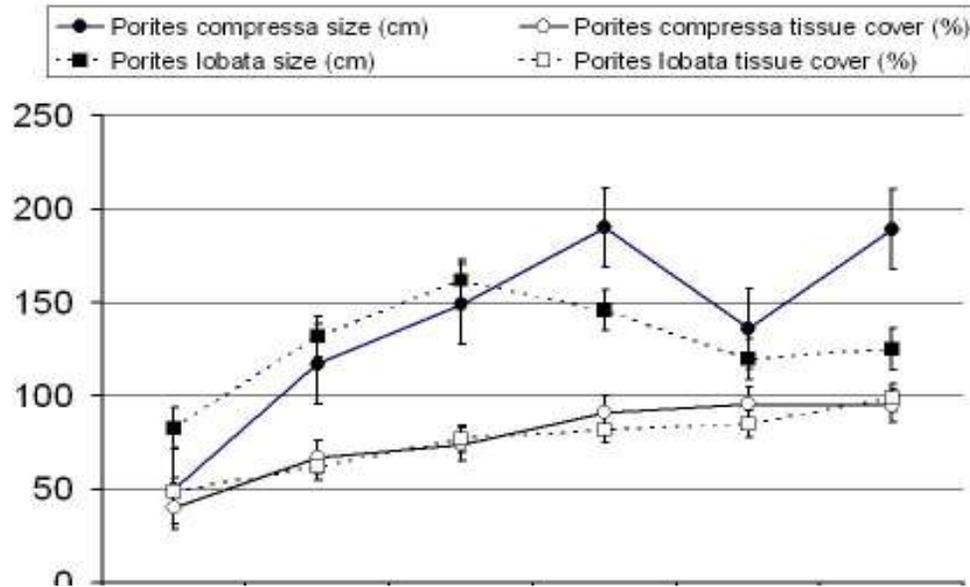


Coral cover, 2010

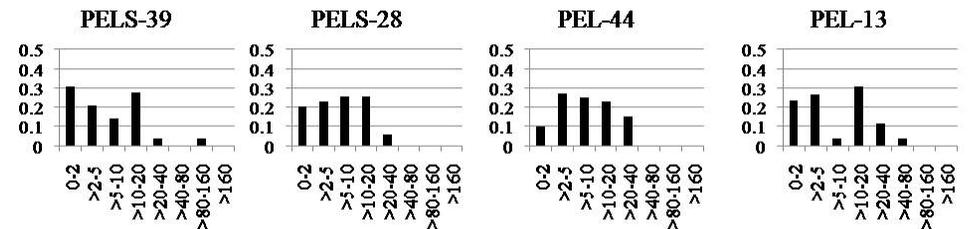
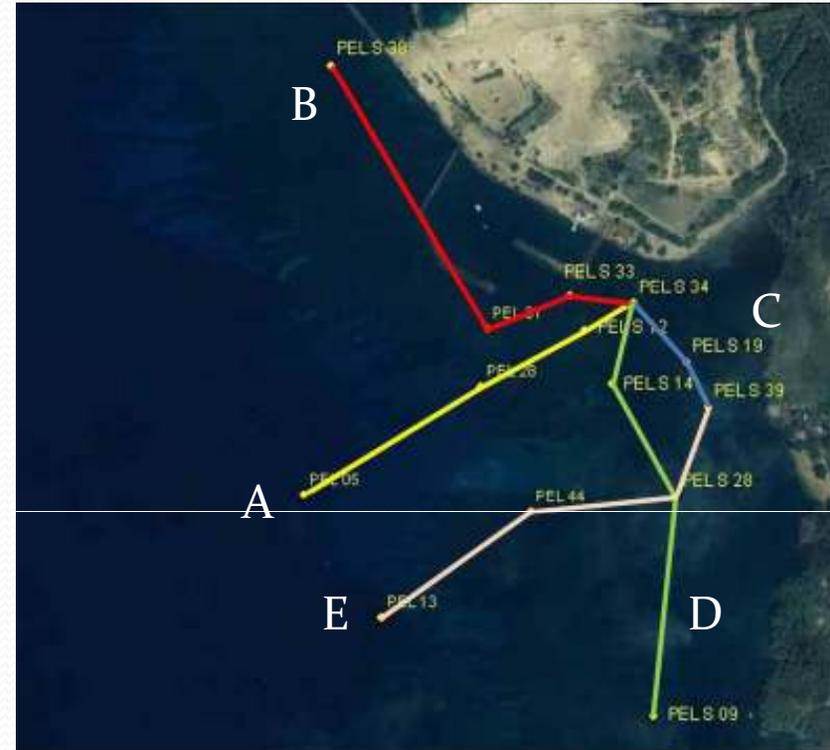
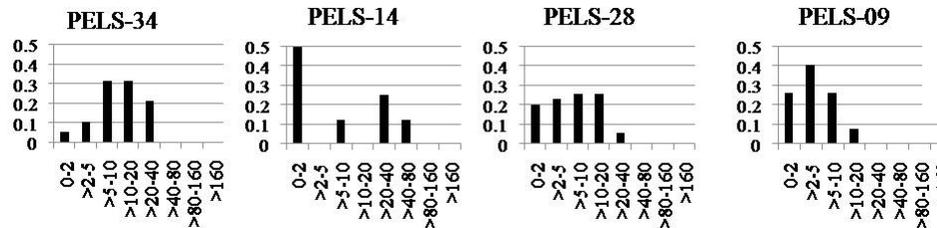
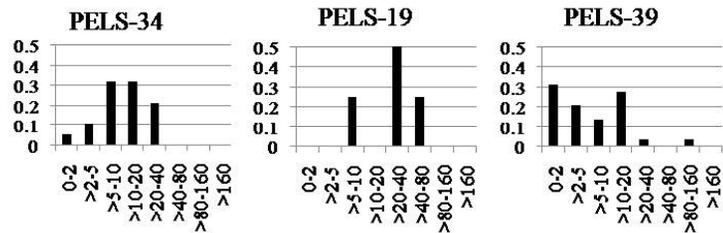
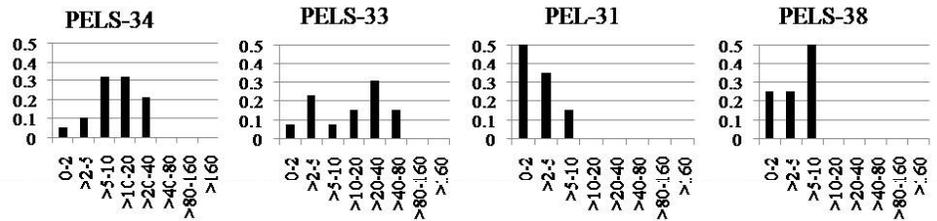
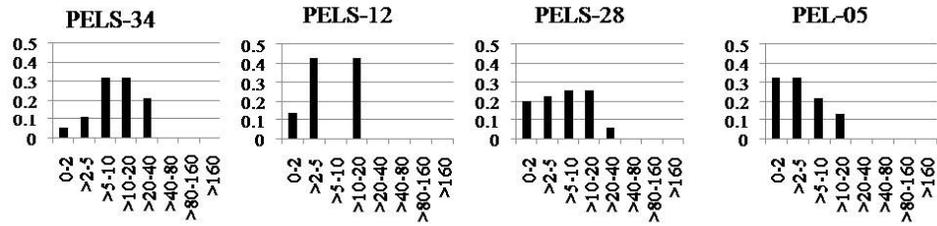




**Study1.
Coral Growth, Colony size, and Live
tissue**



Pattern of colony size

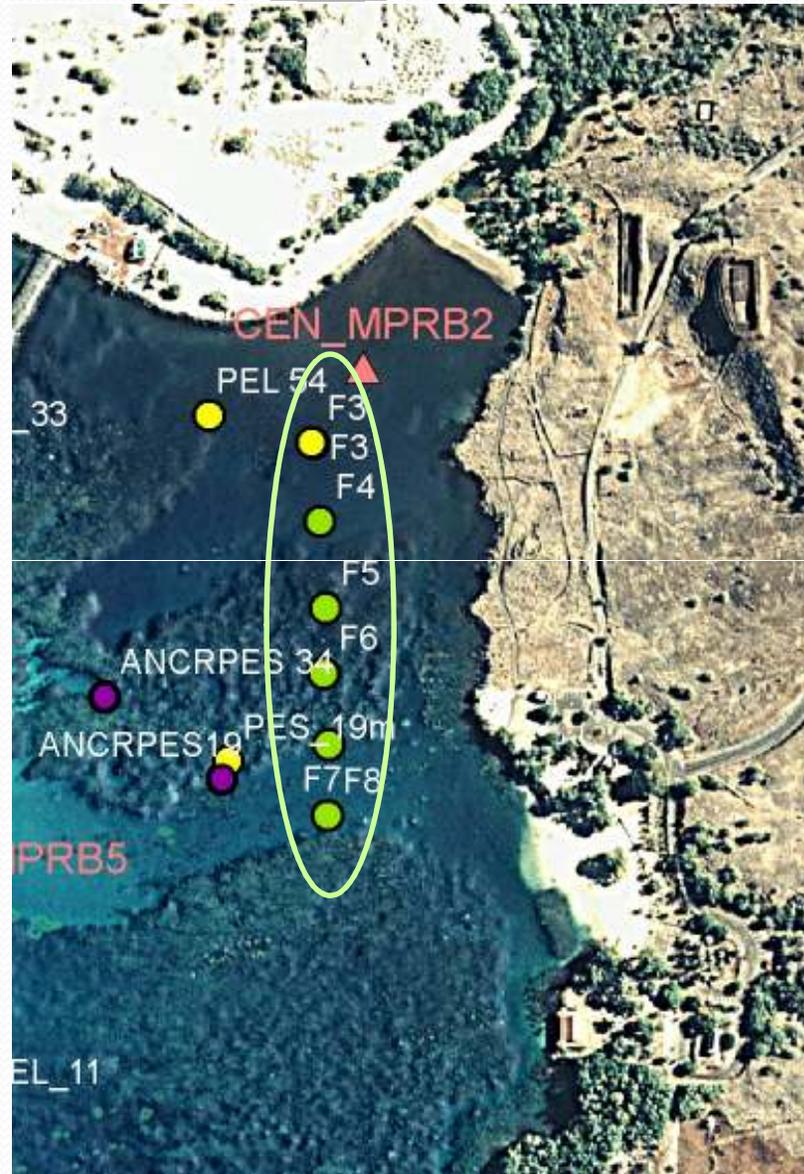


Study 2. Coral settlement, 2010

4 *Montipora*



1 *Porites*

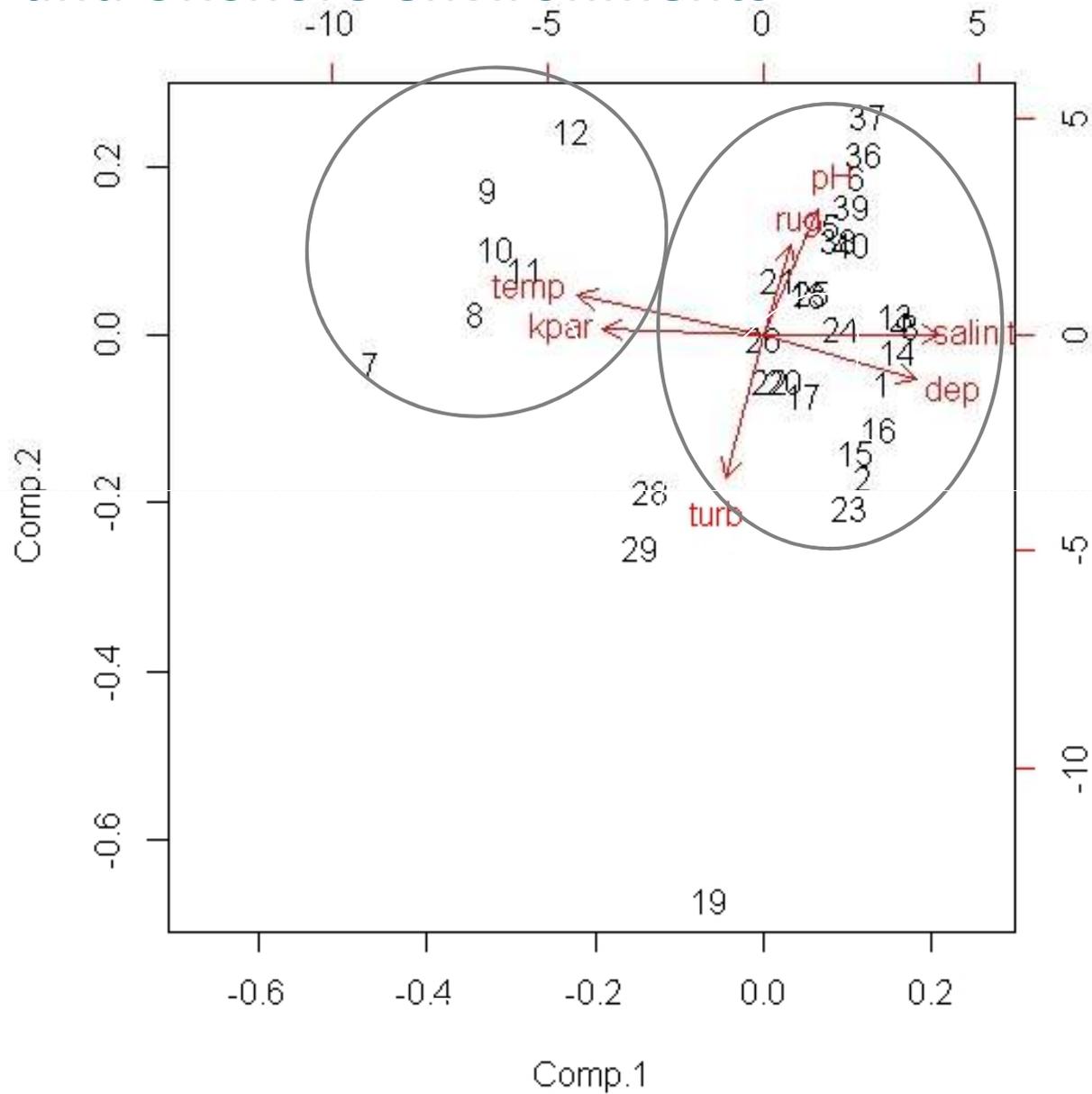


Study 3. Coral settlement, 2011

- Increased samples of settlement tile sets at 38 sites:
 - USGS oceanographic instrument deployment locations
 - TNC biological survey locations
- Relative water quality measurement: light, temperature, salinity, pH, turbidity
- Habitat: rugosity, depth

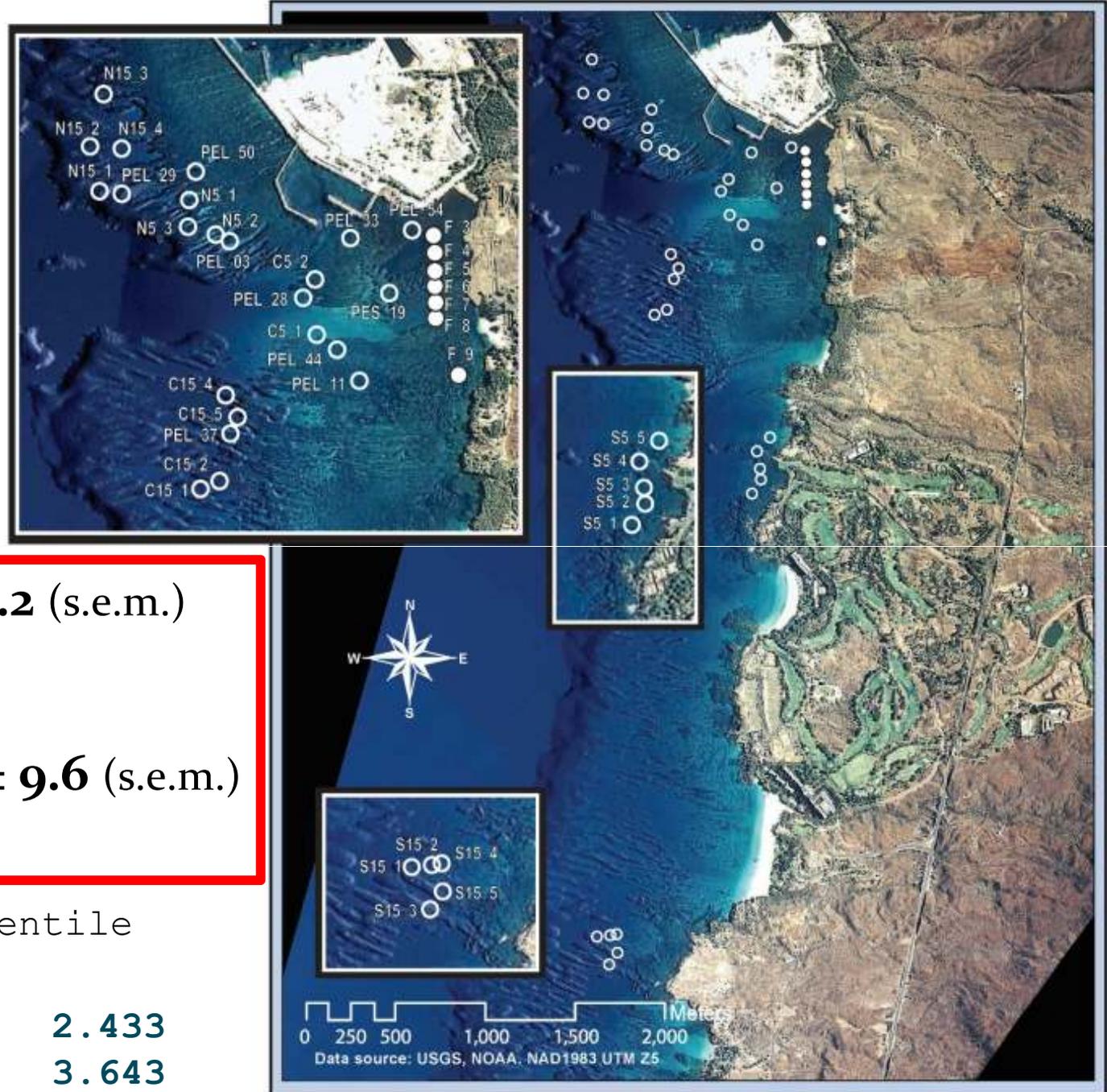


Inshore and offshore environments



2011

Coral Settlement



Inshore: 7.9 ± 2.2 (s.e.m.)
 $\text{m}^2 \cdot 90 \text{ days}^{-1}$

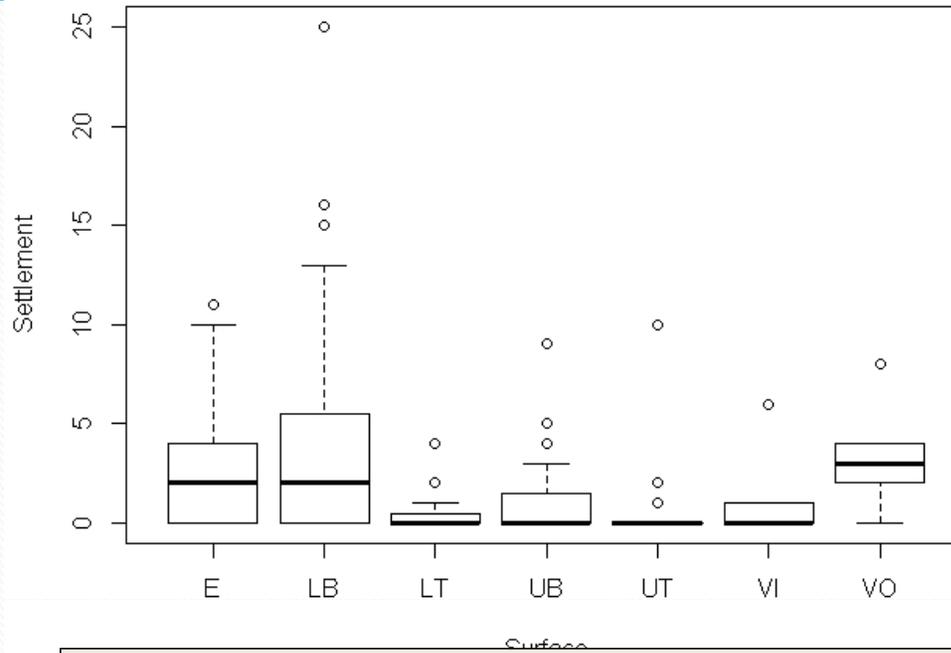
Offshore: 43.7 ± 9.6 (s.e.m.)
 $\text{m}^2 \cdot 90 \text{ days}^{-1}$

Bootstrap percentile
95% CI

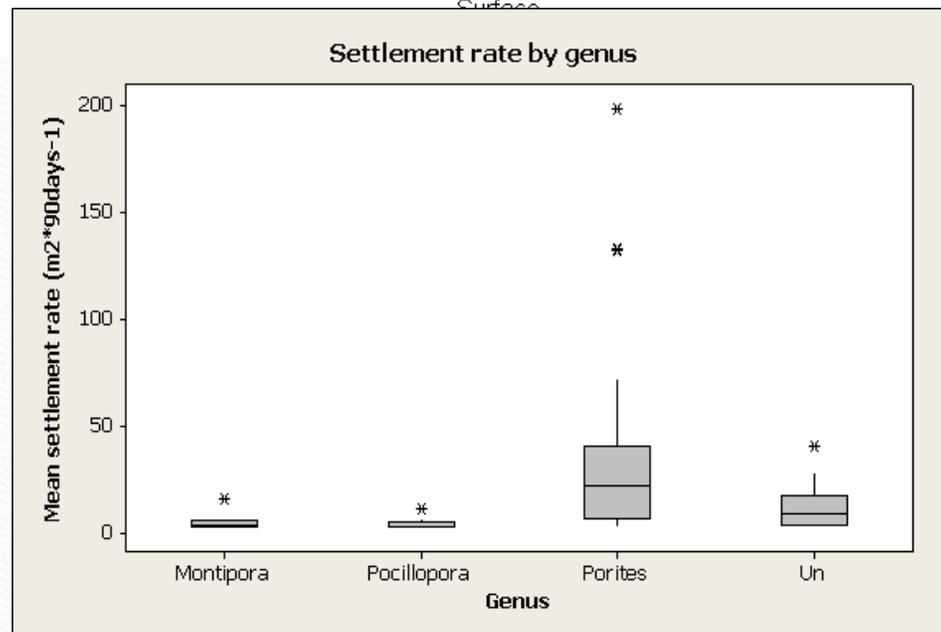
Inshore 1.244, 2.433

Offshore 2.499, 3.643

Settlement by Surface Orientation, 2011



Settlement rate by genus



2011 coral settlement summary

- Inshore and offshore environment
- Inshore: limited circulation
- Significantly less settlement in inshore than offshore
- Settlement limited by available light:
 - Inshore: suspended solids/sediments, smothering
 - Offshore: depth



Study 4. Assessment of long-term change in the reef community

- Chaney et al. (1977): Baseline for marine invertebrates and vertebrates
- Ball (1977): Marine algae
- Tissot (1998): Documenting declines of reef biota between 1976 and 1996
- Stender et al. (2014): Re-evaluation of fish and coral community following Tissot (1998) in 2012

PeerJ

Thirty years of coral reef change in relation to coastal construction and increased sedimentation at Pelekane Bay, Hawai'i

Yuko Stender^{1,2}, Paul L. Jokiel¹ and K'aukei S. Rodgers¹

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ABSTRACT

Coral reefs are being critically impacted by anthropogenic processes throughout the world. Long term monitoring is essential to the understanding of coral reef response to human impacts and the effectiveness of corrective management efforts. Here we reevaluated a valuable coral reef baseline established in Pelekane Bay, Hawaii during 1976 and subsequently resurveyed in 1996. During this time interval substantial impacts occurred followed by extensive corrective measures. Coral and fish communities showed dramatic declines from 1977 to 1996 due to massive harbor construction and suboptimal land management practices on the watershed. More recently, corrective measures in the form of watershed stabilization and fishing regulations have been implemented. Consequently our 2012 survey reveals that coral cover since 1996 has increased slightly accompanied by a significant increase in fish abundance, diversity, and evenness. This improvement can be attributed to lower fishing pressure since 1996 due to reduced shoreline access, tighter fishing regulations and increased monitoring of legal and illegal fishing activities. Stabilization of the coral community can be attributed partially to reduced sedimentation resulting from watershed restoration that included installation of sediment check dams, control of feral ungulates, controlled grazing and replanting of native vegetation. Insights into the mechanism that removes sediment from reefs was provided by a major storm event and a tsunami that remobilized and flushed out sediment deposits. The increase in herbivorous fishes probably played a role in reducing algal competition in favor of corals. The data suggest that the precipitous reef decline in this area has been arrested and offers support for the corrective actions previously undertaken.

Subjects Conservation Biology, Ecology, Environmental Sciences, Marine Biology

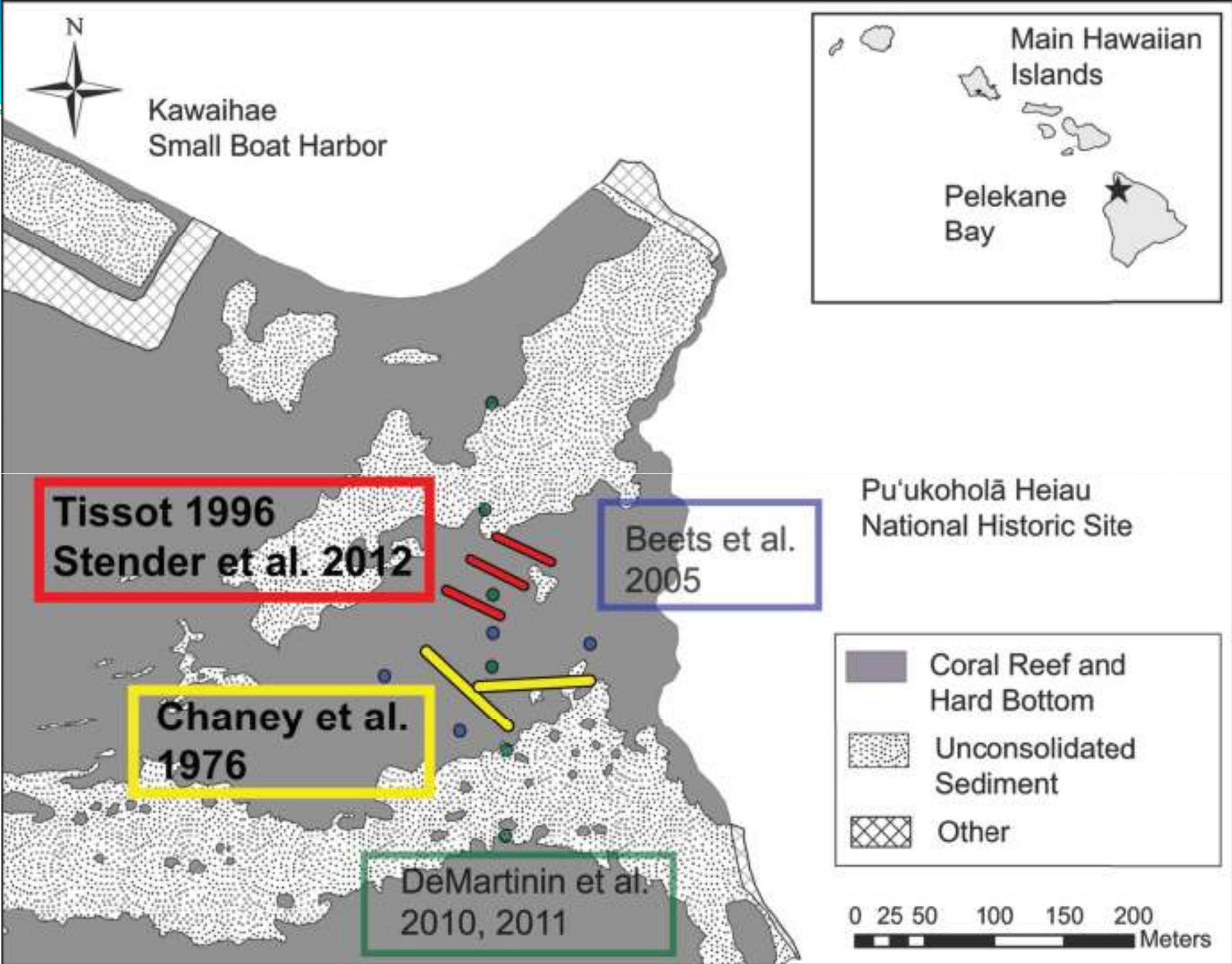
Keywords Coral reefs, Land-based impacts, Hawaii, Long-term monitoring, Sedimentation

INTRODUCTION

Coral reefs have been impacted by anthropogenic processes on a global scale (Bryant et al., 1998; Richmond et al., 2007; Halpern et al., 2008; Wilkinson, 2008). Direct impacts of global climate change on coral reefs is a great concern (Hughes et al., 2003; Hoegh-Guldberg, 2011), but indirect local effects such as altered hydrological processes (Fletcher, 2010) also impose land-based threats to coral reefs. Deforestation, uncontrolled grazing and

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Benthic

Table . Change in total coral cover at Pelekane Bay between 1976 and 2012. One standard errors of the mean are indicated by \pm s.e.m.

Survey year	Month	Author	Mean cover (%) \pm s.e.m.
1976	April	Chaney et al. (1977)	43.45 \pm 2.45
1996	January-April	Tissot (1998)	5.50 \pm 2.26
2012	June	Stender et al. (2014)	6.58 \pm 0.02

- Increased coral richness: 1996 (5 spp.) and 2012 (8 spp.)
- Increased *Porites compressa* cover 1996 (0.7%) and 2012 (2.1%)
- Decreased area covered by silt from 1976 (41.0%), 1996 (30.5%), to 2012 (24.4%)

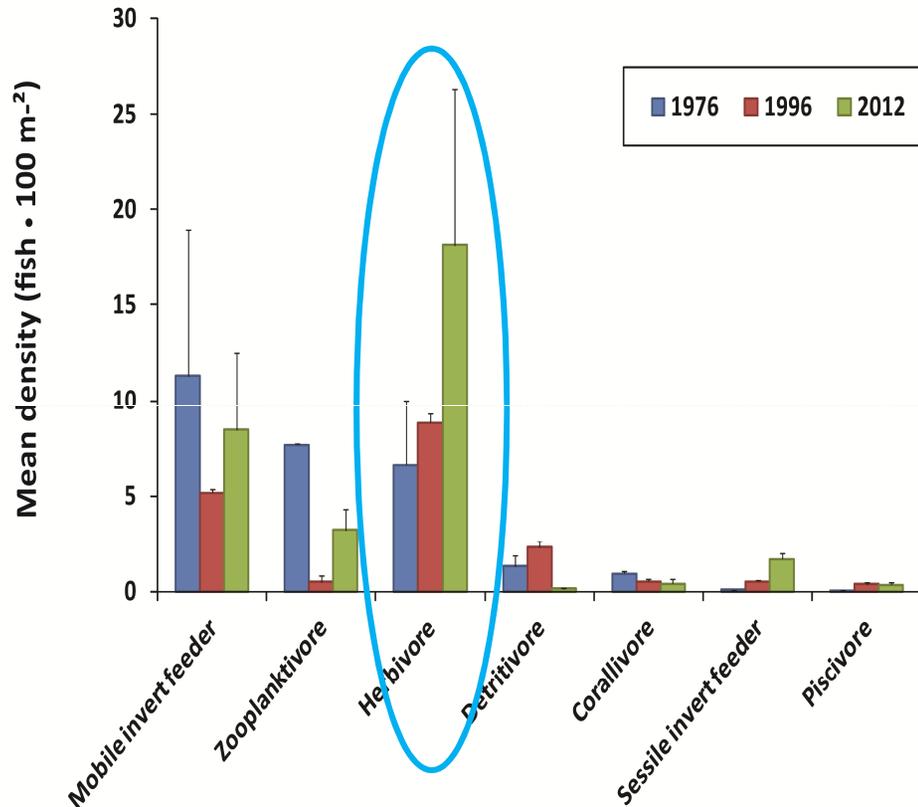
Fish

Table . Comparison of fish assemblage characteristics among surveys.

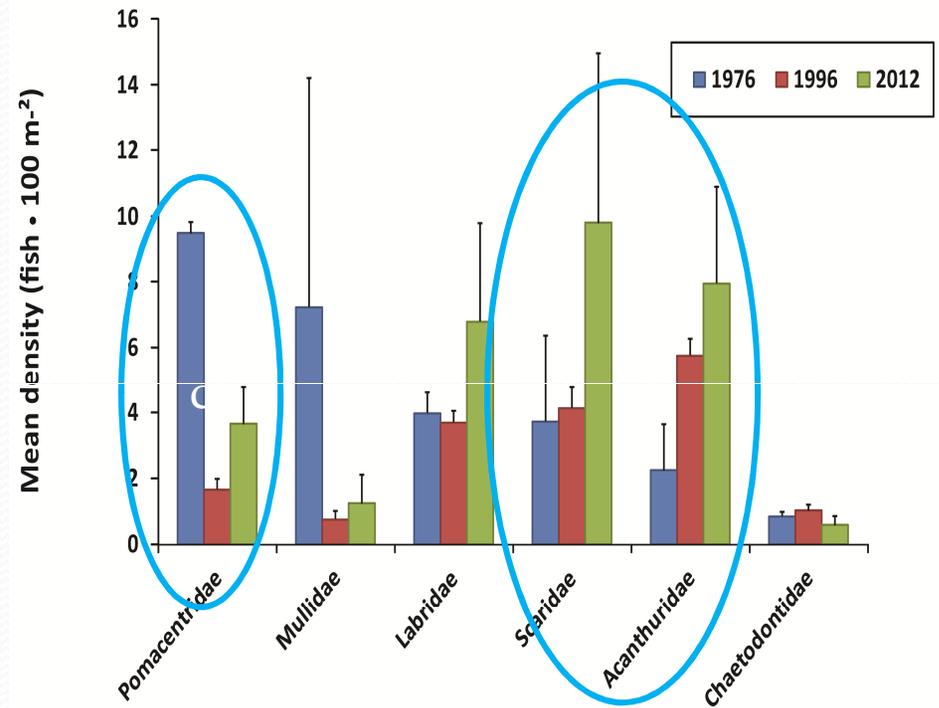
	1976 (Chaney et al.)	1996 (Tissot)	2012 (Stender et al.)
Mean number of fish·100 m⁻²	27.9	18.1	34.5
Species richness	35	39	41
Diversity (Shannon–Weiner)	1.07	1.17	2.46
Evenness	0.69	0.73	0.66

- 1996 and 2012: overall abundance varied by year and transect ($p < 0.000$)
- Greater abundance in 2012 than in 1996 ($p = 0.024$)
- The difference influenced by the outer transect.

By family and guild



Increase in zooplanktivores, herbivores, and sessile invertebrate feeders between 1996 and 2012



Scaridae and Acanthuridae increases in 2012

Pomacentridae declined between 1976 and 1996; increase in 2012

Species rank order

Table. Comparison of most abundant fish species in rank order among surveys.

	1976 (Chaney et al.)	1996 (Tissot)	2012 (Stender et al.)
1			
2			
3			
4			
5			

* Currently accepted name is *Mulloidichthys flavolineatus*.

**Currently accepted name is *Chlorurus spilurus*.



2012 Reef community change summary

- Coral and fish communities: declines from 1977 to 1996
- Changes since 1996
- Fish community improvement:
 - reduced shoreline access
 - increased surveillance
- Coral community stabilization:
 - reduced and remobilized sediment
 - watershed restoration
 - increased herbivores

Settlement 2014

- Settlement tiles: deployment and recovery at Pelekane, Kawaihae, and Puakō (37 sites).
- PAR and suspended solid concentration measurement



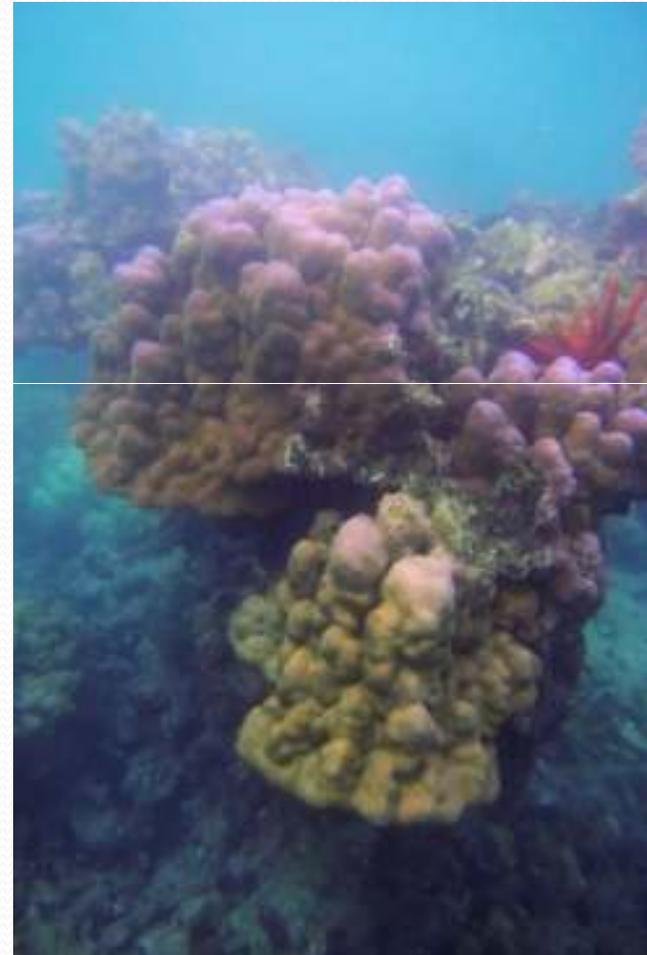
Overall summary and discussion: 2010-2012

- Growth and greater live tissue cover in less turbid areas , partial mortality is common in turbid areas
- Large colonies in turbid areas, small colonies in less turbid areas
- Greater settlement on offshore reefs than inshore reefs
- Stabilized cover of dominant corals inshore
- Minimal threat to offshore reefs by land-based sediment affecting habitat quality
- The potential for local reef recovery with controlled sediment sources and increased water circulation

Overall summary and discussion: 2010-2012

- Coral decline on neighboring reefs (Kawaihae and Puakō) in long term
- Declined coral settlement in Waiaka‘ilio (Martin and Walsh 2014)
- Confounding effects of sediment and thermal stress, 2014?

Station F8, September 2014, elevated water temperature



Porites evermanni

Station F8, F6, and F3



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Temporal Change in Hawaiian Coral Reefs

1 Over a Decade of Change in Spatial and Temporal Dynamics in Hawaiian Coral Reef
2 Communities¹

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4 Abstract: The Hawai'i Coral Reef Assessment and Monitoring Program (CRAMP) was
5 established in 1999 to describe spatial and temporal variation in Hawaiian coral reef
6 communities in relation to natural and anthropogenic factors. In this study, we analyze changes
7 over a 14 year period (1999 to 2012) based on data from 60 permanent reef stations at 30 sites in
8 the main Hawaiian Islands. Overall mean statewide coral cover, richness, and diversity did not
9 vary significantly since initial surveys, although local variations in coral cover trends were
10 detected. The greatest proportion of stations with significant declines in coral cover was found
11 on the island of Maui (0.40) while Hawai'i Island had the highest proportion of stations with
12 significant increases (0.58). Trends in coral cover at some stations varied over time due to acute
13 (e.g. crown of thorns outbreak) and chronic (e.g. sedimentation) disturbances. Stations with
14 increasing coral cover with the potential for recovery from disturbances were identified for
15 possible management actions in the face of future climate change. The Hawaiian archipelago,
16 located in the center of the subtropical Pacific, has experienced a temporary reprieve of slight
17 cooling due to a downturn of temperature since 1998 at the end of the last cycle of the Pacific
18 Decadal Oscillation (PDO). However, temperatures have been steadily increasing over the past
19 several decades and models predict more severe bleaching events to increase in frequency and
20 intensity in coming decades with concomitant decline in Hawaiian corals. Trends reported in this
21 study provide a baseline that can later be used to test this predicted decline associated with future
22 warming.

23

24

25 ¹Manuscript accepted _____

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31

32 Keywords: coral reefs, Hawaiian Islands, monitoring, temporal change

33

Introduction

34 The Hawai‘i Coral Reef Assessment and Monitoring Program (CRAMP) was established
35 in 1999 to test the hypothesis that reef condition is related to anthropogenic and natural forcing
36 functions and that management practices (various levels of protection) can conserve and restore
37 coral reefs through regulating human impact (Brown et al. 2004). Management needs were
38 addressed to develop a baseline and understand the current status and future stability of Hawaiian
39 reefs (<http://cramp.wcc.hawaii.edu>). No statewide long-term monitoring program existed prior to
40 the development of CRAMP. Previous monitoring had been fragmentary, addressing local issues
41 with short term studies by a range of researchers using a variety of methods. Studies conducted
42 at limited spatial and temporal scales can be misleading in the understanding of broad patterns
43 and ecological processes of reefs on a large scale (Hughes and Connell 1999).

Temporal Change in Hawaiian Coral Reefs

44 CRAMP established a robust baseline for a large number of reefs representing the overall
45 diversity in the State of Hawai‘i. Initial results of temporal change after the first three years from
46 1999–2002 were reported by Jokiel et al. (2004). The islands with the highest concentration of
47 human population or highest levels of sedimentation showed the highest declines in coral cover.
48 Coral reef communities experience natural fluctuations over a short duration of several years
49 (Grigg and Dollar 1990). Thus, long-term decadal data are essential to define long-term trends
50 outside natural variation. This report focuses on describing the overall spatial and temporal
51 changes in coral communities spanning the previous 14 years in the main Hawaiian Islands, with
52 an emphasis on comparisons among islands. We also speculate on potential causes of the
53 observed patterns.

54 Materials and Methods

55 To provide a diverse representation of coral reefs in the main islands in the State of
56 Hawai‘i, site selection criteria included: degree of perceived environmental degradation, wave
57 exposure and direction, level of management protection, accessibility, longitudinal range, range
58 of anthropogenic and natural impacts, and level of pre-existing data. Input on site selection for
59 reefs of interest was also received from non-governmental organizations, state agencies, and
60 federal agencies involved with the management of nearshore reef areas in Hawai‘i.

61 Thirty-two permanent long-term monitoring sites were selected on hard substrate with
62 two stations at each site. Generally, this design consisted of a shallow station in < 5 m of water,
63 and a deeper station at depths > 5 m (Table 1).

64 <<Table 1 near here>>

65 At each station, 10 randomly selected 10 m transects were permanently marked using
66 stainless steel pins. Thirty of the sites (60 stations) were initially surveyed between 1999 and

Temporal Change in Hawaiian Coral Reefs

67 2001 with an additional two sites (four stations) added in 2003 and 2004 to fill in spatial gaps
68 and to address concerns about degradation at specific reefs. Detailed methodology is described
69 by Jokiel et al. (2004). The methodology was designed with high statistical power as described
70 by Brown et al. (2004) to distinguish an absolute change of 10% in coral cover annually within a
71 site. This design, focused on changes in percent coral cover within a site since the sites were not
72 randomly selected at the onset.

73 Initially, digital video and the software program PointCount99 (Dustan, University of
74 Charleston) were used to tabulate substrate type. Advances in digital still photo technology led to
75 improved resolution over video frames, so starting in 2004 non-overlapping digital images were
76 used to estimate benthic coverage using the software program PhotoGrid (Bird 2001). Prior to
77 this modification in methodology, an analysis was conducted to ensure that data were
78 comparable between techniques and thus extend the temporal comparison. The variables of
79 interest at each station were percent coral cover, coral species richness, and coral diversity.

80 Over the 14 year survey period, sites were surveyed between two and 14 times (Table 1).
81 Consistent annual sampling was limited by resources or adverse weather conditions.

82 A general linear mixed model (*lmerTest* package) in the R statistical software package (ver.
83 2.15.3) was used for trend estimation of percent coral cover by station (R Core Team 2012).
84 Percent coral cover data were arcsine-square root transformed to meet the assumptions of
85 normality and homogeneity of the variances (Zar 1999). Percent coral cover was the dependent
86 variable with year (1999–2012) and transect (1–10 for permanent transects at each station, n =
87 640) as random effects. Due to the hierarchical nature of the sampling design, transect was
88 nested in station to focus on transects within each year and across years. A standardized
89 covariate was generated for trend estimation with the year variable starting at year 0 (e.g.

90 Starceovich 2013). The fixed effects or effects of interest in the model were station ($n = 64$) and
91 the year covariate (0-13). Restricted maximum likelihood (REML) in the *lmer* function, which is
92 within the *lmerTest* package, was used to estimate variance due to the unbalanced structure of the
93 data because not all sites were visited annually (Spilke et al. 2005). The Kenward-Rogers (1997)
94 approximation to Satterthwaite's degrees of freedom was used to generate the p-value of the t-
95 statistic at $\alpha = 0.05$.

96 Explanatory variables such as wave exposure, human population in the watershed, and
97 precipitation in the watershed were not included in the model since the main focus of the paper
98 was simply to examine statewide trends. In addition, gaps in the data set limited using more
99 complex models that examined statistical differences among islands and depths. Therefore, the
100 results focused on simply tabulating the number of sites among islands and depths that
101 experienced significant changes in coral cover. Regression slope estimates were used from the
102 general linear mixed model for the comparison.

103 Coral species richness and diversity were examined using paired t-tests (MINITAB 14®)
104 to explore the variation in coral species composition. Two sites were removed from the results
105 due to abbreviated sampling. Hakioawa, Kaho‘olawe (1999–2002) has not been resurveyed since
106 2002 and Mahinahina, Maui (2004–2012) was not initiated until 2004.

107

108

Results

109

110

111

The average coral cover on transects statewide in 2012 (24.1%, $SE \pm 0.89$) was not
statistically different ($t = -0.026$, $p = 0.979$) from the average of coral cover on the same
transects when first surveyed between 1999 and 2000 (24.3%, $SE \pm 0.93$) (Fig. 1). Although

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112 average coral cover did not change significantly statewide, 29 stations showed a decline in coral
113 cover of which 14 were statistically significant (Table 1, Figure 1).

114 <<Fig. 1 near here>>

115 Maui had the highest proportion of stations (8 out of 18 stations – 0.44) with a
116 statistically significant decline in coral cover whereas the island of Hawai‘i had the highest
117 proportion of stations with a statistically significant increase (8 out of 12 stations – 0.67).
118 Regression slope estimates from each station (Table 1) support this pattern and indicated that
119 coral cover on Maui experienced the highest number of sites with significant decreases. Three of
120 12 stations (0.25) on O‘ahu showed a significant increase in coral cover with an equal number of
121 stations that had a significant decrease in coral cover (Figure 1). On the island of Kaua‘i, two of
122 the 10 stations (0.20) experienced a significant decline in coral cover with one showing a
123 significant increase and the seven remaining stations (0.70) appearing relatively stable. The
124 largest decline in percent coral cover was found at the Papaula, Maui 10 m station which
125 declined from >50% to <5% over 14 years while the Kamiloloa, Moloka‘i 10 m station showed
126 the greatest percent increase from <1% to >10% from 2000 to 2012.

127 Statewide, shallow stations experienced more significant changes in coral cover over the
128 study period (22 of 33 stations with significant changes 0.67) than deeper stations (7 of 27
129 stations 0.26). Significant increases in coral cover were documented at 10 shallow stations (0.30)
130 compared to 12 stations (0.36) with significant decreases. At deeper sites, four stations (0.13)
131 had significant increases and three stations had significant decreases in coral cover. Hawai‘i had
132 the highest proportion of shallow stations (5 of 6 stations – 0.83) that experienced a significant
133 increase in coral cover. Maui had the largest proportion of shallow stations (6 of 11 stations –
134 0.55) with a significant decline. The deeper stations on Hawai‘i and Moloka‘i had the highest

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135 proportion (0.33) of stations with significant increases compared with the other islands. In
136 contrast, the largest proportion of deep stations with a significant decline in coral cover was on
137 the island of Maui (3 of 7 stations – 0.43).

138 Coral species diversity (Shannon-Weiner) did not vary significantly across the state from
139 1999/2000 to 2012 ($p=0.23$). Coral richness within stations exhibited a significant decrease since
140 the initial surveys (7.4 ± 0.3 in 1999/2000, versus 6.7 ± 0.2 in 2012, $p=0.02$) due to the
141 appearance and disappearance of uncommon species at various stations that represent a very
142 small fraction of the coral cover. The overall number of species recorded from all stations
143 remained stable at 20 species; however species composition varied slightly among the rarer
144 species such as *Leptoseris incrustans* and *Montipora studeri*. This result may have been an
145 artifact of the random point sampling on the images, which may not have detected the rare
146 species every time.

147 Coral cover on the statewide permanent transects was dominated by *Porites lobata*
148 (6.9%) followed by *Montipora capitata* (6.1%), *Montipora patula* (5.0%), *Porites compressa*
149 (3.5%), *Pocillopora meandrina* (1.5%), and *Montipora flabellata* (0.7%). Species composition
150 shifted since the original surveys with four of the main species increasing in cover and two
151 species decreasing. *Montipora patula* experienced the largest percent increase (+83.3%),
152 followed by *Montipora capitata* (+56.8%), *Porites lobata* (+12.7%), and *Montipora flabellata*
153 (+2.4%) while *Pocillopora meandrina* (–36.1%) and *Porites compressa* (–22.9%) exhibited a
154 decrease in percent cover. Hawai‘i Island showed no temporal decreases of the main coral
155 species over the survey period. Total cover of *Montipora flabellata* declined on Maui, O‘ahu,
156 and Kaua‘i, while cover of *Porites compressa* exhibited declines on Moloka‘i and O‘ahu, and
157 cover of *Porites lobata* showed temporal declines on Kaua‘i (Table 2). Species with the strongest

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158 skeletal strengths, *Montipora flabellata* (1.2% mean percent cover at shallow stations, 0.3%
159 mean percent cover at deep stations), *Pocillopora meandrina* (1.9%, 1.1%), and *Porites lobata*
160 (8.2%, 7.2%) had higher mean coral cover in shallower (<5 m) waters compared to deeper waters
161 (>5 m) (Table 2).

162 <<Table 2 near here>>

163 Discussion

164 Compared to the initial CRAMP survey results reported by Jokiel et al. (2004), the
165 number of stations on the island of Maui experiencing a significant decline in coral cover
166 increased from six to eight. In contrast, more stations (seven vs. three) on the island of Hawai'i
167 had a significant increase in coral cover (Fig. 2). Between 1999 and 2002 there were five stations
168 out of the 12 surveyed (0.42) on the most populated island of O'ahu that showed a significant
169 decrease in coral cover compared with only three stations in the present study (0.25). In addition,
170 more stations (three vs. one) on O'ahu are currently experiencing a significant increase in coral
171 cover compared to the initial paper. Kaua'i by comparison, shifted from three stations with a
172 significant increase in coral cover after 2002 to only one station, with the remaining two stations
173 declining in coral cover. Figure 2 summaries the current trends by island for the stations
174 surveyed. Admittedly, many of the stations were initially selected based on perceived threats and
175 stressors to the reef systems and therefore, the figure may represent a bias towards stations that
176 would not improve or were already in decline.

177 <<Fig. 2 near here>>

178 Closer examination revealed that trends in percent coral cover at given stations varied
179 tremendously since the initial CRAMP survey for a variety of potential reasons. Only six of the
180 60 reported trends in Table 1 of the Jokiel et al. (2004) held over the full time period of the

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181 study. This number more than doubled to 13 when including stations that experienced non-
182 significant trends in the earlier study that later were significant with a similar trajectory. The low
183 concordance between surveys at 5 years and at 13 years shows the importance of long-term data
184 records to clarify trends above the background noise and reveal potential roles of acute and
185 chronic disturbances that can significantly alter the trend during an intervening period.

186

187 Most Hawai'i reefs are located on island slopes near deep oceanic waters with high wave energy
188 that flushes sediment and pollutants from the system while moderating temperature. Also,
189 Hawai'i is relatively free of industrial development, mining and other highly polluting activities,
190 although sediment impact resulting from improper land use practices and feral ungulates is a
191 major problem (Hawai'i DBEDT 2006). Although over half of all reefs in the wider Pacific
192 region are currently listed as threatened by the World Resources Institute, Hawai'i has one of the
193 lowest overall threat ratings (Burke et al. 2011). The main Hawaiian Islands occupy a unique
194 geographic position in an area of the north-central Pacific that has escaped major bleaching
195 events (Burke et al. 2011) as well as rapid sea level rise (Leuliette 2012) over the past decade.
196 Thus, overall statewide coral cover and diversity have remained relatively stable since the initial
197 CRAMP survey in 1999, whereas coral cover on reefs in the Caribbean declined by 50% due to
198 bleaching events, storms and a major decline in coral growth (Wilkinson 2004). Nevertheless
199 Hawai'i and other areas of the Pacific with relatively healthy coral reefs are now at a threshold of
200 severe and frequent bleaching events projected for the near future (Donner 2009, Hoeke et al.
201 2011). The Intergovernmental Panel on Climate Change (IPCC 2007) states that within the next
202 few decades the thermal limits of corals will be surpassed in most geographic regions, with the

Temporal Change in Hawaiian Coral Reefs

203 highest impact in the Caribbean and the lowest in the central Pacific (Hoegh-Guldberg 2010,
204 IPCC 2007).

205 Acute disturbances such as storm events (Hanalei, Kaua‘i 2003) or crown of thorns
206 outbreaks (Kahahena Point, Maui 2005) can be seasonal or of a temporary nature (Keough and
207 Quinn 1991). CRAMP stations that showed an acute decline from natural impacts often showed
208 a steady increase in coral cover following the disturbance (Figure 3a). In contrast, stations with
209 chronic, recurrent pressure show inhibited recovery of coral cover (e.g. Mā‘alaea and Honolua
210 Bay, Maui) (Figure 3b). Several stations on each of the main islands exhibited specific
211 disturbance (eg. crown of thorns outbreak, sedimentation, nutrification) followed by recovery.
212 Many of these disturbance/recovery events were also documented by other studies that helped
213 explain the declines in coral cover at these stations.

214 <<Fig. 3 near here>>

215 Many stations on the island of Hawai‘i experienced an overall increase in coral cover
216 during the study period as indicated by the positive regression slopes in percent coral cover
217 (Figure 2). The exceptions were the two stations at Kawaihae along the northern section of the
218 West Hawai‘i coastline (Figure 1). These results are in agreement with data from the Division of
219 Aquatic Resources (DAR) West Hawai‘i Aquarium Project (WHAP) that has developed
220 extensive spatial and temporal data coverage at 24 sites along the West Hawai‘i coastline.
221 WHAP results showed a significant decline in coral cover since 2003 at six of their seven
222 northern sites that encompass the West Hawai‘i coastline (Walsh et al. 2009). In addition, DAR
223 and the Nature Conservancy found drastic declines in reef fishes and associated coral habitat
224 when reviewing historical and recent data at sites near Kawaihae, West Hawai‘i (Minton et al.
225 2012). Minton et al. (2012) found that contributing factors included a decrease in vegetation

226 cover in the adjacent watersheds due to a reduction in rainfall over the past nine years that
227 increased sediment deposition on nearshore reefs. Survey plots in the Pelekane Bay Watershed
228 above the Kawaihae site also showed a decline in vegetation as drought conditions progressed
229 (The Kohala Center 2011). Major sedimentation events occurred during periods of high rainfall
230 (USGS 2006, 2011).

231 A predominant pattern of continued decline in coral cover is clearly evident at open
232 access stations on Maui (Table 1, Figure 1). This has been linked to land-based nutrients (Smith
233 et al. 2005, Smith and Smith 2006, Dailer et al. 2010) and low herbivore populations (Walsh et
234 al. 2009). At sites with low grazing, mainly due to heavy fishing pressure that has removed the
235 herbivores, algae compete with coral for substrate. Walsh et al. (2009) found a relationship
236 between areas with depleted grazers and abundant *Acanthophora spicifera*, a preferred herbivore
237 food, (e.g. Mā‘alaea) and those with little or no *A. spicifera* and abundant grazers (e.g. Honolua
238 Bay). This led to recent management action of the Kahekili Herbivore Fisheries Management
239 Area where removal of herbivorous fishes is prohibited. At Papa‘ula, much of the decline in
240 coral cover has occurred since 2009 when a dramatic increase in the invasive *A. spicifera* was
241 documented (Walsh et al. 2009). In addition to excessive algal growth, other non-indigenous and
242 invasive species may be contributors to the observed declines. Coles et al. (2006) found that
243 enclosed harbors (e.g., Mā‘alaea) and disturbed embayments (e.g., Honolua Bay) generally had
244 higher levels of introduced species than open-ocean reefs. This pattern has also been observed in
245 other parts of the Pacific such as Guam (Pauley et al. 2002) and American Samoa (Coles et al.
246 2003).

247 Steady decline at sites with open access on Maui are correlated with chronic, localized
248 anthropogenic impacts while marine protected areas (MPAs) and deeper sites further from land-

249 derived materials have remained stable or experienced slower declines in coral cover. Selig and
250 Bruno (2010) compared coral cover within 310 MPAs worldwide to unprotected reefs and found
251 that MPAs are not only beneficial to restoration of fish populations but also to corals by
252 indirectly reducing fishing pressure which has been linked to coral degradation and mortality
253 (Wilson et al. 2008).

254 Honolua Bay, a no-take Marine Life Conservation District, is a notable example. Coral
255 cover data from the two stations going back to 1974 documented a period of stability and then a
256 gradual decline beginning in the mid-1990s (Friedlander et al., 2008). It was hypothesized that
257 agricultural practices in the watershed coupled with low coral recruitment levels contributed to
258 the chronic decline in the coral community (Brown 2004). A dramatic decline in coral cover at
259 the MPA at Kanahena Point (Figure 3a) was directly attributed to a crown of thorns (*Acanthaster*
260 *planci*) outbreak (1 per 10m²) in 2005 (Walsh et al. 2009). Since the initial impact reduced coral
261 cover at both the shallow (11.8–1.1%) and deep (33.9–14.5%) stations, there has been a gradual
262 recovery at both stations (shallow: 1.1–4.5%, deep: 14.5–26.3%) over the last seven years. This
263 localized predation event has also resulted in changes in coral community composition with a
264 shift from Montiporid towards Poritid corals. Increases in coral diversity within a reef system
265 such as at this site can increase resistance to future stressors and improve resilience (Carpenter
266 1997; Birkeland and Lucas 1990).

267 The reefs along the south shore of Moloka‘i appear to be primarily influenced by
268 terrestrial sediment input and near shore sediment transport over the past few decades (Field et
269 al. 2008). In response, the Moloka‘i stations from Kamalō to Kamiloloa (east to west) near the
270 harbor (Figure 1) continued to decline due to historical land-derived sedimentation due to
271 improper land management and overgrazing by feral ungulates (Roberts and Fields 2008). The

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272 stations at Kamalō in particular have experienced a slow, steady decline in coral cover. In
273 addition to land-derived sediment impacting the Kamalō stations, two proposed marina
274 developments in the 1970s excavated considerable sediment up current of these monitoring
275 stations (Roberts and Field 2008). The deeper Kamiloloa site, however, has increased in coral
276 cover from 0.9% to 10.0% from 2000 to 2012. This deeper site had the highest level of coral
277 settlement among the Molokaʻi stations (Brown et al. 2008) and may be far enough removed
278 from sources of sedimentation that it is showing signs of recovery from a previous disturbance
279 (e.g. Hurricane Iniki in 1992). The two Pālāʻau stations have remained relatively stable since
280 2000, in part due to the stabilizing influence of the invasive mangroves that have inhibited
281 sediment transport onto the reef (D’lorio 2008).

282 The overall pattern of decline on the island of Oʻahu reported in Jokiel et al. (2004) has
283 stabilized due to increases in coral cover at sites in Kāneʻohe Bay as well as in the marine
284 protected sites at Pūpūkea (Figure 1). Following historical insults of sewage discharge from 1951
285 through 1978, increases in coral cover have been documented in Kāneʻohe Bay near CRAMP
286 sites between 1997 and 2011 (J. Stimson pers com). An extensive rain event in 2006 resulted in a
287 reduction in irradiance and the associated high levels of nutrients caused a dramatic decline in
288 the macroalga, *Dictyosphaeria cavernosa* (Stimson and Conklin 2008). This decline reduced
289 algal dominance and competition for space allowing reestablishment of formerly displaced coral.
290 The one exception in Kāneʻohe Bay was the shallow Kaʻalaea station, which showed a
291 significant decline, attributed to slumping of the upper reef slope. Coral cover was relatively
292 stable at stations located in the Marine Life Conservation District (MLCD) at Pūpūkea and
293 Hanauma Bay. The notable exception was the shallow station at Hanauma Bay which declined
294 significantly in coral cover over the study period and most of the decrease appeared to occur

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295 after 2002. This wave sheltered MLCD on the south shore receives over 1 million visitors a year
296 and has more fragile corals based on the coral assemblage than at the Pūpūkea MLCD on
297 O‘ahu’s north facing shore. Therefore, it is possible that the shallow station was more prone to
298 damage from physical contact (e.g. Rodgers et al., 2003) and changes in the nearshore water
299 quality from high human use than the deeper station.

300 Coral zonation patterns reflect coral morphology, skeletal strength, and wave regimes.
301 Species with stronger skeletons such as *Pocillopora meandrina*, and *Porites lobata* and
302 encrusting species with low relief such as *Montipora flabellata*, showed higher coral cover in
303 shallow waters where wave energy is highest. This pattern of distribution has likely evolved as
304 an adaptive response to disturbance by waves (Rodgers et al. 2003, Storlazzi et al. 2005). Dollar
305 (1982) demonstrated depth stratification of corals in Hawai‘i due to wave stress. Corals
306 exhibiting highly branched morphologies, low skeletal strength and high fracture rates are found
307 in regions with little wave exposure such as embayments and sheltered areas, while lobate and
308 encrusting forms tend to inhabit higher wave energy regions.

309 This study focused on station-specific trends since CRAMP was started in 1999.
310 Identifying stations that are improving or stable despite perceived natural and anthropogenic
311 variations will be crucial to direct management strategies in the face of future climate change.
312 The main Hawaiian Islands occupy a unique geographic position in an area of the north-central
313 Pacific that has escaped major bleaching events (Burke et al. 2011) as well as rapid sea level rise
314 (Leuliette 2012) over the past decade. The long-term trend of increasing water temperature in
315 Hawaiian waters, however, indicates that Hawai‘i may not be buffered indefinitely from these
316 climatic events. In addition, projected changes in the ocean chemistry due to ocean acidification
317 will have profound effects on reef areas globally and in Hawai‘i unless carbon emissions are

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318 reduced substantially (Hoegh-Guldberg et al. 2007). Consequently, it is imperative that reefs be
319 identified that appear to be more resistant and/or resilient to these perturbations. Several of the
320 stations in this study, such as the stations in Kāneʻohe Bay, Oʻahu (Heʻeia 2 m, Moku o Loʻe 2
321 m, Kaʻalaea 8 m), many of the shallow stations on Hawaiʻi Island, and Kanahena Point 10 m,
322 Maui appear to fit these criteria and could act as source populations.

323 The 1999–2000 CRAMP baseline established reliable reference points to evaluate coral
324 cover statewide over time. In addition, comparative studies at the onset (e.g. Brown 2004,
325 Brown et al. 2004) enabled the program to examine earlier temporal data sets at a larger spatial
326 than had been previously attempted. This present study documented the trends at individual
327 stations and found similar levels of improving and declining reefs suggesting that overall
328 statewide coral cover and diversity has remained relatively stable since the initial CRAMP
329 survey. The key strategy will be focusing management efforts on the stations that have been
330 declining in a chronic fashion. Even though many of these reefs may have already been in a
331 degraded state when CRAMP was initiated, the current (2012) results will set a new baseline for
332 assessing future declines and potential recovery at reefs targeted for management actions.

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Captions

Figure 1. Statewide Coral Reef Assessment and Monitoring stations showing change in coral cover and statistical significance from 1999/2000 to 2012.

Figure 2. Mean regression slopes of changes in percent coral cover by island along a longitudinal gradient from west to east. The regression slopes represent changes in percent coral cover over the study period with negative slopes indicating a decline in coral cover, in contrast to positive slopes that signify an increase in coral cover. Error bars are ± 1 SE of the mean. Note that no statistical test was used to evaluate island differences due to gaps in the data set that precluded a more complete analysis at that scale.

Figure 3. a: Scatterplot of percent coral cover from 1999 to 2012 at the Kanahena Point 10 m station on Maui showing the acute impact of the crown of thorns outbreak in 2005. b: Scatterplot of percent coral cover from 1999 to 2012 at the Mā‘alaea 3 m station on Maui showing the steady decline in cover over the same time period. The solid trend line in both plots represents a Lowess function fitted to the data.

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573 Table 1. CRAMP sites showing depth, legal status (O = Open access, PP = Partially protected,
 574 NT = No take), number of years surveyed, coral cover regression slope over the years surveyed
 575 (negative slope indicates decline), and p values. Bold p values indicate statistically significant
 576 trend over the study period. Bold positive slope indicates increase in coral cover with possible
 577 recovery potential.

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Island	Site	Depth (m)	Legal Status	# Yrs Surveyed	Slope	<i>p</i>
Kaua'i	Hanalei	3	O	10	-1.27	<0.001
	Hanalei	8	O	10	-0.41	0.292
	Ho'ai	3	O	4	0.69	0.011
	Ho'ai	10	O	4	0.24	0.222
	Limahuli	1	O	5	-0.69	0.001
	Limahuli	10	O	7	0.16	0.385
	Miloli'i	3	O	3	0.07	0.660
	Miloli'i	10	O	4	0.13	0.592
	Nualolo	3	O	4	-0.05	0.653
	Nualolo	10	O	4	-0.49	0.094
O'ahu	Ala Wai	3	O	2	0.18	0.349
	Ala Wai	10	O	2	-0.15	0.978
	Hanauma	3	NT	5	-1.27	<0.001
	Hanauma	10	NT	5	0.31	0.589
	He'eia	2	O	6	3.97	<0.001
	He'eia	8	O	6	0.16	0.515
	Ka'alaea	2	O	7	-0.83	0.014
	Ka'alaea	8	O	6	0.72	<0.001
	Kahe Point	3	O	5	-0.14	0.552
	Moku o Lo'e	2	NT	8	2.58	<0.001
	Moku o Lo'e	9	NT	8	0.40	0.083
	Pili o Kahi	3	O	5	-0.33	0.051
	Pūpūkea	4	PP	4	0.26	0.258
Pūpūkea	8	PP	4	0.21	0.491	
Moloka'i	Kamalō	3	O	8	-0.83	0.020
	Kamalō	10	O	8	-0.56	0.112
	Kamiloloa	3	O	8	-0.19	0.079
	Kamiloloa	10	O	7	0.69	<0.001
	Pālā'au	3	O	8	0.28	0.373
	Pālā'au	10	O	8	-0.55	0.080
Kaho'olawe	Hakioawa	3	PP	4	0.24	0.541
	Hakioawa	10	PP	4	-1.17	0.524
Maui	Honolua North	3	NT	14	-0.48	0.035
	Honolua South	3	NT	14	-1.64	<0.001
	Kanahena Bay	1	NT	12	0.45	0.086
	Kanahena Bay	3	NT	12	1.06	0.001
	Kahekili	3	O	13	0.90	0.006
	Kahekili	7	O	12	0.47	0.114
	Kanahena Point	3	NT	13	-0.37	0.011
	Kanahena Point	10	NT	13	-1.79	<0.001
	Ma'alaea	3	O	12	-0.84	<0.001
Ma'alaea	6	O	12	-0.56	<0.001	

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	Mahinahina	3	O	6	-0.27	0.807
	Mahinahina	10	O	7	-0.25	0.656
	Molokini	8	NT	13	0.15	0.600
	Molokini	13	NT	13	-0.05	0.721
	Olowalu	3	O	14	-0.37	0.212
	Olowalu	7	O	14	-0.04	0.997
	Papaula	4	O	13	-1.08	<0.001
	Papaula	10	O	13	-4.28	<0.001
	Puamana	3	O	12	-0.02	0.990
	Puamana	13	O	14	0.09	0.282
Hawai'i	Ka'apuna	4	O	3	0.56	0.013
	Ka'apuna	10	O	4	0.47	0.139
	Kawaihae	3	O	3	-0.84	0.002
	Kawaihae	10	O	3	-2.10	<0.001
	La'aloa	3	O	4	1.73	<0.001
	La'aloa	10	O	4	1.83	<0.001
	Laupāhoehoe	3	O	3	1.33	<0.001
	Laupāhoehoe	10	O	3	0.47	0.055
	Leleiwi	3	O	3	1.28	<0.001
	Leleiwi	10	O	3	-0.59	0.082
	Nenue	5	PP	5	1.32	<0.001
	Nenue	10	PP	5	1.18	<0.001

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Table 2. Change in coral composition of main species by island (regression slope) and depth (percent cover). Negative slope indicates a decline, positive slope indicates an increase over all survey years.

Island/Depth	<i>Montipora capitata</i>	<i>Montipora flabellata</i>	<i>Montipora patula</i>	<i>Pocillopora meandrina</i>	<i>Porites compressa</i>	<i>Porites lobata</i>
Hawai'i	0.155	0.051	0.063	0.265	0.027	1.460
Maui	0.292	-0.166	0.124	0.017	0.108	0.378
Moloka'i	0.547	0.034	0.848	0.035	-0.091	0.112
O'ahu	0.557	-0.010	0.029	0.061	-0.116	0.286
Kaua'i	0.137	-0.007	0.625	0.029	0.018	-0.025
Kaho'olawe	0.514	-0.207	0.277	0.169	-0.704	-0.500
Shallow sites (<5 m)	4.13	1.21	1.70	1.89	4.07	8.16
Deep sites (>5 m)	7.06	0.26	6.55	1.13	2.83	7.16

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