



Rebounds, regresses, and recovery: A 15-year study of the coral reef community at Pila'a, Kaua'i after decades of natural and anthropogenic stress events

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ARTICLE INFO

Keywords:

Coral
Sedimentation
Recovery
Re-colonization
Long-term
Hawaii

ABSTRACT

Pila'a reef on the north shore of Kaua'i, Hawai'i was subjected to a major flood event in 2001 that deposited extensive sediment on the reef flat, resulting in high coral mortality. To document potential recovery, this study replicated benthic and sediment surveys conducted immediately following the event and 15 years later. Coral cores were analyzed to determine coral growth rates and density. Our results suggest that significant reduction in terrigenous sediments has led to partial ecosystem recovery based on coral species and colony increases, more balanced size frequency distributions, improved coral condition, and enhanced coral recruitment despite lack of recovery of large dead coral colonies. However, within this 15-year period, episodic storms and a bleaching event impeded the recovery process, preventing full recovery and continuously threatening the coral reef community. As climate change progresses, the intensity and frequency of these disturbances are predicted to increase.

1. Introduction

Coral reef communities are increasingly exposed to the cumulative impacts of multiple disturbances that may lead to the loss of individuals, taxa, and resilience. Recovery from disturbances requires resilience but may instead result in phase-shifts to alternate stable communities (i.e. macroalgae; Hughes et al., 2010, Ortiz et al., 2018). Community composition and structure of reef building corals can be altered by natural disturbances such as episodic storms and wave stress (Dollar, 1982; Connell et al., 1997). Inshore corals commonly experience intense wave disturbance, high irradiance, large fluctuations in seawater temperature and chemistry, and exposure during low tides. These potentially stressful conditions may occur in isolation or simultaneously. Local anthropogenic disturbances add to these physical stressors, reducing resilience of resident coral communities (Johannes, 1975; Bachtiar et al., 2019; Hughes et al., 2019; McWilliam et al., 2020). Human-induced stressors can be acute, such as direct impacts of ship groundings (Negri et al., 2002; Carilli et al., 2009), or chronic, as seen in impacts to reefs from non-point source pollution and heavy fishing pressure (Hughes, 1994; Fabricius, 2005; Hughes et al., 2010). Impacts

also include direct effects from visitors. Shallow reef flats in Hawai'i are prime tourist locations that receive over ten million visitors annually (Dbedt, 2019) and are commonly subjected to reduced water quality, abrasion, and breakage among other human induced stressors (Rodgers et al., 2003; Lachs and Oñate-Casado, 2020; Severino and Rodgers, 2019).

Primary global concerns include the increasing effects of climate change. Regional widespread bleaching events have occurred globally since the 1980's with increasing frequency, intensity and geographic extent (Hoegh-Guldberg, 1999; Mora et al., 2013; Hughes et al., 2019). The first widespread bleaching event in the main Hawaiian Islands occurred in 1996 with a second affecting the unpopulated northwest Hawaiian Islands in 2002 (Jokiel and Brown, 2004a). Recovery from these events was rapid with no large-scale mortality reported (Jokiel, 2004). From 2014 through 2017 an unprecedented global-scale bleaching event resulted in widespread coral mortality. Hawai'i was no exception, with a statewide average of 35% coral mortality and over 60% coral loss in select regions (Neilson, 2014; Kramer et al., 2016). Along with bleaching events, the intensity and frequency of storms are increasing by 3 to 5% (Emanuel, 2013; Giambelluca et al., 2013;

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<https://doi.org/10.1016/j.marpolbul.2021.112306>

Received 29 April 2020; Received in revised form 1 March 2021; Accepted 24 March 2021

Available online 26 August 2021

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Longman et al., 2020; Murakami et al., 2020). These storms amplify runoff containing freshwater, nutrients, and sediment that can be detrimental to nearshore organisms (Rodgers et al., 2021).

Sediment pollution is a devastating human-induced disturbance, often caused by modifications directly or adjacent to existing coastal ecosystems that may have acute and/or chronic impacts on inshore coral communities (e.g. Ennis et al., 2016). For a comprehensive review of the negative impacts of sedimentation and associated turbidity due to coastal dredging activities see Erfteimeijer et al. (2012) and Jones et al. (2016). Poorly managed alterations of natural landscapes can lead to a release of excess terrigenous materials towards shore, intensifying impacts of sedimentation on nearshore coral reefs (Jokiel et al., 2002; Fabricius, 2005; Bartley et al., 2014; Storlazzi et al., 2015). Sedimentation can facilitate coral mortality due to burial (Grigg and Birkeland, 1997), increased susceptibility to disease (Brown and Howard, 1985), abrasion (Glynn et al., 1989), decreased light levels (Rogers, 1990; Davies, 1991), and altered habitats (Jokiel et al., 2014). Sub-lethal effects include reduced reproductive output, lower recruitment rates (Birkeland, 1977), suppressed accretion rates, decreased calcification (Randall and Birkeland, 1978; Carilli et al., 2009), morphological changes (Dustan, 1975; Brown et al., 1986), metabolic shifts (Rogers, 1979; Te, 2001), behavioral alterations, and increased pathological disease and bleaching (Brown and Howard, 1985). Sediment laden with chemicals and heavy metals can produce adverse secondary effects in corals that may dramatically affect physiological processes (Glynn et al., 1986). Moreover, effects of sediment may interact with other stressors such as wave disturbance, nutrient enrichment, light, and seawater temperature (Storlazzi et al., 2004; Storlazzi et al., 2012; Weber et al., 2006; Fisher et al., 2019), influencing coral-algal competition (McCook, 2001) and the re-establishment and recovery of coral dominated communities (Nugues and Roberts, 2003; Wolanski et al., 2004; Jokiel et al., 2014; Gil et al., 2016).

While recent research and management efforts continue to focus on the development of thresholds for lethal/sublethal effects of sedimentation and associated turbidity on corals (Erfteimeijer et al., 2012; Jones et al., 2016; Tuttle et al., 2020), spatial-temporal variability of a coral community and the potential interactions among environmental stressors make generalizations of sediment thresholds difficult and unrealistic. Additionally, more studies focus on immediate impacts (Pearson, 1981; Rogers, 1990; Brown et al., 2002; Jones et al., 2020; Tuttle et al., 2020) rather than long-term monitoring of coral reefs following acute and/or chronic sedimentation events (Fabricius, 2005; Australian Institute of Marine Science, 2019).

The research outlined here describes the outcomes of several converging events, both anthropogenic and natural, that began in the 1990s and gravely affected the condition of Pila'a reef on the island of Kaua'i, Hawai'i. Surveys conducted in 2002 after a heavy rainfall in 2001 that caused massive mudslides revealed recent and previous coral mortality that were both likely tied to the land modifications, which began around 1993 (Jokiel et al., 2002, Fig. 1a). These direct human impacts resulted in chronic sedimentation that likely occurred with each heavy rainfall. From initial surveys in 2002 to surveys conducted 15 years later in 2017, we document the long-term changes that have occurred at Pila'a following identical methodologies at the same locations for both years. The 2002 surveys represent the baseline for Pila'a reef, with no prior data available. Researchers and managers from the University of Hawai'i's Coral Reef Ecology Laboratory, and the State of Hawai'i's Division of Aquatic Resources (DAR), participated in the collaborative effort to assess the reef damage at Pila'a in 2002 following the sedimentation event. The beaches and reefs at Pila'a have limited public accessibility providing a unique opportunity to study reef stress dynamics, mortality, and recovery in an area with limited human use (Rodgers et al., 2017a, 2017b). In 2017, we returned to Pila'a to investigate coral community recovery since the acute sedimentation event. This rare opportunity allows us to better understand the responses of coral communities on an ecological time scale.

2. Background

2.1. Site background

Pila'a reef is located off the northeastern shore of Kaua'i, Hawai'i (Fig. 1a). The land slopes immediately upwards from the eastern sector of Pila'a beach, reaching ~46 m elevation within a linear distance of 182 m. The mountainous topography adjacent to the reef and the prevailing Northeasterly Trade Winds produce orographic precipitation that increases with elevation. The Pila'a watershed (Fig. 1b; 652 ha; State of Hawai'i GIS) receives an average annual rainfall of approximately 150 cm (nearshore) and 200 cm at higher elevation, and is drained by the Pila'a Stream. An extensive outer reef crest stretches the length of the inner reef flat that protects the inner reef from large ocean waves and swell. Coral reef flats, massive coral heads, sandy bottom pockets, and deep and shallow areas contribute to the highly complex topography that provides numerous, diverse habitats. Pila'a reef is naturally divided into eastern and western sectors, delineated by a central channel that extends seaward from the mouth of Pila'a Stream.

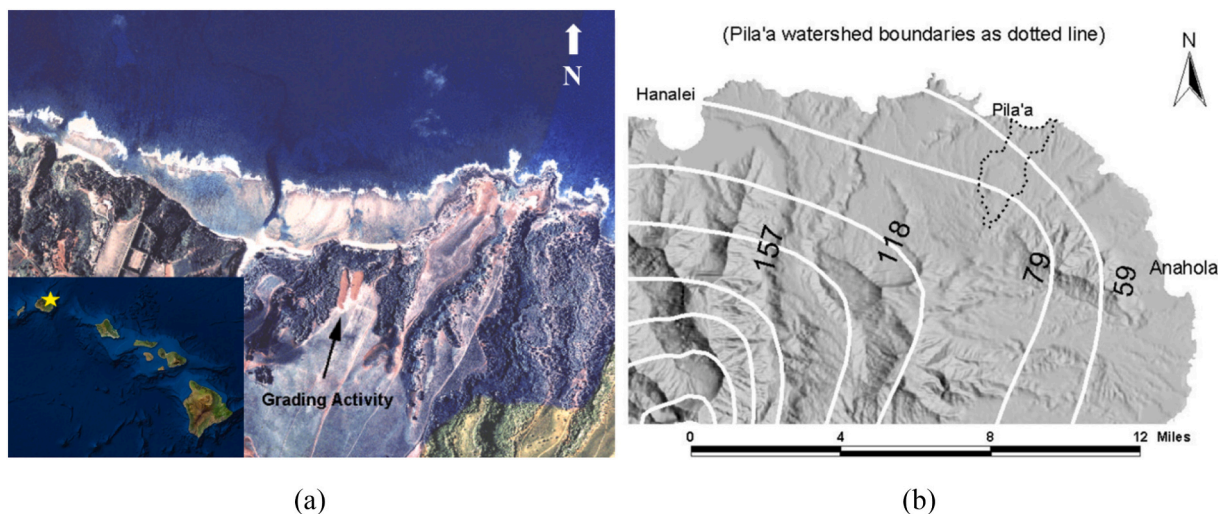


Fig. 1. (a) Map showing the watershed where grade and fill operations were ongoing prior to 2001 (indicated by arrow) with inset of the Hawaiian Islands, and (b) map of the Pila'a watershed annual rainfall contours (in inches) from Jokiel et al. (2002). Original source: State of Hawai'i GIS.

Under typical conditions, watershed runoff drains directly into this deeper channel and is carried by strong currents beyond the reef (Jokiel et al., 2002). The eastern sector has sandy beaches, a wide reef crest, and is sheltered from ocean swell by a peninsula. The reef crest in the western sector tapers towards the rocky shoreline and is more exposed. Much of the reef in the eastern sector is consolidated and forms a relatively flat, shallow pavement while the structures are patchier with shallow, narrow channels in the western sector. On the reef flat, circulation slows as it moves shoreward, curving inward to converge at the central channel where a strong outgoing rip current is formed. The channel current flushes seawater out to the open ocean and is especially strong during the incoming tide (Jokiel et al., 2002). The central channel also functions as a natural barrier between the sectors with circulation dynamics that result in two structurally different coral habitats.

2.2. Eastern sector

Intensive grading in the 1990s of shoreline slopes and a stream in Pila'a Valley resulted in exposure of the shallow eastern Pila'a reef to extensive sedimentation (Fig. 1a). Aerial imagery from the National Oceanic and Atmospheric Administration (NOAA) shows extensive vegetation removal adjacent to the eastern sector between 1993 and 2000. These anthropogenic alterations coupled with a heavy rain event in November 2001, caused mudslides that deposited on the order of hundreds to thousands of tonnes of fine, red sediment on the eastern (impacted) nearshore reefs (Jokiel et al., 2002). This event resulted in high coral mortality in the eastern sector as indicated by post-storm surveys that attributed only those colonies with unequivocal signs of recent mortality to that event. The eastern reef flat at Pila'a is more heavily impacted than the adjacent western reef by freshwater, sediment, and nutrient exposure from flood events due to stream proximity and local circulation patterns. Historical stream discharge records suggest that several other severe flood events may have occurred between 1991 and 1995, likely impacting the coral reef. Stream gauge records from 1957 to 2002 at Halaulani Stream, which drains a portion of the watershed into the sea adjacent to Pila'a, showed anomalously high mean daily flow (Fig. 2) in December 1991 (521 cubic feet per second; cfs), February 1994 (879 cfs), and November 1995 (625 cfs). Interestingly, the stream gauge reading for the devastating event in 2001 (126 cfs) was several times lower than for the events in the 1990s. Based on

the number and sizes of recruits observed on large, dead coral colonies during the 2002 surveys, the timing for the loss of these colonies was deemed consistent with the heavy rainfall that occurred in the 1990s.

According to Erfemeijer et al. (2012), strong water motion that re-suspends sediment and clears out turbid waters, is the most significant factor mitigating coral mortality following acute or chronic sedimentation events. Weak neap tides following a flood event, likely exacerbates the initial runoff stress (Jokiel et al., 2002). The November 2001 event at Pila'a reef also occurred during a weak neap tide and when offshore wave energy was low. Most of the mud that had flowed onto the reef settled and remained throughout the winter, despite strong winter surf conditions (Jokiel et al., 2002). The sediment was re-suspended during high tides and settled during low tides. This resulted in chronic smothering conditions for corals and other sessile reef organisms. Much of the sediment that was deposited onto the eastern reef flat was still evident in September of 2002 (Jokiel et al., 2002). Although the duration of chronic re-suspended sedimentation from the 2001 storm event has not been quantified, researchers determined from short term recovery surveys that prolonged storm activity in late 2002 and early 2003 had flushed much of the sediment from the eastern nearshore reef (Jokiel and Brown, 2004a). Thus, it is estimated that corals in the eastern sector were impacted by heavy sediment for at least one year following the mudslide event. All grading activity ceased following the 2001 sediment event.

2.3. Western sector

Whereas damage from the mudslide to the eastern sector was evident in 2002, no visible damage was observed in the western sector. A strong storm event later occurred in November 2003, resulting in extensive fragmentation in the western sector, reducing live coral coverage from 14 to 6% (Jokiel and Brown, 2004b). The sediment-impacted eastern sector was largely sheltered from this storm. Thus, the original 2002 survey data used for comparison in this study did not include results from the 2003 storm event.

Natural and anthropogenic events acting at different timescales are important factors determining the community structure and recovery dynamics in both sectors at Pila'a reef. Here we report the continuation of the research begun in 2002 and what is known regarding past disturbances to document the advances and regresses towards recovery

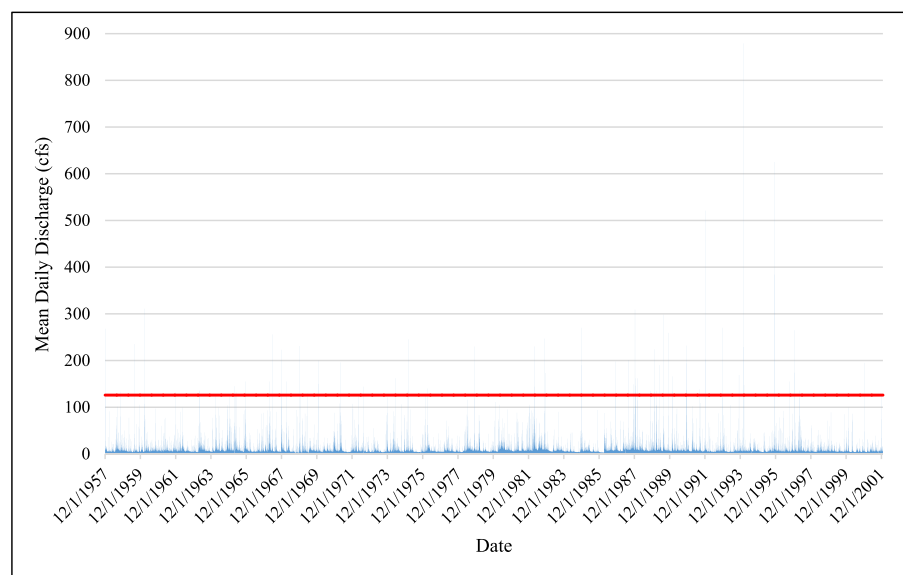


Fig. 2. Stream gauge records from 1957 to 2002 at Halaulani Stream (USGS station 16,097,500) near Pila'a. The red line indicates the maximum discharge recorded during the 2001 storm event. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

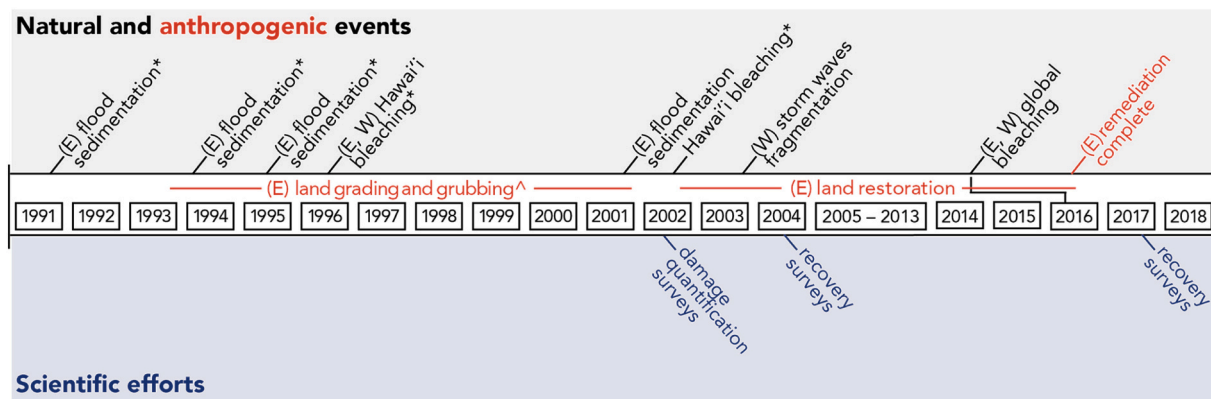


Fig. 3. Timeline from 1991 through 2018 of major events at Pila'a reef, Kaua'i. Sectors affected in (), E = eastern, W = western. * = potential, unconfirmed effects, ^ denotes estimated timeline.

(Fig. 3).

3. Materials and methods

In 2017, surveys were identically conducted to replicate original surveys initiated in 2002 (Jokiel et al., 2002) to determine potential recovery in the coral reef community over the past 15 years. The 2002 surveys represent the baseline for Pila'a reef, with no prior data available. These surveys included 25 m benthic transects, massive *Porites* colony assessments, coral cores, and sediment analyses. From these assessments we obtained data on coral condition, size frequency distributions, recruitment, calcification rates, live cover, species composition, and sediment grain-size and composition. We present the primary findings here from the principal assessments in 2002 and the recent re-surveys in 2017 (cores, benthic transects, massive colony assessments, and sediment comparisons). Although we are able to compare across years to determine recovery, no baseline data were available prior to the sediment event to determine the rate of recovery.

3.1. Hydrological conditions

Historical precipitation and stream discharge records were compiled to examine the frequency of recurring storm events that were equal to or greater than the heavy rainfall event in November of 2001 that caused the massive mudslides at Pila'a reef. Records from 2001 to 2017 were collected to assess hydrological conditions and distinguish severe weather events that may have occurred between the first event, which prompted the initial 2002 surveys, and the 2017 surveys. Rainfall data were obtained through the National Oceanic and Atmospheric Administration (NOAA) National Centers for Environmental Information (NCEI) Climate Data Online. The rain gauge at Koloko Reservoir (USC00514758), approximately three kilometers southwest of the study site, was used as a proxy for rainfall at Pila'a as no rainfall data were available for the site. Stream discharge data for Halaulani Stream was acquired through the United States Geological Survey (USGS) National Water Information System (16,097,500; U.S. Geological Survey, 2020) to identify high stream flow following the 2001 flood event. There is no stream gauge installed at Pila'a stream, and previous research comparing two separate streams near the Pila'a stream watershed suggest Halaulani Stream as the most similar and comparable to Pila'a stream characteristics based on drainage area and near proximity (Jokiel et al., 2002).

3.2. Benthic coral surveys

3.2.1. Benthic transects: U25 and I25 surveys (established 2002, replicated 2017)

During the original 2002 surveys, no signs of sedimentation-induced stress were observed in the western sector; thus, the west side of the channel was assumed a "control" (unimpacted; U25 surveys) site and the east side of the channel was classified as impacted (I25 surveys). Benthic transects 25 m in length were established to compare the sediment-impacted east to the unimpacted west. Surveys in 2017 replicated those conducted in 2002 (Jokiel et al., 2002) at their original locations (Fig. 4).

Ten 25-m transects in each of the impacted (east; I25-1 to I25-10) and unimpacted (west; U25-1 to U25-10) sectors were relocated using GPS map78S (Fig. 4). Data were collected on species, size (longest planar cross-section), abundance, and condition of all corals found within a 2×25 m area (50 m²). Condition of each coral colony was assigned a category from those used in the 2002 surveys: "Normal", "Bleached", "Dying", and "Dead." However, observations in 2017 found coral colonies that were paling or recently dead, which did not fit the former categories listed. Therefore, "pale" and "recently dead" condition categories were added to adequately characterize coral condition. Consequently, data had to be combined for analyses to allow for comparability with original data. The 2017 category "Pale" was combined with the "Normal" category for analyses, and the 2002 category "Dead" and "Dying" were combined to compare with the 2017 category "Recently dead". The list of categories for coral conditions and descriptions are provided in Table 1. For bleaching comparability, surveys in 2002 and 2017 were both conducted during the late summer.

3.2.2. Massive *Porites* spp. colony comparisons

Eleven of the original twenty-three large *Porites* coral heads surveyed in 2002 (Jokiel et al., 2002) were relocated and resurveyed in 2017 (Fig. 5). The colonies in the east were originally selected as evidence of sediment impact and included most of the largest colonies found in that sector. Due to the lack of large colonies in the west, no data were collected at the unimpacted site. The remaining colonies of the initial 23 surveyed were excluded from the analysis either due to original error in GPS coordinates, differences in diameter, or substantial erosion, which precluded a positive match. Species, size, and percent live tissue were recorded as per the original survey (Jokiel et al., 2002). Colony size was determined by measuring the planar length and width. In the 2017 surveys, species, size, and condition of any coral recruits that had colonized the larger coral heads were included.

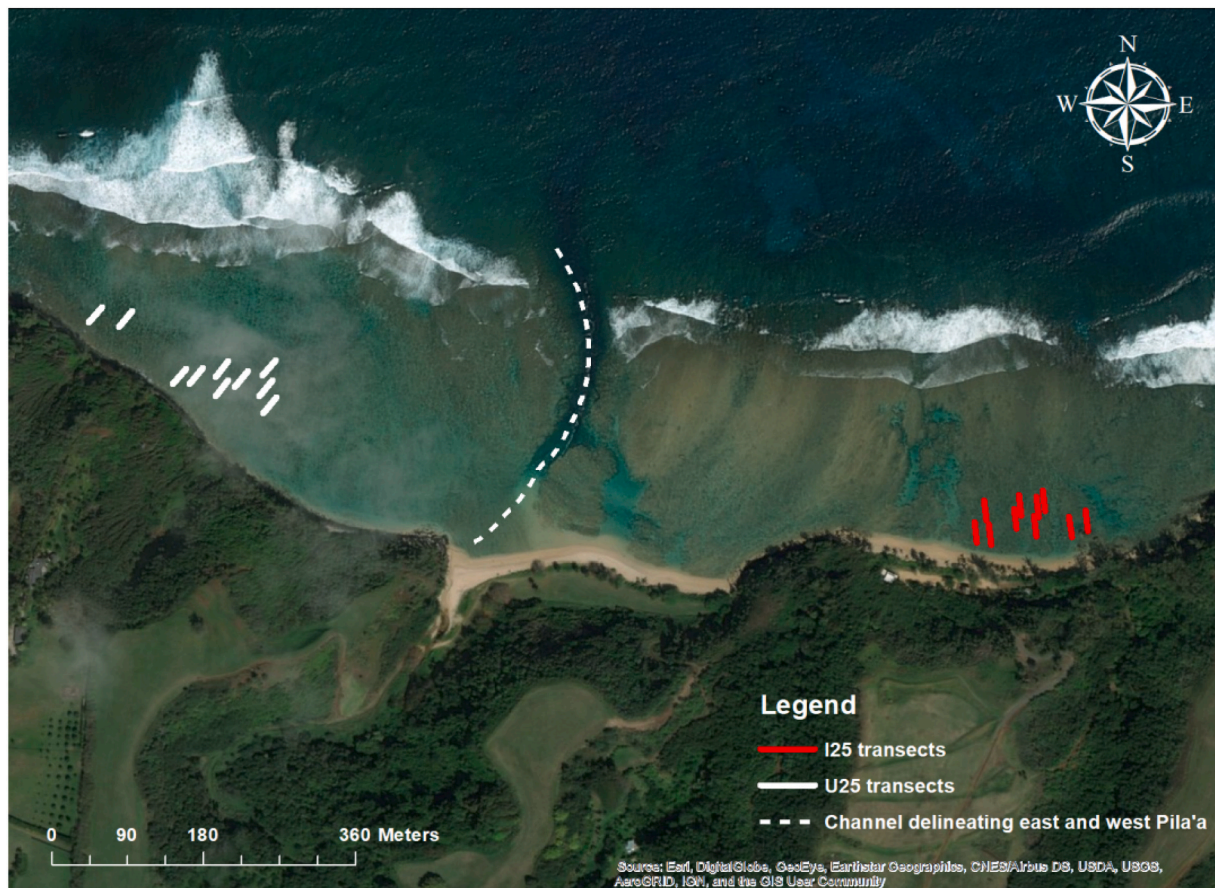


Fig. 4. Map showing locations of 25-meter transects (white lines = unimpacted, red lines = impacted) surveyed in 2002 and 2017 on the Pila'a reef flat. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Descriptions of condition categories assigned to each coral colony recorded in benthic surveys.

Category	Description
Normal	Corals exhibited normal tissue pigmentation with no signs of ongoing necrosis
Pale	Corals exhibited loss of pigmentation
Bleached	Corals exhibited white skeleton over 80% or more of the colony
Dying	Bleached corals exhibited signs of tissue loss and/or algal overgrowth
Recently Dead	Corals exhibited no live tissue and were newly colonized by algae
Dead	Corals exhibited no live tissue and were overgrown with algae or covered in sediment but were still distinct and attached to the substrate.

3.3. Statistical analyses

The statistical computing programs, R (version 3.3.1), the integrated development environment, RStudio Desktop (version 1.0.136), and PRIMER 5.0 were used to conduct the analyses.

3.3.1. Impacted and unimpacted sites (I25 1-10, U25 1-10)

The analyses of the 20 transects comparing impacted to unimpacted sites by year (2002 and 2017) were conducted on the statistical computing program, R (version 3.3.1) and its integrated development environment, RStudio Desktop (version 1.0.136) R Core Team 2020. The package “Vegan” in R was used to analyze species composition (Table 2). Coral cover data showed skewness following arcsine transformations,

thus a non-parametric test was used.

3.3.2. Frequency of live colonies and species composition

Colonies were summarized by the lowest taxa/species and mapped on an NMDS ordination plot to explore patterns of coral composition among transects across years. Species composition was analyzed using a non-metric multidimensional scaling (NMDS) to examine dissimilarity by year and site. Permutational multivariate analysis of variance (PERMANOVA, Anderson, 2001) was performed to determine whether the different sampling years and sites explain variation in species composition. As post-hoc analyses, an analysis of similarity (ANOSIM, Clarke, 1993) and similarity percentage analysis (SIMPER) were performed, investigating which pair-wise comparisons were likely influencing the overall effect of year on the dissimilarity of species composition. Species data were square-root transformed and Wisconsin double standardization was applied. Distance matrices were constructed and applied to the above analyses. A difference in number of species was analyzed using a two-way ANOVA with year and site followed by post-hoc Tukey HSD (Table 2).

3.3.3. Number of live coral colonies

Frequencies of live coral colonies were analyzed to examine changes in abundance between years, sites, and conditions. Since live coral counts are always non-negative and likely non-homogeneous, a generalized linear model (GLM) with a non-Gaussian distribution can be used to examine the effects of independent variables on the response variable (Zuur et al., 2007). A GLM with negative binomial distribution (NB) was applied to the count of live colonies, examining effects of years, sites, and condition. The upper and lower limit of a 95% confidence interval

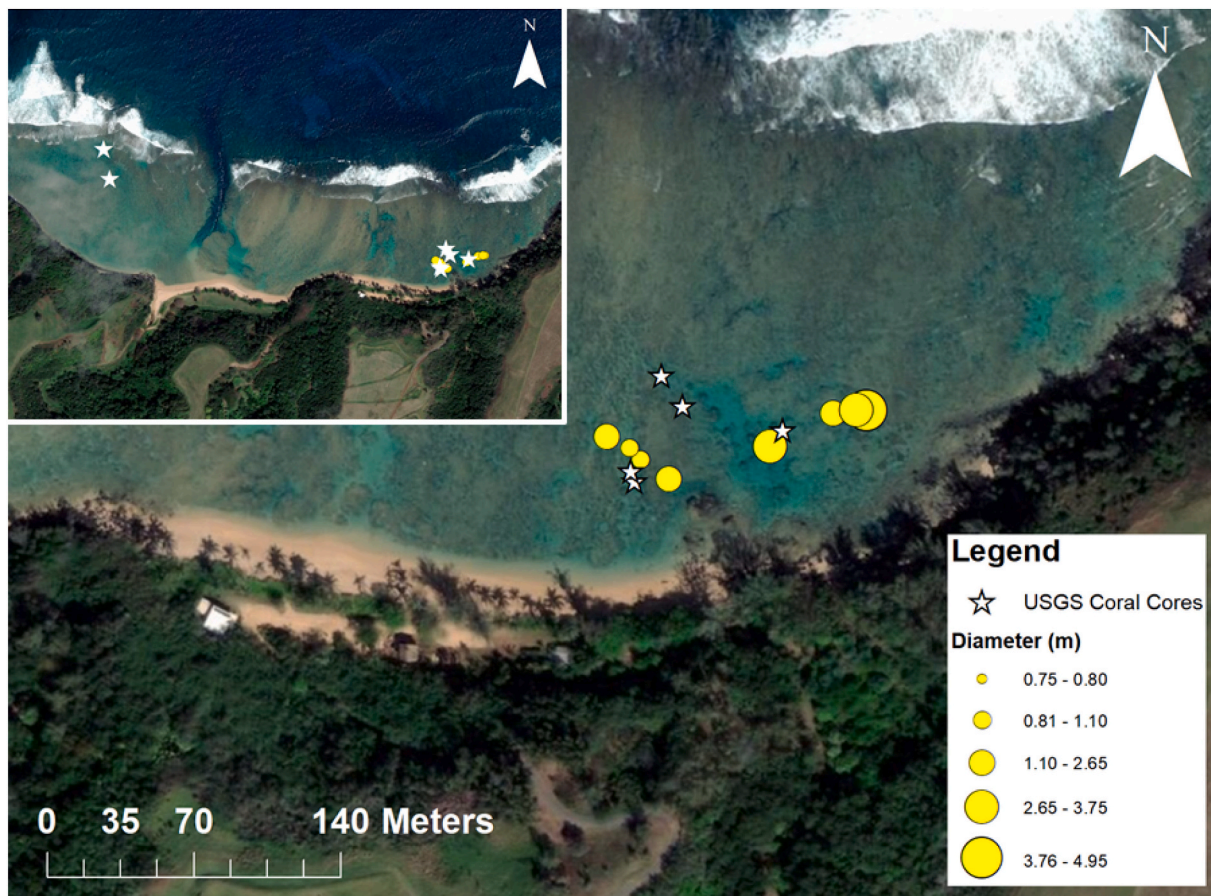


Fig. 5. Map depicting locations of large coral heads originally surveyed in June 2002 and revisited in June 2017 ($n = 11$). Yellow circles show size classes of original colonies; White stars indicate locations of coral cores collected. Inset image shows the location of two additional coral cores collected in the unimpacted western zone. Service Layer Credits: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Analyses, response, and statistical tests used in comparing transects between years.

Analysis	Response	Test
Live coral cover between 2002 and 2017 at impacted and unimpacted sites	% coral cover	Kruskal-Wallis tests
Species composition between 2002 and 2017 at impacted and unimpacted sites	Species and abundance, distance metric: Bray-Curtis similarity	nMSD PERMANOVA with ANOSIM, SIMPER
Number of species between 2002 and 2017 at impacted and unimpacted sites	Number of species	Two-way ANOVA
Number of live coral colonies by condition between 2002 and 2017 at the impacted and unimpacted sites	Colony counts in each condition (Normal, Bleached, Dead)	Generalized Linear Model with the negative binomial distribution
Number of live coral colonies in different size classes between 2002 and 2017 at impacted and unimpacted sites	Colony counts in each size class (cm)	Generalized Linear Model with the negative binomial distribution

was calculated to find substantial differences in the number of colonies in combinations of categories. Additionally, frequencies of live coral colonies were analyzed to examine changes in the abundance by years, sites, and by size class to investigate the demographic change between years. A GLM with poisson, negative binomial distribution, and a GLM

with zero-inflated NB were run and compared to explore over-dispersion, AIC, and results of likelihood ratio tests for comparisons. Since no significant difference was seen between GLM with NB and GLM with NB and zero-inflated models, a GLM with NB was applied to the colony count data, examining effects of year, site, and size class. The smallest and the largest size classes were pooled with the next closest size category because the average of each was less than one colony. The analysis was run on the dataset with these modified size classes as follows:

- A ≤ 5 (includes $< 2, 2-5$) cm.
- B $> 5 - \leq 10$ cm.
- C $> 10 - \leq 20$ cm.
- D $> 20 - \leq 40$ cm.
- E $> 40 - \leq 80$ cm.
- F > 80 (includes $> 80-160, > 160$) cm.

3.4. Coral cores

Using SCUBA and a submersible pneumatic hand-held drill, 2.5-cm diameter cores were collected from pre-selected *Porites* spp. colonies with minimal disturbance to the coral and surrounding environment (methods described in Prouty et al., 2009). Drill holes were capped with prefabricated Portland-carbonate cores to prevent bioerosion. Four coral cores (Pila1I, Pila 2I, Pila 6I, and Pila 7I) were collected from the sediment-impacted site and two coral cores (Pila 4U and Pila 5U) were collected from the unimpacted site in the west (Fig. 5). Additionally, shallow core tops (< 6 cm depth) from a visibly-dead, large *Porites* colony were collected from the impacted site to estimate time of mortality.

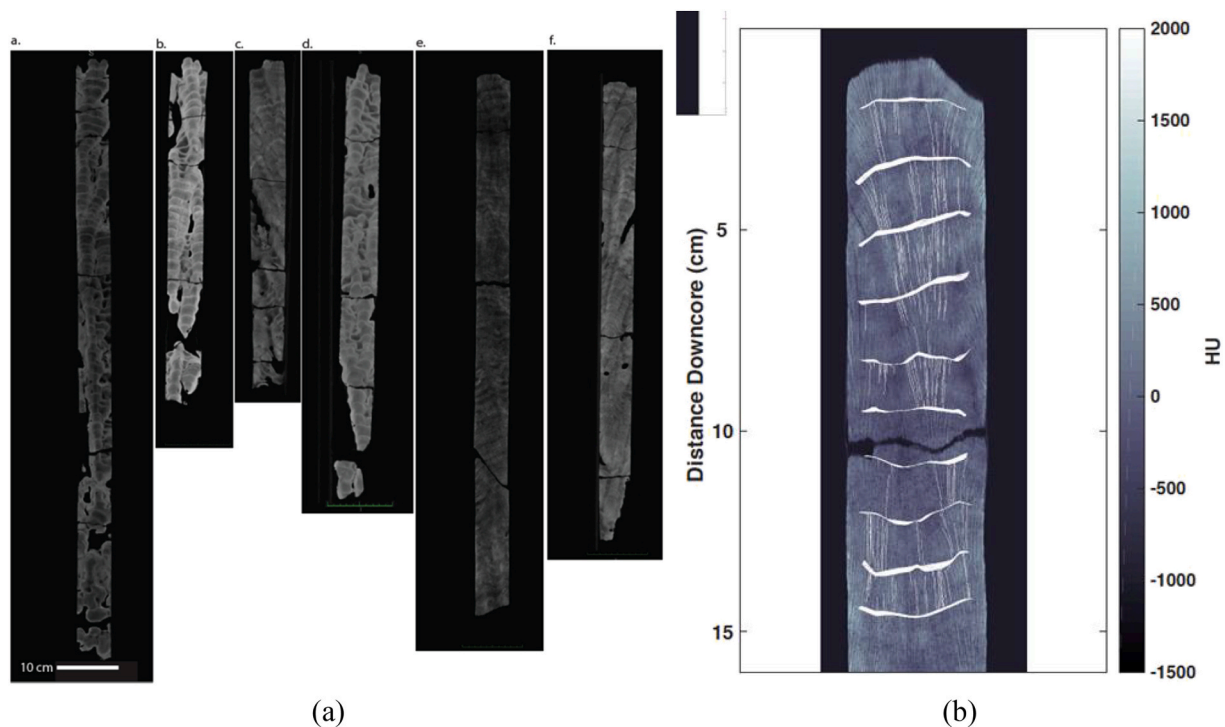


Fig. 6. (a) Computerized tomography (CT) scans of coral cores collected in the sediment-impacted eastern reef area. a. Pila1I, b. Pila2I, c. Pila6I, and d. Pila7I and in the unimpacted region to the west, e. Pila4U and f. Pila5U. CT scan images were used to calculate the proportion of the skeleton eroded by boring organisms. (b) Computerized tomography (CT) scans of the upper 20 cm of coral skeletal growth of Pila4U collected in the unimpacted west. Location of low-density (white) bands used for developing coral chronologies with coral CT. Variability in density is measured in “Hounsfield Units” (HU) and typically varies annually as a function of season.

Coral cores were analyzed for density (g cm^{-3}), extension (cm yr^{-1}), and calcification rates ($\text{g cm}^{-1} \text{yr}^{-1}$) at Woods Hole Oceanographic Institution (WHOI) Computerized Tomography (CT) Scanning Facility following methods described in Crook et al. (2013). This approach uses a Siemens Volume Zoom Spiral Computerized CT Scanner to reveal the high- and low-density couplets that constitute each annual growth band (Cantin et al., 2010; Crook et al., 2013; Prouty et al., 2014; Saenger et al., 2009). The distance between the high-density bands was used to calculate the average annual linear extension (growth) rates. The proportion of skeletons eroded by boring organisms (>1 mm boring diameter) was calculated using CT scan images from coralCT (DeCarlo and Cohen, 2016; Fig. 6). The total volume of CaCO_3 removed relative to the total volume of the individual *Porites* coral core was calculated based on previously established methods by Barkley et al. (2015) and DeCarlo et al. (2015). Coral life spans were calculated based on annual growth rates and core lengths. Life span for the dead specimen (core tops) was determined by comparing bomb-derived radiocarbon (^{14}C) values to reference bomb-curves from Hawai'i (Demartini et al. 2018). Accelerator Mass Spectrometry (AMS) radiocarbon (^{14}C) dating was conducted at the National Ocean Sciences Accelerator Mass Spectrometry (NOSAMS) facility at WHOI.

Coral cores were cut into 5–10 mm slabs using a diamond blade band saw and cleaned in an ultrasonic bath using deionized water. Coral slabs were prepared and analyzed at the University of California at Santa Cruz's Marine Analytical Lab using a Photon Machine 193 nm ArF excimer laser and a Thermo X-series II quadrupole ICP-MS. Samples and standards were pre-ablated with a scan speed of 400 m s^{-1} and a laser pulse rate of 40 Hz (1 pulse per 10 m) to remove any material that had accreted to the surface of the coral skeleton slab during coral cutting and handling. Samples and standards were ablated with a scan speed of 40 m s^{-1} and a laser pulse rate of 10 Hz (1 pulse per 4 m). Samples were bracketed by three standards: NIST 610, NIST 612, and JCP-1 (a Japanese ground coral standard). Two parallel tracks spaced horizontally

2.5 mm apart were along the major growth axis along the length of each coral. Elemental concentration data were background-corrected, drift-corrected, and calibrated using a MATLAB script following similar methods described in Sinclair et al. (1998). Samples were calibrated using the concentration data reported for the NIST 610 standard. The NIST 612 and JCP-1 standards were used to check the calibration and to assure that major biases are not introduced due to matrix differences. All concentrations were normalized to ^{43}Ca to account for variations in coral surface architecture and density (Fallon et al., 1999). Spurious outliers in the dataset were removed when individual points deviated more than three standard deviations from the mean before and after the individual sample, similar to the approach of using a 10-point running median to remove outliers as reported in Sinclair et al. (1998). The chronology for the coral Ba/Ca time series was based on annual linear extension rates derived from the CT analysis. The Ba/Ca time-series was resampled at equal time steps using Arand TIMER software (Howell et al., 2006) to yield sub-weekly resolution. In addition, trace metal analysis was conducted via solution ICP-MS on water and sediment samples collected from each coral site and the nearby stream for comparison with coral elemental concentrations.

3.5. Sediment analyses

Bulk replicate sediments were collected from seven locations on Pila'a reef flat in 2002 and 10 comparable locations in 2016 for comparison. Approximately 500 cm^3 of sediment were collected by hand along transects at each site and secured in Fisher brand $9 \times 18 \text{ cm}$ sample bags. Identical methodology was employed in both years for collection and processing (Parker, 1983; McManus, 1988; Craft et al., 1991).

3.5.1. Sediment grain-size

Subsamples were taken from each of the two replicates collected

from each location. Standard brass sieves were used to determine size fractions in accordance with the Wentworth scale (Folk, 1980): >2.0 mm (granule), >500 μm - <2 mm (coarse and very coarse sand), >250-<500 μm (medium sand), >63-<250 μm (fine and very fine sand), and <63 μm (silt/clay; USA Standard Testing Sieve: A.S.T.M.E.-11 specifications). To determine the relative proportions of each size fraction, each sample was collected onto pre-weighed Whatman 114 wet strength filters, then air-dried and weighed three times to account for changes in humidity and averaged. Particularly large pieces were discarded to reduce variability and eliminate overweighting by a single piece of material.

3.5.2. Sediment composition by loss on ignition (LOI)

Sediment was processed for composition analysis following two weeks of air-drying. To determine the inorganic-organic carbon fraction, 20 g of bulk sediment per sample was finely ground using an IKA microfine grinder model A1 BS1. Ground subsamples were oven-dried for 10 h at 100 °C, cooled in a desiccator, and weighed. To remove the organic fraction, 10 g of the ground subsample was placed in a muffle furnace for 12 h at 500 °C, cooled in a desiccator, and weighed. For removal of carbonate material, samples were placed in a muffle furnace for 2 h at 1000 °C, cooled in a desiccator, and weighed. The remaining sample after initial incinerations represented terrigenous material, and loss on ignition values were then used to calculate proportions of each sediment component (organic, carbonate, terrigenous).

4. Results

4.1. Hydrological conditions

Long term averages for mean monthly precipitation and stream discharge are shown in Table 3. Total daily precipitation from 2001 to 2017 is shown in Fig. 7, and mean daily discharge for Halaulani Stream is shown in Fig. 8.

4.2. Benthic coral surveys

4.2.1. Live coral cover

In 2002, the difference in coral cover between impacted and unimpacted sectors was significant ($n = 20$, $df = 1$, $p < 0.001$; Supplemental Fig. 1), with much higher cover in the unimpacted west. We found no statistical difference in live coral cover between the two sectors in 2017. When comparing across years, a statistically significant increase in coral cover ($n = 20$, $df = 1$, $p = 0.01$) was found in the impacted eastern sector from 2002 to 2017 while no statistically significant difference was found in coral cover in the unimpacted west across years.

4.2.2. Species composition

A compositional shift in coral species has occurred in the 15 years between surveys. A total of 10 species were reported in the impacted east in 2002 compared to 11 in the unimpacted west. Data on the large number of recently dead corals in 2002 provided a baseline of live corals just prior to the sediment event in 2001. These data shows that prior to the sedimentation event, the dominant species in the impacted area were *Porites compressa*, *Pocillopora meandrina*, *Montipora capitata*, and *Montipora patula*, in descending order. In the unimpacted west, *P. compressa*, *M. capitata*, and *Porites lobata* dominated. In the 2017 impacted area surveys, we found no change in numbers of Montiporids

but an approximate 50% decline in *P. compressa* and a 43% decline in *P. meandrina* from the 2002 baseline. In the unimpacted area only small numbers of recently dead colonies were counted and these were not attributed to the sedimentation event since they were outside the impact zone, thus no change in species dominance in the west was reported as a result of the sediment event.

In 2017, the total number of species increased from 10 in 2002 to 12 in the impacted east with the addition of two new species: *Porites lichen* and *Pocillopora eydouxi* (Supplemental Fig. 2a). In the unimpacted west, the number of species increased from 11 in 2002 to 17 with the additions of *Cyphastrea agassizi*, *Lobactis scutaria*, *Pocillopora damicornis*, *P. eydouxi*, *Psammocora stellata*, and *Porites lichen*. Species dominance shifted to *M. capitata* and *P. compressa* in the impacted east with a 438% and 389% increase, respectively, in total colony numbers. *Cyphastrea ocellina*, *M. patula*, *M. capitata*, and *Pavona varians* were dominant in the unimpacted west in 2017 with *C. ocellina* counts increasing from one colony in 2002 to 200 colonies in 2017. *Montipora patula*, *M. capitata*, and *P. varians* abundance increased by 403%, 141%, and 1625%, respectively. *Montipora flabellata*, *P. damicornis*, and *P. brighami* colony numbers decreased by more than 50% from 2002 to 2017 in the impacted east. In 2017, in the unimpacted west, *M. flabellata*, *P. compressa*, and *P. lobata* all decreased substantially.

4.2.3. Impacted vs. unimpacted

Species assemblages were highly dissimilar in the impacted east as compared to the unimpacted site in 2002 (ANOSIM R-statistic = 0.83, $p < 0.001$, Supplemental Fig. 2b). The R-statistic in ANOSIM is the ratio of within-group and between-group dissimilarity ranking where the ranking of 1 indicates the highest level of dissimilarity and 0, none. This dissimilarity can be largely attributed to the much higher numbers of *P. compressa*, *P. lobata*, *M. flabellata*, and *P. duerdeni* in the unimpacted west as compared to the impacted east. Likewise, the dissimilarity in 2017 between sectors ($R = 0.55$, $p < 0.001$) was driven primarily by larger numbers of *C. ocellina*, *M. patula*, *P. varians*, and *P. brighami* in the unimpacted west. Notably, the dissimilarity between sectors decreased from 2002 to 2017.

4.2.4. Comparison between years

Species composition in the impacted eastern sector was highly dissimilar between 2002 and 2017 ($R = 0.73$, $p < 0.001$) driven by large increases in colonies of several species and a decline in one. High dissimilarity in the unimpacted sector between years ($R = 0.83$, $p < 0.001$) is due in large part to a great increase in the diminutive species *C. ocellina*, and of *P. varians* and *M. patula* in 2017.

4.2.5. Size class and condition

A relatively small AIC, McFadden pseudo- R^2 (82% condition, 72% size class), and over dispersion indices suggested that the GLM with negative binomial distribution, including 3-way interactions was the best fit for these analyses. There were significant overall effects of year ($p < 0.001$), site ($p < 0.001$), size class ($p < 0.001$), and condition ($p < 0.001$) on the number of colonies, indicating that the variation in the number of coral colonies was affected by these factors. A significant 3-way interaction suggests that the year-size interaction varies by site and the year-site interaction varies across conditions.

A significantly greater number of live (normal and bleached) coral colonies was observed in 2017 ($n = 508$) than in 2002 ($n = 148$) in the impacted east with even greater differences in the unimpacted west

Table 3

Long term averages (from 2001 to 2017) for mean monthly precipitation (mm) and mean daily discharge (cfs) from the Koloko rain gauge (USC00514758) and USGS Halaulani stream gauge (16097500).

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Mean Monthly Precipitation (mm)	141.6	169.7	293.1	134.0	163.0	114.6	123.9	114.2	101.9	151.2	183.0	201.8
Mean Daily Discharge (cfs)	8.7	12.0	17.0	10.0	9.9	8.3	7.7	8.7	7.9	9.1	13.0	12.0

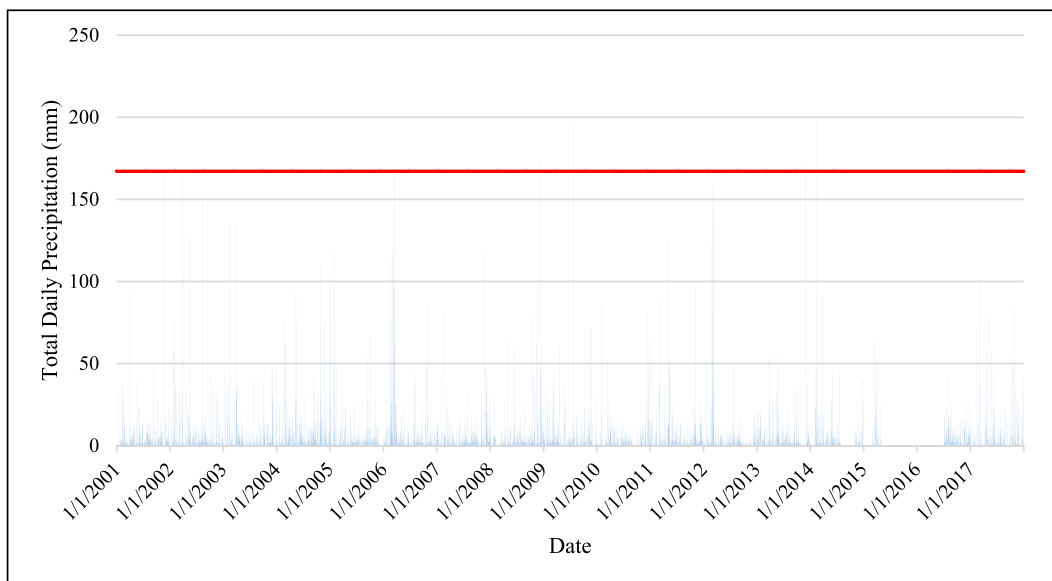


Fig. 7. Total daily precipitation (mm) from the Koloko reservoir rain gauge from 2001 to 2017. The red horizontal line depicts the amount of rainfall that occurred during the 2001 storm event. Note the data gap for rainfall between May of 2015 to June of 2016. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

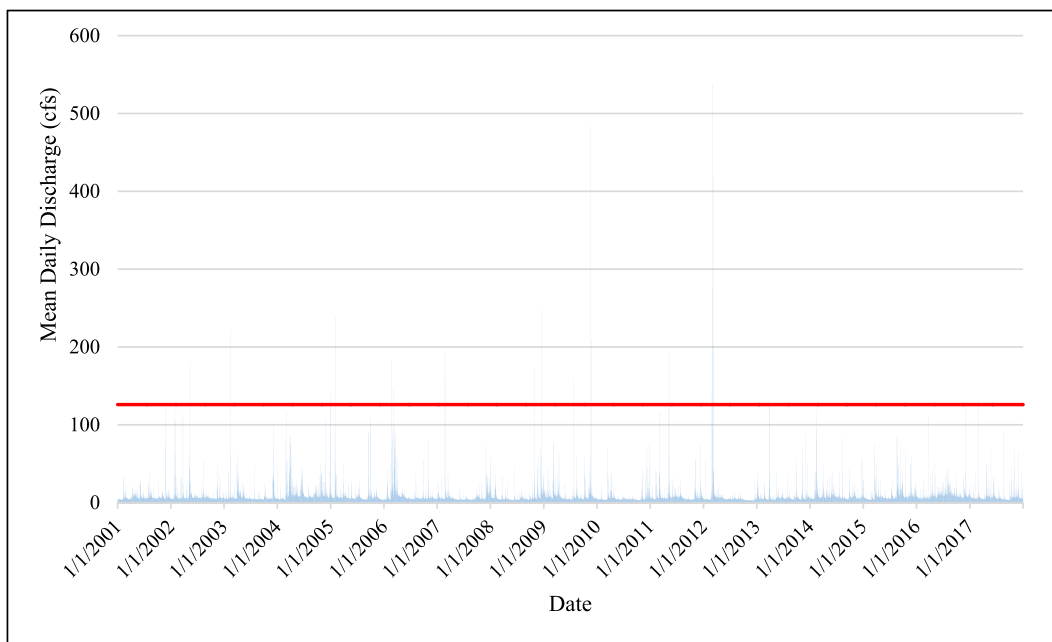


Fig. 8. Mean daily discharge in cubic feet per second (cfs) for Halaulani Stream from 2001 to 2017. The red horizontal line depicts the discharge recorded during the 2001 storm event. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(2017 $n = 986$, 2002 $n = 396$; Fig. 9a and b). Live coral cover increased from 2002 to 2017 in the impacted east in all size categories except the <2 cm and the two largest size categories (80–160 cm and >160 cm). Similarly, increases occurred in all size classes except the three largest in the unimpacted west from 2002 to 2017. In both sectors, size class distribution was strongly skewed towards smaller sizes from 2 to 40 cm. The number of bleached colonies was higher in 2017 than in 2002 across all sites and in 2017, bleached colony numbers were higher in the unimpacted west than in the impacted east (Supplemental Table 1).

4.2.6. Massive *Porites* colony comparisons - eastern sector

Eleven of the original 23 massive *Porites* colonies surveyed in 2002 were located and re-surveyed in 2017. Seven of these colonies suffered full mortality from the 2001 sedimentation event. A colony with 5% live tissue in 2002 was entirely dead in 2017. Three colonies with 40%, 45%, and 60% live tissue in 2002 increased to 83%, 90%, and 90% respectively, in 2017 (Table 4). Ten species of corals recruited onto the 11 large colonies re-surveyed in 2017. Nearby large colonies had up to 110 recruits (Supplemental Fig. 3).

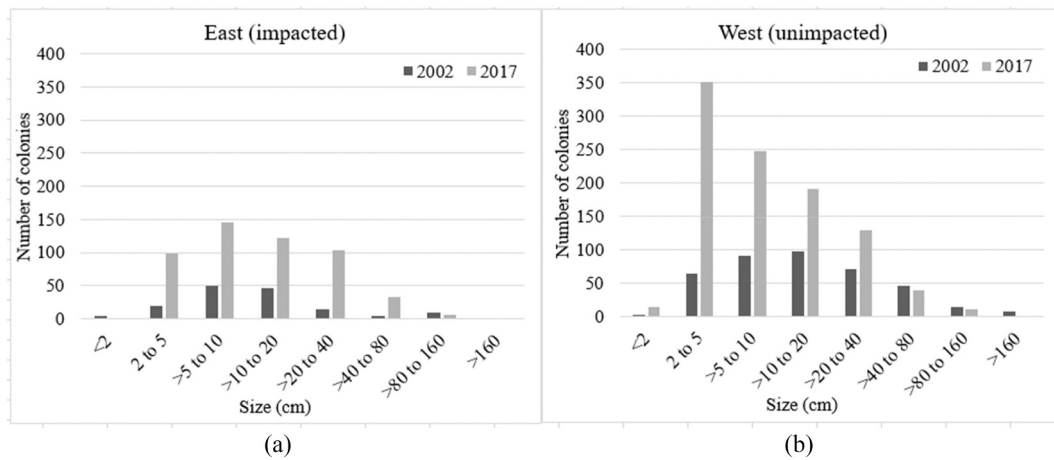


Fig. 9. Number of live coral colonies by size class in the (a) impacted east and (b) unimpacted west.

Table 4

Identification, GPS coordinates, diameter, percent live tissue, and number of recruits found on massive coral colonies assessed in the sediment impact zone at Pila'a in 2002 and 2017. Diameter in 2017 is recorded as the length of longest cross-section in meters.

Colony	Latitude	Longitude	2002 Diameter (m)	2017 Diameter (m)	2002% Alive	2017% Alive	Number of recruits
1	22.21214	-159.35809	1	0.7	5	0	1
2	22.2121	-159.35799	1	1.1	0	0	5
3	22.21205	-159.35795	1	1.1	0	0	1
4	22.21205	-159.35795	1	0.8	0	0	1
5	22.21205	-159.35795	1	1	0	0	1
6	22.21204	-159.35797	0.5	0.75	0	0	8
7	22.21197	-159.35782	2.5	2.65	0	0	6
8	22.2121	-159.35739	3	3	0	0	12
9	22.21223	-159.35712	1.5	1.95	45	90	2
10	22.21225	-159.35702	2	3.75	40	83	9
11	22.21225	-159.35698	3	4.95	60	90	1

Table 5

Coral coring locations on Pila'a reef collected in June 2017. Coral growth parameters (average \pm SD) quantified by computerized tomography (CT) for growth rate, density, and calcification rates, percent volume erosion, and lifespan. Pila1I, Pila2I, Pila6I, and Pila7I were collected in the impacted east. Cores Pila4U and Pila5U were collected in the unimpacted west.

Coral ID	Length	Latitude (WGS84)	Longitude (WGS84)	Species	Bioerosion volume (%)	Growth rate (cm yr ⁻¹)	Density (g cm ⁻³)	Calcification (g cm ⁻² yr ⁻¹)	Lifespan (years)
Pila1I	102	22.21196	-159.3579	<i>P. lutea</i>	8.2	1.34 \pm 0.27	0.89 \pm 0.06	1.18 \pm 0.19	76
Pila2I	57.5	22.21201	-159.35799	<i>P. compressa</i>	10.81	1.39 \pm 0.22	0.98 \pm 0.06	1.35 \pm 0.18	41
Pila6I	52	22.21226	-159.35777	<i>P. compressa</i>	9.58	1.54 \pm 0.27	0.71 \pm 0.07	1.07 \pm 0.15	34
Pila7I	67.5	22.21238	-159.35785	<i>P. compressa</i>	4.25	1.30 \pm 0.26	0.91 \pm 0.07	1.17 \pm 0.19	52
Pila4U	82	22.21385	-159.36548	<i>P. lobata</i>	<1	1.20 \pm 0.16	1.11 \pm 0.08	1.32 \pm 0.19	68
Pila5U	59.5	22.21448	-159.36562	<i>P. lobata</i>	2.61	1.21 \pm 0.28	1.13 \pm 0.10	1.37 \pm 0.31	49

4.3. Coral cores

Average coral growth rates (e.g., linear extension) varied between 1.20 ± 0.16 cm yr⁻¹ and 1.54 ± 0.27 cm yr⁻¹ and are higher compared to those reported from sediment-impacted sites in Molokai, Hawai'i and Guam (Table 5). According to the calculated growth rates, lifespans of individual *Porites* spp. colonies ranged between 34 and 76 years for coral cores collected from living specimens. Estimated time of death from a dead colony in the impacted region is between 2009 and 2012, according to age-dating using reference bomb curves from Hawai'i (DeMartini et al., 2018). Average (\pm SD) density ranged from 0.71 ± 0.07 to 1.13 ± 0.10 g cm⁻³ and calcification rates averaged 1.07 ± 0.19 to 1.37 ± 0.31 g cm⁻² yr⁻¹. Percent bio-erosion volume ranged from less than 1% to 10.8%, noticeably lower than those reported from West Maui where nutrient-laden groundwater is accelerating bio-erosion rates (Prouty et al., 2017). Comparing the average growth parameters over the life span of the corals revealed a spatial

difference between the impacted sites in the east and the unimpacted sites in the west. Except for calcification rates, all measured growth parameters (i.e., growth rate, density, and bio-erosion volume) from the sediment-impacted site in the east were statistically different from cores analyzed at the unimpacted, control site in the west (4C, 5C) (Student's *t*-test $P < 0.05$). Compared to the control site, growth rate and density were lower and percent bio-erosion volume was higher at the impacted site (Table 5).

Interannual variability in coral growth parameters was observed. For example, extension and calcification rates declined between 2000 and 2011 from the Pila2I record and rates appear to inversely track density. In comparison, changes in growth parameters at the control site, as captured in the Pila4U record, were more gradual and merge in the last decade. The high-resolution Ba/Ca time-series displays high variability in both records. However, baseline values are similar across the reef flat, centered at 5 U, consistent with the range in Ba/Ca baseline values reported from Molokai (4 to 6 $\mu\text{mol mol}^{-1}$; Prouty et al., 2010). Periods of

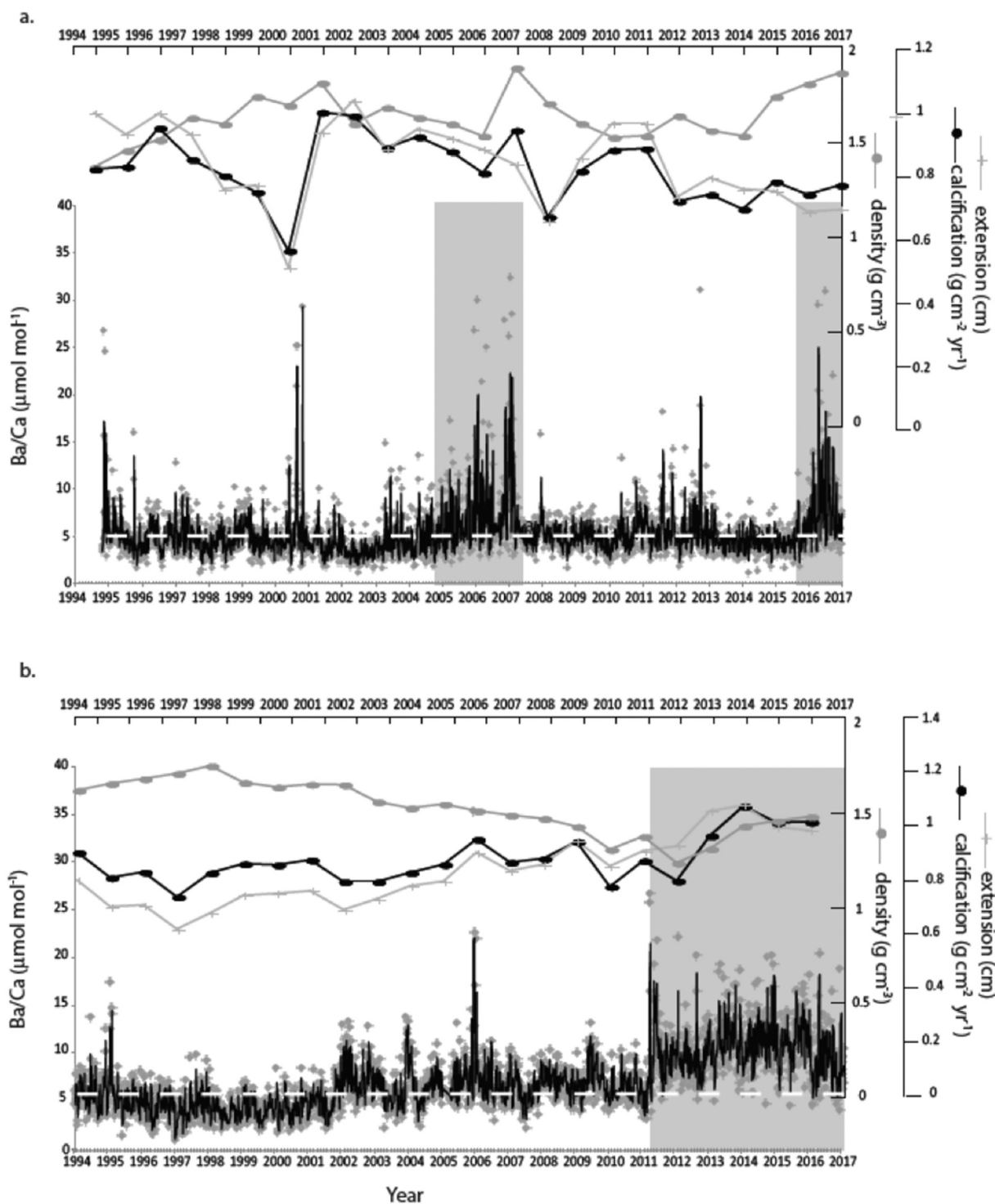


Fig. 10. High-resolution time-series of barium:calcium (Ba/Ca) ratios from the (a) impacted site (Pila2I) and the (b) unimpacted region (Pila4U). Running mean (2-pt; black) superimposed on sub-weekly Ba/Ca data points (grey diamonds). Shaded grey areas represent periods of elevated Ba/Ca ratios above baseline (dashed white line). Corresponding annually derived coral growth parameters (density, calcification and extension rates) are also shown for the period of overlapping skeletal growth.

elevated Ba/Ca values punctuated both records at Pila'a. A sharp increase in Ba/Ca values occurred between 2000 and 2001. These values were concurrent with a decrease in calcification and extension rates, with Ba/Ca values peaking at $30 \mu\text{mol mol}^{-1}$, enriched by six times relative to baseline values. A period of sustained enrichment occurred between 2005 until mid-way through 2007, and again throughout 2016 at the impacted site, as captured in the Pila2I record. Increases in Ba/Ca

values at the control site, shown for Pila4U, are not synchronous with the impacted site. Instead, baseline Ba/Ca values increase starting in 2002, and again display a sustained enrichment in 2011 through 2016 (Fig. 10a and b). This latter enrichment is marked by an increase in extension and calcification relative to the previous two decades.

Table 6

Mean sediment composition and grain size fractions (% of total) shown with standard deviation in 2002 and 2016 separated by Pila'a east and west sectors.

		WEST (unimpacted)		EAST (impacted)	
		2002	2016	2002	2016
Composition	Organics	3.2	3.2 ± 0.1	4.9 ± 2.0	3.7 ± 0.5
	Carbonate	93.3	94.3 ± 0.3	81.2 ± 13.5	93.2 ± 1.3
	Terrigenous	3.5	2.5 ± 0.2	13.9 ± 11.6	3.2 ± 0.8
Grain size	Gravel /coarse	96.8 ± 0.6	89.3 ± 3.9	73.8 ± 13.6	87.4 ± 8.5
	Medium sand	2.9 ± 0.5	8.15 ± 4.6	6.6 ± 6.5	7.0 ± 5.0
	Fine sand	0.1 ± 0.1	2.0 ± 0.6	4.8 ± 2.7	4.7 ± 5.9
	Silt/clay	0.2 ± 0.1	0.51 ± 0.3	14.8 ± 13.7	0.90 ± 0.8

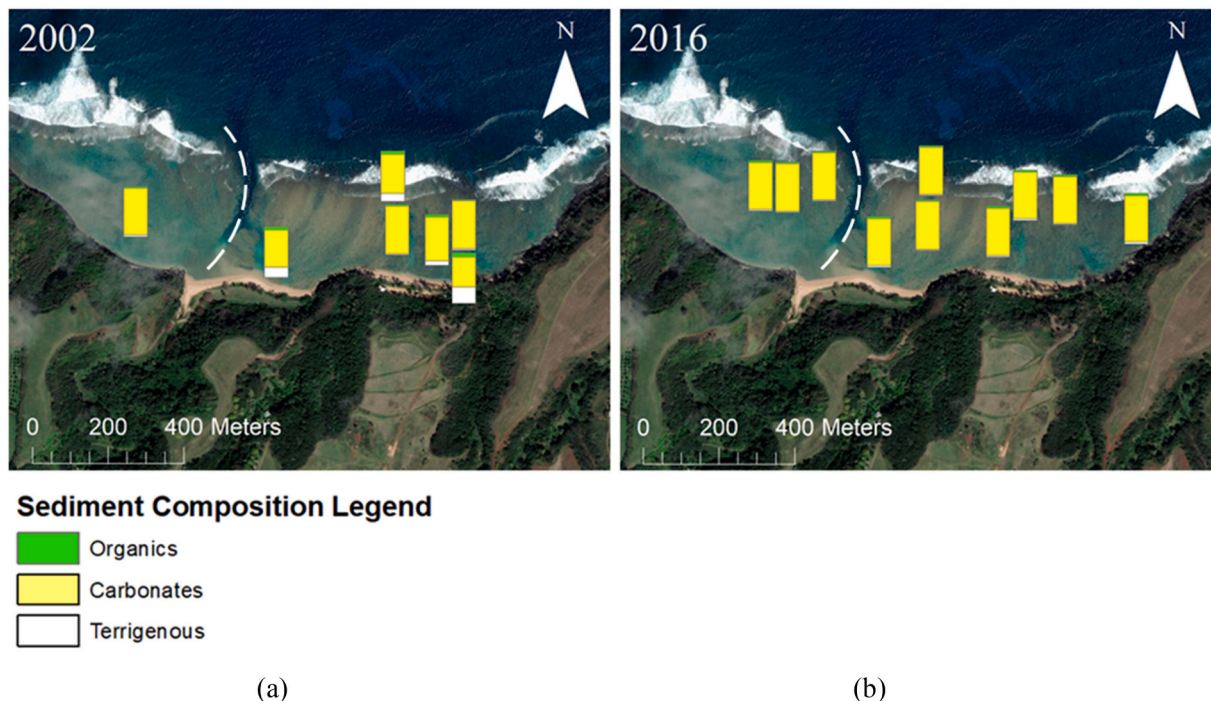


Fig. 11. Sediment composition by location in percent of the total in (a) 2002 and (b) 2016 at Pila'a, Kaua'i. The channel that divides the east and west reef is delineated by the white dashed line. Service Layer Credits: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community.

4.4. Sediment analyses

Mean fine silt/clay sediment significantly decreased in the impacted eastern sector 15 years after the large sediment event in 2001, declining from 15.0% of total sediment grain sizes to 0.9% in 2016 ($p = 0.024$). Similarly, mean organic (4.9%) and terrigenous (13.9%) components of the sediment substantially decreased from 2002 to 3.7% and 3.2% in 2016, respectively. Inversely, CaCO_3 increased from 81.2% in 2002 to 93.2% in 2016 (Table 6, Fig. 11a and b).

In the unimpacted west, mean fine silt/clay sediment was similar in 2002 (0.2%) and 2016 (0.5%) (Table 6). No statistical differences in percent organics were detected between 2002 (3.2%) and 2016 (3.2%). CaCO_3 and terrigenous fractions were also similar between 2002 (93.3%, 3.5% respectively) and 2016 (94.3%, 2.5%).

In 2016 at the impacted site in the east, there were only slightly higher organics (3.6%) than at the reference site in the west (3.2%) and low silt/clay composition in the east (0.91%) and west (0.52%). This was in concert with other Kaua'i organic percentages (3–4% range) (Rodgers, 2005).

5. Discussion

Results of this study comparing surveys conducted in 2002 to replicate surveys in 2017, found significant changes in species assemblages, size-frequency distributions, recruitment of corals onto large, dead colonies, and increases in number of coral colonies and species, indicating a partial coral community recovery on the impacted reef flat. Statistically higher coral cover was found in the unimpacted west in 2002 while no significant difference was found in coral cover between the two sectors in 2017. These results support partial system recovery over the 15-year period. In addition, coral cores indicate historical temporal patterns of increased linear extension and calcification rates since 2001. Significant reductions have been established in fine-grain sediments and organic and terrigenous components of sediments from 2002 to 2016 in the impacted eastern sector and no significant changes in sediment fractions or composition in the unimpacted western sector provides additional supporting evidence of partial recovery from the initially documented sediment event. Slow coral growth rates prevent full recovery in a 15-year period while repeated periodic disturbances inhibit system equilibrium. These data may help explain why the recovery process appears to be perpetually at an early or intermediate

stage.

During this 15-year period from 2002 to 2017 documented disturbances on the Pila'a, Kaua'i reef flat include the flood event that resulted in a massive mudslide, depositing sediment on the eastern reef flat in 2001, sediment resuspension and high stream discharge events, a storm event causing extensive coral fragmentation in the western sector in 2003, and a widespread bleaching event that affected the entire main Hawaiian Islands in 2014/2015. Surveys following the flood and wave events found significant damage. The 2001 sediment event caused severe mortality in the impacted east as compared to the unimpacted west (Jokiel et al., 2002). Reports from the 2003 high surf anomaly in the west reported a reduction of coral cover from 14% to 6% and a loss of 30% of the coral colonies surveyed prior to the wave event. These waves did not impact the more protected eastern sector that reported a significant increase in live coral colonies (Jokiel and Brown, 2004b). The 2014/2015 bleaching event was documented throughout the main Hawaiian Islands (Kramer et al., 2016). On the north shore of Kaua'i, 50% and 89% bleaching was reported (Neilson, 2014). Although no follow up surveys were conducted to determine the levels of mortality on Kaua'i, the rest of the state ranged from no mortality to over 50%.

Pila'a reef is actually two reefs with different wave and current patterns that differentially influence the effects of natural and anthropogenic disturbances. The land grading that began in the 1990s had a pivotal effect on the eastern sector as this, coupled with heavy rainfall, resulted in large amounts of terrigenous inputs, likely several times from 1994 to 2001, on an initially healthy but increasingly degraded reef as time passed. The short return intervals between events, as evidenced by historical temperature, meteorological data, and recruitment data from our surveys, show that recovery has not progressed unhindered. This is especially apparent in the eastern sector. In the years following the largest sediment event in 2001, several storm events and high stream discharges likely deposited sediment onto the reef. A year of chronic resuspension of sediment following the 2001 mudslide likely also impacted coral spawning and recruitment (Padilla-Gamiño and Gates, 2012; Padilla-Gamiño et al., 2014; Lacks, 2000).

In the Hawaiian archipelago, reef-building coral species composition is generally homogeneous and most Hawaiian species can be found wherever favorable substrate exists (Grigg, 1983). Successional recovery after disturbance is determined by the frequency, duration, and severity of the disturbance, as well as the possibility of recruitment. Wave energy is the primary driver of post-disturbance species composition on seaward reefs but on sheltered reefs and areas with strong human impacts, the primary mechanism controlling community structure is anthropogenic disturbance (Grigg, 1983; Rodgers, 2005). The Pila'a sedimentation event in 2001 was due to anthropogenic land modifications however, chronic, nearshore resuspension of fine mud sediment continued to occur through 2004 despite the fact that, by then, most of the seaward sediment had been flushed out of the system. In 2017, we found that successional recruitment was underway, but the majority of nearshore massive *Porites* spp. colonies had not survived.

In addition to the sediment stressors occurring during our study period from 2002 to 2017, a stochastic flood event, breaking all historical precipitation records, occurred in 2018, after our surveys, heavily impacting coral cover on this shallow reef flat (Rodgers et al., 2021). In response to the massive freshwater input, algae and an invasive octocoral were able to overgrow and outcompete coral for recruitment space. These continual assaults to the coral reef community do not allow full recovery, keeping the system in constant flux. Successional climax through modeling has been reported on undisturbed reefs to take between 17 and 200 years, depending on growth and dominance (Maguire and Porter, 1977). Although Grigg and Maragos (1974) estimate a 50-year period to reach full recovery of community equilibrium in Hawai'i, the process is likely extended or cannot reach equilibrium due to the increasing frequency and severity of periodic environmental disturbances.

5.1. Hydrological conditions

During the storm event of November 2001, the highest daily total rainfall was 167 mm, which is substantially high when compared with mean monthly rainfall records from Table 3. Recent records show that rainfall exceeded 167 mm five times since the 2001 event. The highest daily stream discharge mean during the 2001 storm event was 126 cfs. Subsequently, mean daily discharge that exceeded this amount occurred 23 times from 2002 to 2017 (Fig. 8). This average flood frequency of 1.4 times per year (24 events/17 years) is identical to the calculations from previous research that utilized historical records over a 45-year period (Jokiel et al., 2002). These data suggest that Pila'a reef recovery may be hindered by chronic flooding, and freshwater input.

5.2. Benthic surveys

Coral species composition at Pila'a reef has changed since 2002 and trends towards smaller, encrusting colonies. Declines in *Pocillopora meandrina* and an increase in other species suggest successional patterns of recovery are underway. This is consistent with the assessment by Jokiel and Brown (2004a, 2004b) that conditions at Pila'a reef had improved, much of the fine sediment had been flushed from the system, and signs of recovery were already apparent. Ecological succession is defined as the process of recovery, whereby a sequence of species or groups of species is present at different times following a disturbance to an ecosystem. Pioneer species are generally robust, arrive early, and are able to succeed despite harsh conditions of the changed environment (Hobbs, 2009). Succession on new reef substrate or following coral mortality generally begins with macroalgae followed by the pioneer coral species *P. meandrina* (Grigg, 1983). Colonizers that may eventually dominate include species with wave-tolerant morphologies, i.e., encrusting *Montipora* spp., or slow-growing, dense skeleton species such as *Porites lobata*. Competitive species, i.e., *Porites compressa*, are also among the first species to appear after disturbance. Our results are consistent with these known patterns of succession and recovery on Hawaiian reefs, however, changes in environmental conditions may result in changes to the overall community species distribution. For example, we observed a Chrysophyta golden-brown algae bloom in 2016, a notable increase in cyanobacterial mats in 2017, and a prominent octocoral, *Sarcothelia edmondsoni*, bloom in 2018 that were all confined to the eastern and central channel nearshore area near stream input. These benthic shifts are likely the result of the heavy rain and freshwater flood events with associated nutrient and sediment laden runoff and likely contributed to coral stress through increased competition for suitable growth substrate.

Coral growth rates are not fast enough for new colonies to reach larger size classes in the 15-year recovery period assessed. However, fifteen years after a mass mortality event, we might expect to see a more developed mid-range size class grouping. Several factors, including increased SSTs, waves, and heavy rainfall events, are likely contributing to the small skew. The predominance of small *M. capitata* and *M. patula* colonies may be due to loss of tissue leading to colony fragmentation where more small "individual" colonies are recorded. 2014 marked the beginning of a multi-year warming event that resulted in worldwide coral bleaching and mortality through 2017. Mean temperatures at Pila'a were nearly 2 °C higher in the east where coral bleaching was more prevalent in 2017. The bleaching threshold for Hawaiian corals is 29–30 °C, a 1–2 °C increase above the upper summer maxima (Jokiel and Coles, 1977; Coles et al., 1976). June temperatures at Pila'a were within this range in the east (29.7 °C) and near the threshold in the west (28.9 °C). Although bleaching was not observed in 2002, 24% of corals were bleached in 2017. The endemic species *Montipora flabellata* is in current decline at Pila'a and was observed as the first to bleach severely in Kane'ohe Bay in 2014 (unpublished data, A. Richards Donà). It is possible its decline at Pila'a is due to temperature increases, which further illustrates the complicated dynamics of loss and recovery at Pila'a.

5.3. Coral cores

Ba sourced from fine-grained components of terrestrial soil is a useful proxy for the amount of land-based sediment to the coral environment (e.g. Fleitmann et al., 2007; Grove et al., 2012; McCulloch et al., 2003; Prouty et al., 2010). For example, at Pila'a, the stream sediment sample yielded a Ba concentration of 365 ppm, consistent with Ba concentration of transitional volcanic from basalt to alkali lava composition, characteristic of alkalic cap lavas of the Koloa Volcanics (Clague and Dalrymple, 1988). This is presumably the parent material to the weathered soil. Rivers transport Ba that is adsorbed onto fine-grained suspended clay particles in freshwater and desorbed under low salinity values upon contact with seawater (Coffey et al., 1997). Accordingly, water samples collected at the mouth of the stream were enriched in Ba, 11 ppb, relative to seawater, which was below detection. Ba is then incorporated into the coral lattice in close proportion to the surrounding environment concentration (e.g. Lea et al., 1989). Therefore, with rivers providing between 50 and 70% of the total dissolved Ba load to the nearshore environment (Carroll et al., 1993; Li and Chan, 1979), the coral Ba/Ca records suggest several periods of terrestrial sediment loading in the eastern sector of the Pila'a reef. This included an episodic, rapid event between 2000 and 2001, with Ba/Ca values quickly returning to or below baseline value, as well as periods of elevated Ba/Ca values over several years which might suggest sustained sediment loading or chronic exposure, possibly from increased runoff or resuspension of legacy sediment (Esslemont, 2000). The 2001 event coincides with a decrease in coral extension and calcification, and a rapid increase, suggesting either rapid recovery and/or inter-annual variability that is independent of sediment loading given the decline observed in 2008–2009, and overall lower values over the last decade.

In contrast to the impacted site, Ba/Ca values in the western sector display a long-term trend in Ba/Ca enrichment, with stepwise increases between 2002 and 2011, when baseline Ba/Ca values remain elevated (Fig. 10b). This trend coincides with a gradual decline in density and gradual increase in extension and calcification. As discussed in Prouty et al. (2010), variability in coral Ba/Ca values is a function of both sources and sinks, with sediment storage capacity altering the temporal input of the Ba/Ca signal. However, no acute signal from a mass mortality event was observed in either the coral Ba/Ca record or coral growth parameters in the coral core collected from the west.

5.4. Sediment

Changes in sediment composition and grain-size over the recovery period indicate a significant decrease in terrigenous sediment that led to high mortality in the coral community in 2002. Fine sediments in the impacted area have declined by an order of magnitude, are currently similar to the unimpacted reference site in the west, and are currently within the range of other sites on the island of Kaua'i (Rodgers, 2005). A similar pattern of reduction was found in the organics and terrigenous sediment components linked to watershed impacts. The likelihood of recovery from an acute sediment event is higher than from a chronic sedimentation event. Reef recovery from chronic cases has only been shown when other anthropogenic or natural stressors were halted and if the physical or biological environments have not been altered (Connell, 1997; Erfteimeijer et al., 2012; Philipp and Fabricius, 2003). These findings along with an increase in CaCO₃ between 2002 and 2016 suggest that substantial sediment elimination has occurred, creating a sustainable environment for community recovery.

6. Conclusion

The partial recovery on the shallow Pila'a reef flat over the past 15 years are the result of successive impacts from episodic sediment and stochastic storm, bleaching, and flood events that have influenced the biological communities. Many systems are in a constant state of flux,

never reaching equilibrium, and must be managed in a manner that reflect these changes. Management approaches may no longer be based on return to a near pristine state or an earlier baseline, since shifting baselines will be more prevalent as effects of climate change advance in frequency and intensity. The results of this research will assist managers in better understanding of the rates and processes of recovery and provide them with realistic expectations for coral recovery. Research and mitigation managers can plan accordingly in reducing watershed impacts and developing management strategies that will encompass periodic disturbance. Research results can also be integrated into system modeling to improve recovery prediction capabilities. Conservation and preservation efforts can be guided by the recovery processes described in this study to develop more efficient approaches based on scientific research. Providing managers with robust scientific data to improve their planning capabilities will offer a greater chance of success in future endeavors and allow for adaptive management strategies.

CRediT authorship contribution statement

Ku'ulei S. Rodgers: Conceptualization, Methodology, Validation, Investigation, Resources, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition. **Angela Richards Donà:** Methodology, Software, Validation, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Yuko O. Stender:** Methodology, Software, Validation, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Anita O. Tsang:** Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Ji Hoon J. Han:** Investigation, Formal analysis, Data curation, Writing – original draft, Writing – review & editing. **Rebecca M. Weible:** Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Nancy Prouty:** Conceptualization, Resources, Formal analysis, Writing – review & editing, Visualization. **Curt Storlazzi:** Conceptualization, Writing – review & editing. **Andrew T. Graham:** Investigation, Formal analysis.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The foundation for this project was developed by Dr. Paul Jokiel whose visionary insight and interest in Pila'a made this research possible. Funding for this project was provided by the Hawai'i Division of Aquatic Resources. This is University of Hawai'i HIMB contribution number 1846 and UH SOEST contribution number 11284. Coral cores were collected under the Hawai'i Division of Aquatic Resources (DAR) Special Activities Permit # 2018-15. Extensive impact to the Pila'a reef ecosystem was confirmed and legally validated on 14 February 2014 by the Hawai'i State Supreme Court following several appeals. The ruling in favor of the State of Hawai'i's Department of Land and Natural Resources (DLNR) has provided the opportunity to monitor the rate of reef recovery and document any future changes at Pila'a. The Coral Reef Ecology Lab at the University of Hawai'i's Hawai'i Institute of Marine Biology (<http://coralreefecologylab.com>) working in conjunction with the State of Hawai'i's DAR, and the U.S. Geological Survey (USGS) Pacific Coastal and Marine Science Center have partnered to evaluate the recovery of the Pila'a reef, determine historical sedimentation, and document future changes. We acknowledge the extensive field contributions made by Ka'ilikea Shayler, Mckenna Allen, Paul Murakawa, Kazuki Kageyama and Brian Nielsen of DAR. Any use of trade, firm, or product names is for descriptive purposes only and does not imply

endorsement by the U.S. Government.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marpolbul.2021.112306>.

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