



Structure and development of Hawaiian deep-water coral communities on Mauna Loa lava flows

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ABSTRACT: Submarine lava flows on the leeward flank of the Island of Hawai'i, USA, were examined by submersible and remotely operated vehicles to understand the structure and development of deep-water coral communities. Three sites were selected where historically documented lava flows crossed older prehistoric flows, providing 3 pairs of lava substrates of different ages (61/400 yr, 134/2000 yr, 143/2330 yr) to compare and contrast with a nearby older coral community (15 000 yr) growing on fossil carbonate. The number of coral taxa, abundance, and colony size increased with substrate age on the 3 historical lava flows and fossil carbonate site, but not on the prehistoric flows. The faster-growing Coralliidae were the dominant taxa forming patches on the peaks of ridged terrain, while the slower-growing Antipatharia and Isididae were less abundant except at the fossil site where the community was dominated by the slowest-growing corals (including *Kulamanamana haumeae*). A multivariate analysis of similarity of coral communities on lava flows found site, rather than substrate age, to be a better explanation for why paired flows were ecologically the same despite considerable age differences. The data suggest that hot, turbid, mineral-rich water from the more recent historical lava event re-initialized the community succession of the adjacent prehistoric lava substrate. Coral mortality would be greatest close to the edge of the historical flow with the expectation that survivorship would increase with distance from the impact. The survey transects were too short to detect a significant increase in the total coral community, but an increase was evident for the Coralliidae.

KEY WORDS: Deep-sea coral · Cold-water coral · Hawai'i · Community succession · Habitat preference

1. INTRODUCTION

Deep-water corals are ecosystem engineers that slowly modify the benthic environment into a unique habitat (Roberts et al. 2006, Parrish & Baco 2007, Long & Baco 2014). The branching skeletal morphology of colonies provides additional structure and complexity to the seafloor, which is integral to supporting increased biodiversity (Grigg 1993, Parrish 2006, Waddell & Clarke 2008, Tsounis et al. 2010). In Hawai'i, USA, higher fish densities co-occur in envi-

ronments associated with deep-water corals (Parrish 2006), with fish often using coral branches as shelter (Boland & Parrish 2005). Furthermore, dense patches of deep-water coral have been documented as foraging areas for numerous species, including the endangered Hawaiian monk seal *Monachus schauinslandi* (Parrish et al. 2002).

Deep-water corals are also a source of raw material for the jewelry trade (Roberts et al. 2006, Born et al. 2010, Tsounis et al. 2010). Exploited for centuries in the Mediterranean Sea and across the Pacific Ocean

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(Grigg 2002, Tsounis et al. 2010), harvested species of deep-water coral are currently among the most valuable living marine resource in terms of unit price, grossing between US\$3000 and \$16 000 kg⁻¹ (Grigg 1993, 2010, Tsounis et al. 2010). The high value and demand for these corals have sustained active coral fisheries globally for decades, impacting coral populations and associated organisms (Roberts 2002, Grigg 2004, Tsounis et al. 2006, 2010). Hawai'i has one of the few managed deep-water coral fisheries and has instituted a policy of selective harvesting which restricts the fishery by minimum colony size and annual total weight (WP RFMC 1979). The target species include the pink corals *Pleurocorallium secundum* (formerly *Corallium secundum*; Figueroa & Baco 2015) and *Hemicorallium laauense* (formerly *Corallium laauense*; Figueroa & Baco 2015), the gold coral *Kulamanamana haumea* (formerly referred to as *Gerardia*; Sinniger et al. 2013), and to a lesser extent, bamboo corals of the family Isididae. The full reported depth distribution of these species in the main Hawaiian Islands is between 231 and 576 m with the majority of colonies occurring below 400 m (Parrish & Baco 2007, Long & Baco 2014).

Establishing a timeline for community development and recovery is central to the development of better resource management practices and the preservation of key habitats for deep-water coral (Waddell & Clarke 2008). Much of what has been learned about deep-water corals in Hawai'i was prompted by fishery needs (Parrish 2007) and has focused on describing depth distribution (Grigg 1974), growth rate (Roark et al. 2006, Parrish & Roark 2009) taxonomic and genetic diversity (Ardila et al. 2012, Figueroa & Baco 2015), and stock size (Grigg 2002). Most deep-water coral species exhibit slow growth, low rates of recruitment, and low natural mortality (Roberts et al. 2006, Parrish & Roark 2009, Roark et al. 2009). Due to the slow growth and long-lived nature of these organisms (100s–1000s of years), there has been little study of community succession and recovery from disturbance.

This study aimed to characterize the development of deep-water coral communities using Hawaiian

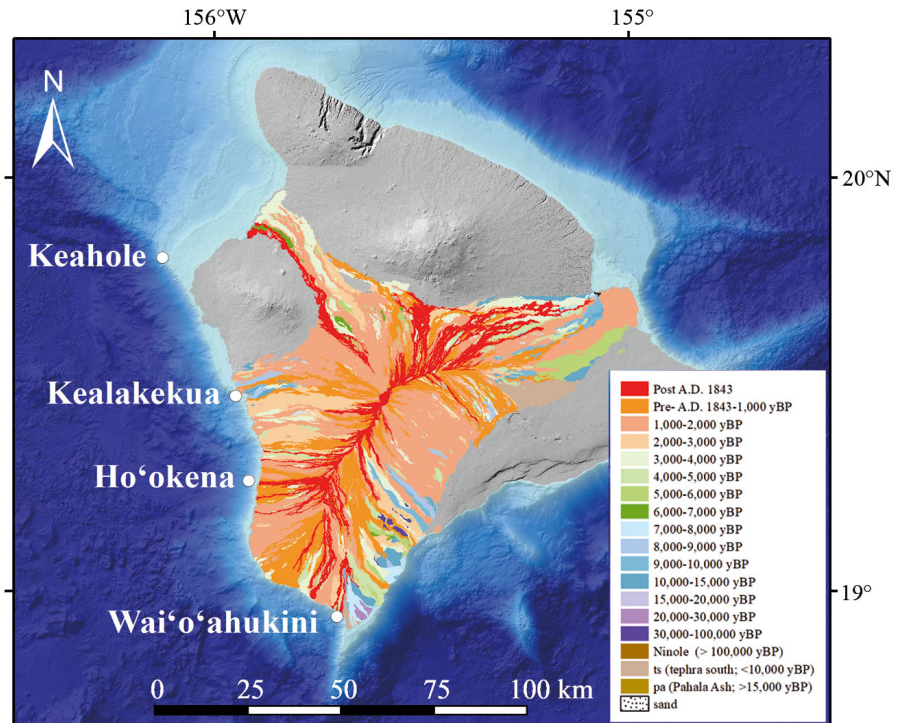


Fig. 1. Boundaries of Mauna Loa lava flows on the Island of Hawai'i, USA, with age as years before present (yBP) shown in color (ranging from oldest in purple and brown to most recent in red; 1:50 000 scale). Labeled place names indicate the general location of the 4 deep-water coral survey sites

lava flows, which have repeatedly generated new and overlapping layers of volcanic substrate throughout the Holocene and Pleistocene, as large-scale 'coral settlement plates' (Fig. 1). This approach can quantitatively measure the rate of colonization and describe stages of deep-water coral community development in a manner analogous to the shallow-water coral community work using lava flows (Grigg & Maragos 1974). The ages and boundaries of Hawai'i's high-volume submarine lava flows are well studied and provide defined areas with a known maximum age of each deep-water coral community (Lockwood & Lipman 1987, Rubin et al. 1987, Lockwood 1995, Moore & Chadwick 1995). The lava flows sit on a single 90 km stretch of coastline all oriented in a westerly direction, reducing the potential for environmental factors that can confound comparisons across broader geographic scales. Coral communities were observed across a range of substrate ages by surveying historical lava flows of known ages and extending the surveys past the boundary of the younger, historical flow onto the adjacent prehistoric lava flow. This design also allowed for an investigation into the potential disturbance effect a new lava flow may have on coral communities growing on the adjacent, older substrate.

2. MATERIALS AND METHODS

2.1. Study design

Six lava flows of successively increasing age (61, 134, 143, 400, 2000, and 2300 yr) were surveyed at 3 sites, with 2 distinct lava flows located at each site, to characterize the development of deep-water coral communities on newly formed volcanic substrate. Each site (Ho'okena, Kealakekua, and Wai'o'ahukini) contained a lava flow of 'historical' age that overlapped an adjacent lava flow of 'prehistoric' age. Historical lava flows occurred between 1950 and 1868 C.E. and were documented in written records at the time of occurrence, while prehistoric lava flows occurred prior to European contact and the introduction of written records between 1611 C.E. and 319 B.C.E. and were radiometrically dated. In addition, a fourth site (Keāhole) located on a drowned fossil carbonate platform, estimated to have been at deep-water coral depths for 15 000 yr, was surveyed as an example of a far older and more mature coral community to contrast with the lava flow sites. Transect surveys were conducted at fixed depth contours (400 and 450 m), and video analysis was used to characterize the geomorphology and community ecology at each site and on each lava flow.

2.2. Site selection

All 6 lava flows selected for study were identified as high-volume flows that extended to offshore depths greater than 500 m. The surveys were conducted using the Hawai'i Undersea Research Laboratory (HURL) submersible 'Pisces V' (28–30 September 2011) and the remotely operated vehicle (ROV) 'Deep Discoverer' belonging to NOAA Ship 'Okeanos Explorer' (30 August 2015). Prior to the dives, the area of the lava flows at each site had been examined using 5 m resolution multibeam bathymetry data in order to identify the boundaries between the historical and prehistoric lava flows (e.g. HURL dive numbers P4-082, R-221-222, etc.; Moore & Fornari 1984, Moore et al. 1987, Moore & Chadwick 1995, Garcia & Davis 2001, Wanless et al. 2006). High-volume lava flows create a distinct 'debris cone' on the ocean floor, which often appears as a wide ridge-like feature or possesses a different gross morphology compared to the surrounding substrate. In order to confirm the estimated age of each lava flow, rock samples were collected and sent to the US Geological Survey Hawaiian Volcano Observatory for radiocarbon and

geochemical analysis that measured the ratio of trace elements and surface weathering (Budahn & Schmitt 1985, Tilling et al. 1987, Moore & Clague 2004).

The drowned fossil carbonate platform at Keāhole surveyed by 'Pisces V' (21 June 2012) was formed in shallow water by hermatypic corals during the Pleistocene before subsiding to its current depth due to lithosphere flexure as a result of the growing mass of the volcanoes (Moore & Fornari 1984, Ludwig et al. 1991, Moore et al. 1996). Based on the rate of island subsidence of 2.2 mm yr⁻¹ (Moore & Fornari 1984, Ludwig et al. 1991, Moore et al. 1996), and the rapid sea-level rise associated with the end of the last glacial period (Chappell 1983), the carbonate platform reached the minimum depth of growth for deep-water coral, i.e. 350 m (Ludwig et al. 1991, Grigg 2002), approximately 15 000 yr ago (Fig. 2). The offshore carbonate platform is devoid of lava flows and other evidence of geological disturbance, suggesting relative stability since its formation in shallow water during the Pleistocene. Therefore, the age of the coral community growing on the carbonate platform is assumed to be a maximum of 15 000 yr and, at the very least, much older than the communities observed growing on the Holocene lava flows.

The northernmost lava flow site was located offshore from Kealakekua Bay south of Kona. The historical lava flow surveyed was on a branch of the 1877 C.E. flow (134 yr) that originated from a submarine vent within the bay (Moore et al. 1985). The prehistoric substrate was determined by stratigraphy position and identified as the Ka'awaloa lava flow, which occurred approximately 2000 yr ago (Lockwood & Lipman 1987; Fig. 2). Farther south on the Mauna Loa coast at the Ho'okena site, the historically dated substrate originated from the 1950 C.E. Ka'apuna flow (61 yr), and the prehistoric substrate was radiometrically dated to 402 ± 33 yr (Lockwood 1995; Fig. 2). At the Wai'o'ahukini site, near the southernmost point of the island, a survey of the eastern branches of the 1868 C.E. flow (143 yr) was paired with the prehistoric Kā'iliki'i lava flow, radiometrically dated to 2330 ± 50 yr (Lockwood 1995; Fig. 2).

2.3. Survey methodology

Survey transects on all lava substrates varied in length (Table 1) but maintained a constant depth of 400 and 450 m. The pilots were able to follow the isobath within a 5 m variation and navigate around terrain while maintaining a consistent speed and altitude above the seafloor to obtain quality video for

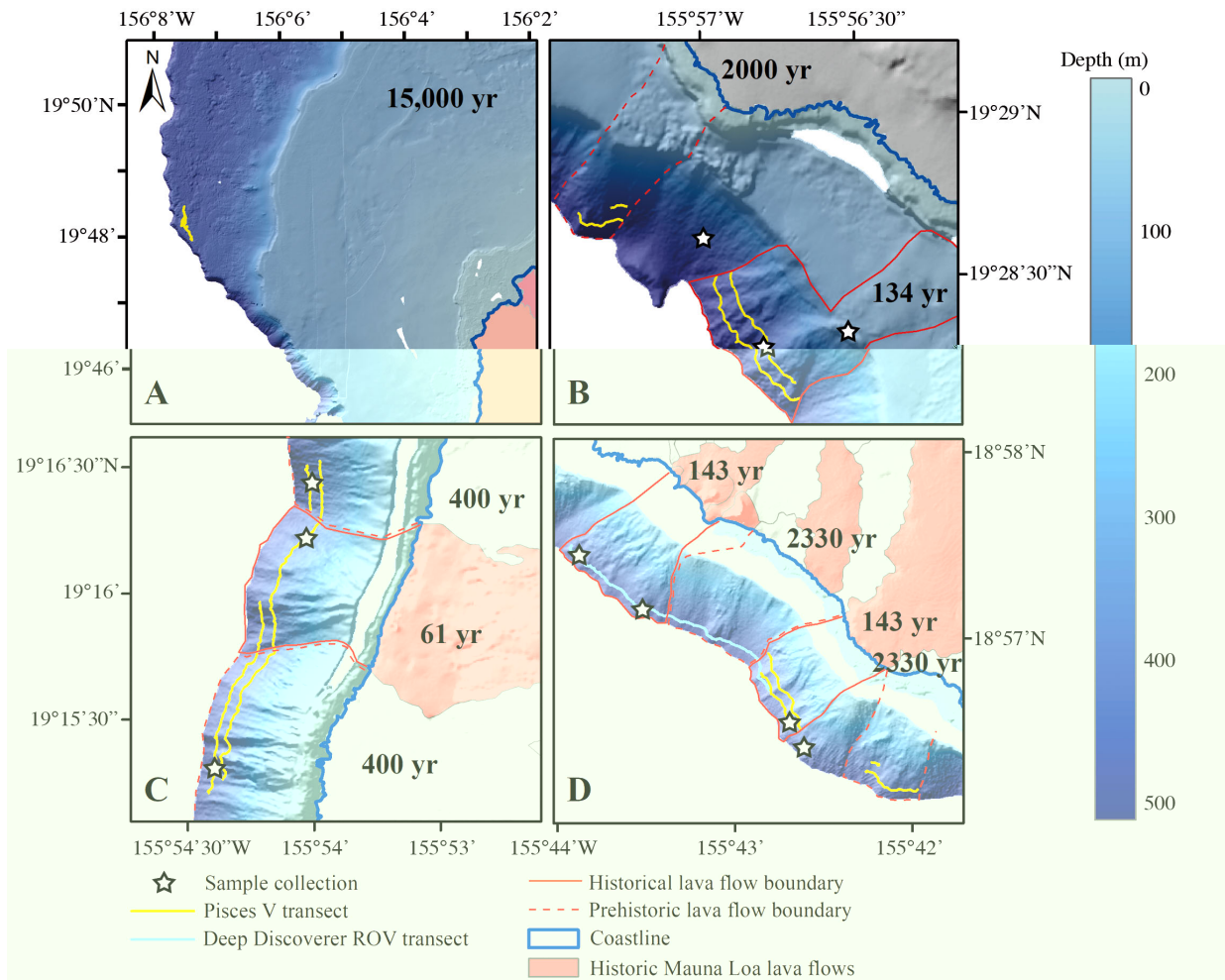


Fig. 2. Bathymetric maps of (A) Keāhole, (B) Kealakekua, (C) Ho'okena, and (D) Wai'o'ahukini. Transects lines of the submarine 'Pisces V' (yellow) and ROV 'Deep Discoverer' (blue) survey at each site. Lava flow boundaries are traced in solid red for historical lava flows and dashed red for prehistoric flows, with the age of the substrate indicated

quantitative analyses. Video from each transect was recorded with a high-definition camera system with calibrated parallel lasers for measurement of corals. The average field of view for the 'Pisces V' MINI-ZEUS HDTV camera system was approximately 7.2 ± 2.7 m (mean \pm SD) looking along the slope at a ~ 2 m altitude above bottom. The Insite Pacific 'Zeus Plus' HD camera system on the 'Deep Discoverer' ROV had an average field of view of 10.4 ± 2.37 m at ~ 2 m altitude above bottom. Transect length and average field of view were multiplied to estimate survey area.

Observed coral colonies were identified to the lowest possible taxonomic level (Long & Baco 2014). Corals that could not be identified with certainty due to small size or poor visibility were given the designation of 'unidentified coral.' Soft, non-branching species of Alcyonacea, Pennatulacea, and single-polyp Scleractinia were not included in the ob-

servations because they were not considered large, habitat-forming species. The location of each coral observed along each transect was determined using the video time code from when the colony was ob-

Table 1. Length and area of each survey transect as defined by dive site and age of the substrate

Site	Age (yr)	Track length (km)	Area (m ²)
Ho'okena	61	1.55	11 194
Kealakekua	134	2.09	15 072
Wai'o'ahukini	143	1.72	12 371
Ho'okena	400	3.38	24 304
Kealakekua	2000	0.44	3152
Wai'o'ahukini	2330	0.79	5715
Keāhole	15 000	3.06	22 032
Total		13.03	93 840

served and corresponding tracking data from the dive. When possible, the height and diameter of colonies were measured in Coral Point Count (CPCe) 4.1. Measurements were calibrated within the program using the camera-mounted laser points within the video frame. If both laser points were not easily discernible, no measurement was made.

The TrackLink 5000HA USBL (LinkQuest) system on the 'Pisces V' calculated the position of the sub every 10 s. The USBL system on the 'Deep Discoverer' recorded the ROV's position every second throughout the dive. Since the time interval of the tracking data differed between the 2 vehicles, the frequency of track points was reduced to be equivalent to that recorded by the 'Pisces V.'

2.4. Terrain

Seabed topography influences coral colonization (Genin et al. 1986, 1992, Grigg 1993, Dolan et al. 2008, Tong et al. 2012). The characteristics of the terrain were quantified using 5 variables calculated in ArcGIS 10.2 with bathymetry and backscatter data (Smith 2016): substrate hardness, aspect, slope, curvature, and bathymetric position index (BPI; Bryan & Metaxas 2007, Verfaillie et al. 2007, Wilson et al. 2007, Dolan et al. 2008). Backscatter data were scaled between 0 and 255 to provide a relative measure of substrate hardness to identify areas of sediment accumulation versus bare bedrock (Flemming 1976, Smith 2016). Focal statistics tools calculated aspect, slope, and curvature using a 3×3 pixel moving window. BPI was calculated using Benthic Terrain Modeler 3.0 set at an inner radius of 1 (5 m) and outer radius of 9 (85 m). Values for each variable were extracted for each track point along the survey transect within ArcGIS and merged with the coral presence and abundance data. Due to the inherent non-normal distribution of the data, nonparametric tests (described in Section 2.5) were selected to describe seabed topography and coral associations so as not to impose assumptions on the relationships among terrain properties (McCune & Grace 2002). The survey was split between historical lava flow and adjacent prehistoric flow to span the covariates and minimize spatial autocorrelation, which has been effective in studies using continuous underwater survey transects (Foster et al. 2014).

Frequency distributions of the variables and coral occurrence were compared to identify non-random distributions. Substrate hardness and slope were split into 10 bins bounded by the minimum and maximum

values in the data. Aspect, which describes the orientation of the slope, was binned so that the median of each bin was 1 of 8 cardinal directions (N, NE, E, SE, S, SW, W, and NW). Curvature and BPI were split into 2 unit-wide bins bounded by the minimum and maximum values within the data set. Chi-squared tests identified where the distribution of coral presence deviated from the expected distribution established by the total terrain (IMB SPSS v24). Since corals often grow in dense beds separated by areas without corals (0 values), the data were normalized using an $(n+1)$ log transformation for a linear regression of coral abundance and the terrain variables (IMB SPSS v24). For this study, areas of high coral abundance were defined as track point locations when 10 or more colonies were observed within the video frame.

2.5. Coral community

Each survey recorded species accumulation, Shannon diversity index (H'), taxa richness, abundance, community composition, maximum colony size, and size frequency of Coralliidae colonies. The data were normalized using 100 m sub-transects for the area surveyed on each lava flow at each survey site. Unidentified coral colonies were tallied with total coral abundance but not used in any other analysis. Community composition was calculated using major taxa: Coralliidae, Isididae, *Kulamanamana haumaeae*, Antipatharia, and other Alcyonacea. Maximum colony size and Coralliidae size frequency were measured using colony surface area (height × width). Surface area provided a more consistent estimation of actual colony size, since oblique camera angles occasionally obscured the measurement of either colony height or width. Without both height and width measurements, the colony was excluded from the size-frequency analyses. To better understand changes in community growth over time, the size-frequency distribution of the most abundant taxa, Coralliidae, was calculated by binning colony size at 100 cm² intervals.

Nonparametric analyses were used on the derived coral-related variables (density, diversity, colony size) in IBM SPSS v24 and Primer v7. A series of independent tests of variance identified which lava flows showed the expected pattern of increasing diversity and abundance with substrate age. For lava flows where the coral community did not reflect the age of the substrate, a multivariate analysis of similarity (ANOSIM, Primer v7) examined species and relative abundance across the 6 lava flows for effects from the 3 sites, historical or prehistoric age, and potential

ridge effects. The data were subjected to a fourth-transformation and 0-adjusted Bray-Curtis similarity matrix prior to conducting the 3-way crossed ANOSIM (Clarke & Gorley 2015). Because similarities within a site could be due disturbance by the historical lava flow to the prehistoric flow, a cluster analysis was performed to assess if coral abundance increased with distance from the historical flow. The effect of distance, as well as the occurrence of ridge-like terrain on coral abundance, was calculated for prehistoric flows from the edge of historical flows out to 600 m. Variables, where significant differences were attributable to distance from the edge of the historical flow, were used in a follow-up correlation analysis that accounted for the differences in age among the prehistoric flows. For all analyses, statistical significance was defined at an alpha level of 0.05 (Siegel & Castellan 1988).

3. RESULTS

3.1. Terrain and community composition

All sites consisted of hard substrate with patches of sediment influenced by varying degrees of slope.

Keāhole (15 000 yr) had the highest proportion of sediment patches, and the slope ($<10^\circ$) differed from the 3 lava sites (25–36°). All sites had a similar average aspect, with the terrain dominated by south-, west-, and southwest-facing features. Curvature was also similar, with no concavity or convexity for nearly half the survey. BPI was more variable between sites, and the high frequency of areas with positive BPI corresponded to prominent ridge features that were conspicuous on multibeam maps.

A total of 8058 upright, arborescent coral colonies comprising 22 different taxa were enumerated in a survey area of 93 840 m². The deep-water coral communities were composed of 90% Coralliidae, 4% Isididae, 2% other gorgonians, 2% Antipatharia, and 2% *Kulamanamana haumea*, and had an average taxa richness of 9.86 ± 6.96 (SD) across all sites. Corals were observed most frequently in areas with positive $0 < \text{BPI} < 6$ associated with the crest of ridges and boulders (Fig. 3). This was especially evident at Kealakekua and Ho'okena, where the chi-squared value of the terrain and coral presence was significant ($\chi^2_{11} = 32.92$, $p < 0.001$, $N = 100$; $\chi^2_{11} = 23.45$, $p < 0.01$, $N = 100$). On these flows there was also a significant positive relationship, although weak, between coral abundance and BPI ($R^2 = 0.04$, $p = < 0.001$;

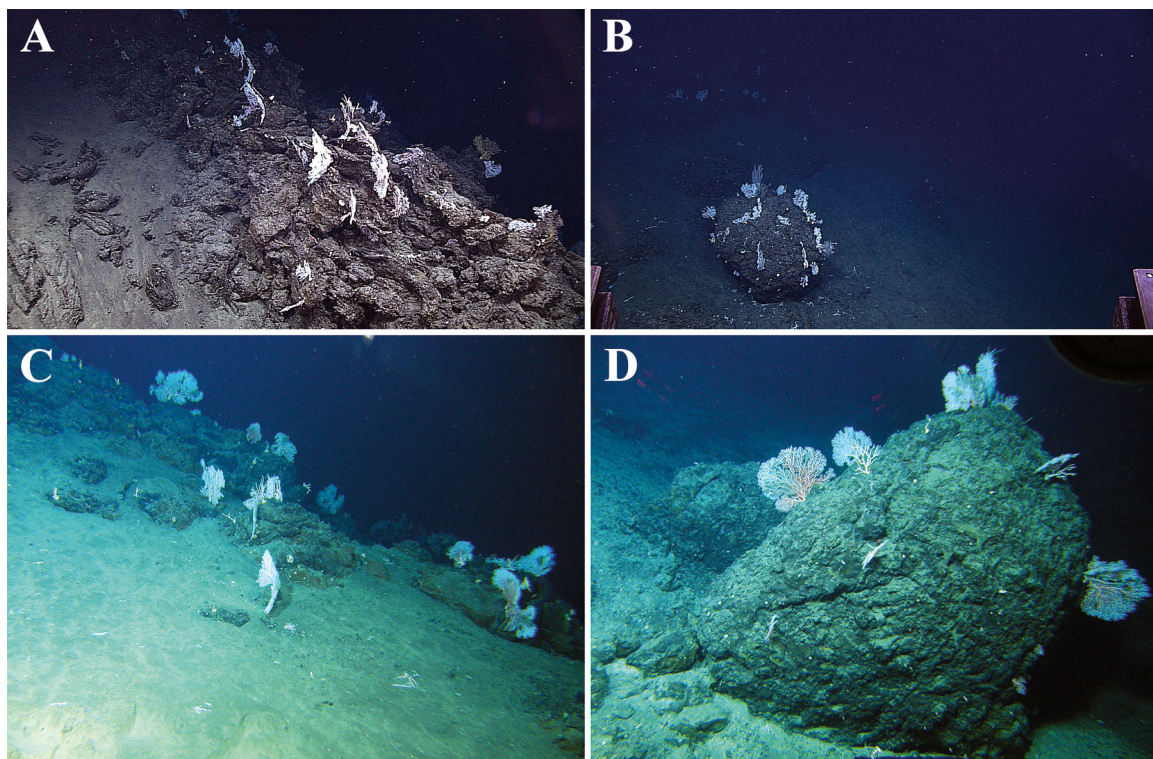


Fig. 3. *In situ* imagery of coral colonies clustered exclusively on the tops of (A,C) ridges and (B,D) boulders, which are areas where the bathymetric position index (BPI) is highly positive

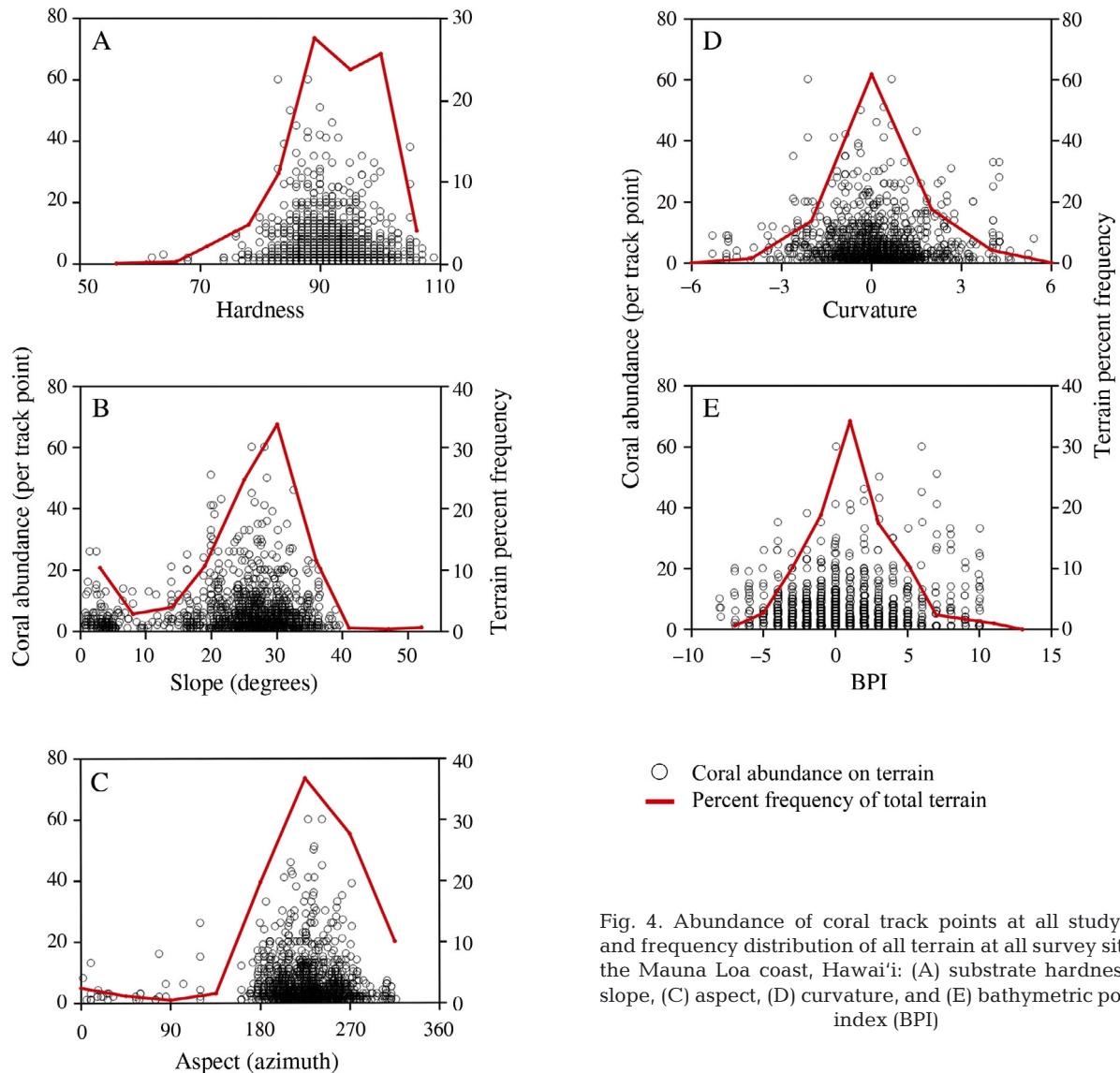


Fig. 4). Of the surveyed terrain, 64 % displayed positive BPI and high densities of coral colonies. The other 4 terrain variables were not significant in either the presence–absence or abundance analysis.

3.2. Substrate age effects on coral community

The substrate age variable did not explain the maturity of the coral communities across all 6 lava flows. Comparisons of coral communities of the pre-historic lava flow to the corresponding overlying historical lava flow showed no significant difference (addressed in greater detail in Section 3.3). Excluding the prehistoric flows from the analysis, the expected relationship of community maturation with substrate age emerges for the remaining 3 historical

Fig. 4. Abundance of coral track points at all study sites and frequency distribution of all terrain at all survey sites on the Mauna Loa coast, Hawai'i: (A) substrate hardness, (B) slope, (C) aspect, (D) curvature, and (E) bathymetric position index (BPI)

lava flows and fossil carbonate site. Tests among the historical lava flows (61–143 yr) showed that all coral variables were significant between sites, with the biggest difference being between the oldest site (143 yr) and the 2 youngest sites (Isididae: $\chi^2_2 = 30.65$, $p < 0.001$, $N = 68$; Coralliidae: $\chi^2_2 = 30.79$, $p < 0.001$, $N = 68$; *K. haumea*: $\chi^2_2 = 15.62$, $p < 0.001$, $N = 68$; Antipatharia: $\chi^2_2 = 7.66$, $p < 0.05$, $N = 68$; other Alcyonacea: $\chi^2_2 = 27.56$, $p < 0.001$, $N = 68$). A partial correlation analysis of substrate age and the coral community controlling for ridge effect showed significant correlations for all taxa: Isididae ($r = 0.66$, $p < 0.001$), Coralliidae ($r = 0.589$, $p < 0.001$), *K. haumea* ($r = 0.455$, $p < 0.001$), Antipatharia ($r = 0.320$, $p < 0.0010$), and other Alcyonacea ($r = 0.559$, $p < 0.001$). Rate of species accumulation over the surveyed area and total species richness increased within the first 143 yr

of development (Fig. 5). The youngest substrate, 61 yr (1950), showed the lowest species richness and fastest species accumulation, with the number of taxa observed reaching an asymptote within 1 km of distance surveyed. The 134 yr (1868) substrate had a 2-fold increase in species accumulation over the same distance surveyed as the 61 yr flow, while the 143 yr flow showed the highest species richness, 6 times greater than the 61 yr flow and 2.5 times greater than the 134 yr flow. On the 15 000 yr substrate at Keāhole, species richness was similar to that observed at Wai'o'ahukini, but greater than at Kealakekua and Ho'okena, which are spatially closer to Keāhole.

The taxa that were missing from the youngest substrate (61 yr) included Isididae, *K. haumea*, and the group of other Alcyonacea (Fig. 6). On the 134 and 143 yr substrates, Isididae and other Alcyonacea appeared in higher numbers, while *K. haumea* comprised 1% of the community only on the 143 yr lava flow. For context, *K. haumea* comprised 19% of the Keāhole coral community growing on the 15 000 yr substrate. At Keāhole, the taxa evenness was greater than on the lava flow substrates. Coralliidae comprised 28% of the Keāhole community while 50% or more of the lava flow community was Coralliidae.

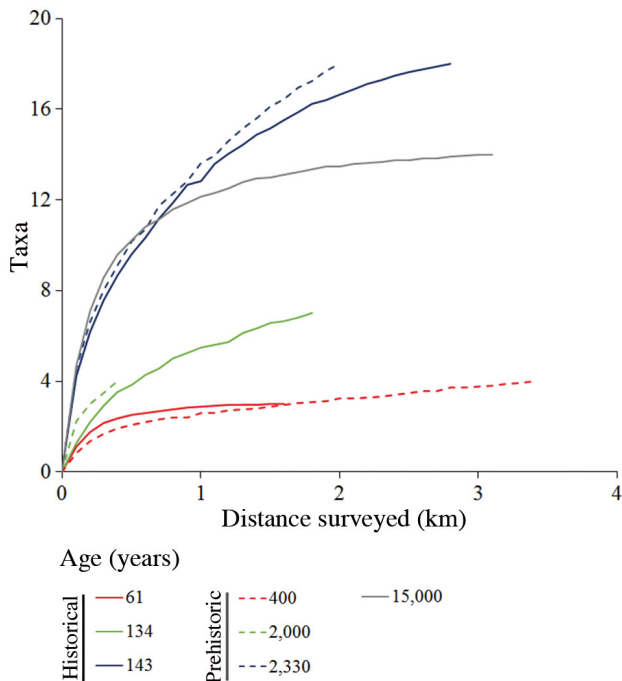


Fig. 5. Species accumulation curves for the number of species observed vs. the distance surveyed (km) across each aged substrate. Solid lines indicate historical lava flows and fossil carbonate substrates, while dashed lines indicate prehistoric lava flow substrates. The color indicates survey site: Ho'okena (red), Kealakekua (green), Wai'o'ahukini (blue), and Keāhole (grey)

Largest colony size increased with substrate age, which was most obvious for the slowest-growing taxon, *K. haumea* (linear growth of 2.2 ± 0.2 mm yr^{-1} ; Roark et al. 2006), which had a significant relationship with substrate age ($R^2 = 0.999$, $p < 0.05$). In addition to colony size, the parasitic life history of *K. haumea* was indicative of community age. The colonies observed on the oldest of the historical lava flows (143 yr) were in the 'midas' stage of development, the initial colonization phase when the zooanthid rapidly spreads and subsumes the bamboo host (Parrish 2015). The colony collected on the adjacent prehistoric flow (2330 yr) appeared to be older, as the host skeleton was entirely encased and was in the earliest stages of creating a proteinaceous skeletal matrix needed to grow larger. For context, the *K. haumea* observed on the 15 000 yr Keāhole substrate were mature colonies fully encased in thick protein skeleton growing to heights more than 1.4 times the size of colonies seen on the lava flows.

The faster-growing Coralliidae colonies (linear growth $0.25\text{--}0.43$ cm yr^{-1} ; Roark et al. 2006) were observed in larger numbers, and the frequency of corals in larger size classes increased with substrate age ($\chi^2_{24} = 94.34$, $p < 0.001$, $N = 661$; Fig. 7). On the

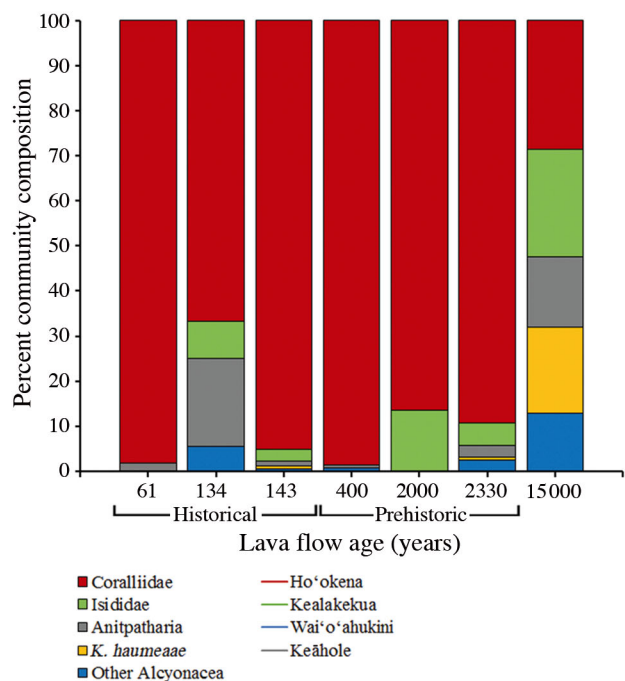


Fig. 6. Community composition of the major deep-water coral taxonomic groups, Coralliidae (red), Isididae (green), Antipatharia (grey), *Kulamanamana haumea* (yellow), and other Alcyonacea (blue) on aged substrates. Color boxes surrounding the flow age indicate spatially adjacent substrates: Ho'okena (red), Kealakekua (green), Wai'o'ahukini (blue), and Keāhole (grey)

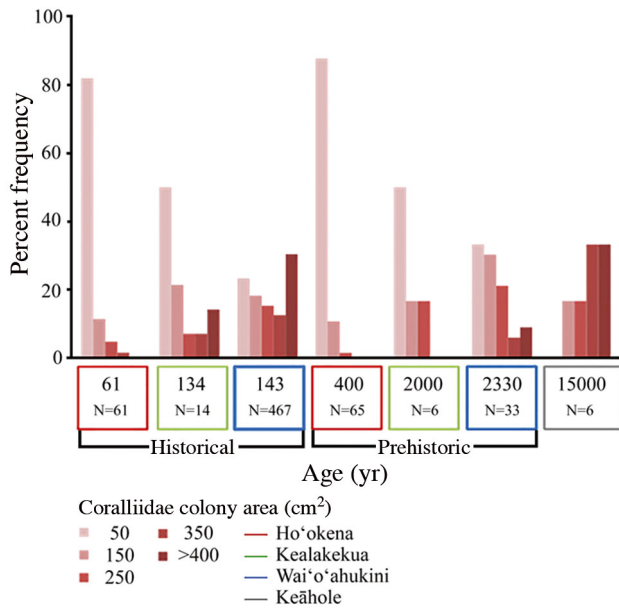


Fig. 7. Size-frequency distribution of Coralliidae area on aged substrates. The median value of each bin represents size class, and number of colonies measured is indicated below the substrate age. Color boxes indicate spatially adjacent substrates: Ho'okena (red), Kealakekua (green), Wai'o'ahukini (blue), and Keāhole (grey). The number of colonies measured using the vehicle-mounted laser system is indicated below the substrate age

61 yr flow at Ho'okena, 98% of the colonies observed were smaller than the minimum reproductive size (14 cm; WPRFMC 1979, Grigg 1993). The largest colony observed was 16 cm, estimated to be 20–40 yr old based on its size and the growth rate of Hawaiian Coralliidae (Roark et al. 2006). At Kealakekua on the 134 yr flow, 92.36% of the colonies observed were under the minimum reproductive size. Of Coralliidae colonies on the 143 yr flow at Wai'o'ahukini, 56% were under reproductive size. On the oldest substrate, 15000 yr at Keāhole, all colonies observed were of reproductive size.

3.3. Historical lava events re-initializing coral communities on adjacent prehistoric flows

Across all 6 lava flows (historical and prehistoric), the site variable was more important to community structure than the age of the lava substrate. Taxa accumulation curves (Fig. 5), community composition, total coral and Coralliidae abundance (Fig. 6), the size frequency of the most abundant coral taxa, Coralliidae (Fig. 7), and diversity, evenness, and richness (Fig. 8) did not differ significantly between pre-

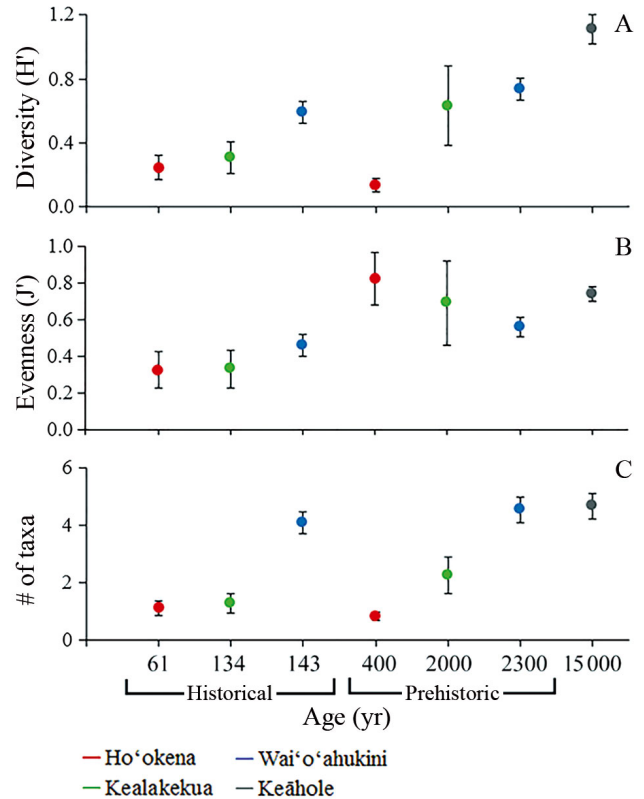


Fig. 8. Values for (A) Shannon diversity, (B) Pielou's evenness, and (C) taxa richness from each aged substrate were normalized across the distance surveyed for each aged substrate using 100 m sub-transects. Bars represent the standard error between sub-transects. The color indicates spatially adjacent substrates: Ho'okena (red), Kealakekua (green), Wai'o'ahukini (blue), and Keāhole (grey)

historic and historical lava substrates at the same location. The Shannon-Wiener diversity index (H') showed the lowest diversity (Fig. 8) at the Ho'okena site where the flow of 61 yr overlapped the 400 yr lava flow, supporting only 2 taxa and the greatest percent Coralliidae. The diversity of the Wai'o'ahukini site with the 143 yr flow overlapping the flow of 2330 yr had a high proportion of Coralliidae in comparison to the other species observed on the flows. Both of these lava substrates had the most coral taxa (18 and 19 taxa, respectively) but lacked evenness, making the communities less diverse than the carbonate Keāhole site (15000 yr).

There was no direct correlation between total coral abundance or Coralliidae abundance with increasing age for the 7 substrates (Total: $r = 0.007$, $p = 0.99$; Coralliidae: $r = 0.22$, $p = 0.63$). The highest coral abundance observed was on the oldest historical lava flow, 143 yr at Wai'o'ahukini, and the location of the next highest abundance was the adjacent prehistoric

flow, 2330 yr. The substrates at the more northern lava flow sites, Kealakekua and Ho'okena, displayed very low abundances of coral (>2 colonies 100 m⁻²). Finally, the size frequency distribution of coral communities among adjacent lava flows of contrasting age did not significantly differ.

Multivariate analysis of coral species examining the effect of site, historical/prehistoric lava age, and presence of ridges showed that only site was significant (3-way crossed ANOSIM: $R = 0.453$, $p < 0.01$). This pattern persists for each lava flow pair even when the substrate ages differ by centuries to millennia, indicating that the disturbance from the more recent historical lava event may determine the shared ecological state at the site. The impact of the historical lava events (heat, turbidity, mineral-rich water) on the adjacent coral communities of the prehistoric lava flows should decrease with distance from the edge of the more recent flows. However, a cluster analysis of the transect data divided into 100 m segments ($N = 6$) on the old flows showed that the impact to the community persisted for the slower-growing older corals out to the farthest distance surveyed. Only the faster-growing Coralliidae exhibited potential for significant differences among close and distant clusters (K-Means cluster analysis accounting for ridge effects: $F = 18.4$, $p < 0.001$). Follow-up partial correlations accounting for ages of the different flows confirmed that the number of Coralliidae did significantly increase with distance from the edge of the new flow (Mann-Whitney: $Z = -2.23$, $p < 0.05$). A 2-step cluster analysis showed that the size of colonies clustered into 2 groups, with the smallest size bin close to the boundary of the historical lava flow and the largest size bin at the farthest distance away from the boundary. Follow-up tests confirmed that this size difference was significant ($\chi^2_5 = 23.8$, $p < 0.001$, $N = 897$).

4. DISCUSSION

4.1. Community development of deep-water precious corals

Deep-water coral communities that did not suffer subsequent disturbance from lava flows (61, 134, 143 yr lava flows and 15 000 yr Keāhole carbonate platform) showed a pattern of community development with time. The youngest lava flow (61 yr) exhibited low coral density and low diversity dominated by relatively small colonies of calcitic sea fans from the family Coralliidae. These pioneer species grow in

height at 0.25–0.43 cm yr⁻¹ and have an average lifespan of 80–100 yr (Grigg 1974, 2002, Druffel et al. 1995, Andrews et al. 2005, Roark et al. 2006). The older of the historical lava flows (134 and 143 yr) exhibited higher taxonomic diversity and a larger size structure of Coralliidae colonies. A greater abundance of often taller and slower-growing species from the octocoral family Isididae and the hexacoral order Antipatharia were observed. Isididae have a unique skeletal structure composed of calcite internodes connected by proteinaceous nodes. The lifespan recorded for some species is 70–220 yr (Roark et al. 2006, Tracey et al. 2007, Andrews et al. 2009). Antipatharia (black corals) have exclusively proteinaceous skeletons, with longevity of deep-water species reported between 198 and 4250 yr (Wagner et al. 2012). The 143 yr old lava flow at Wai'o'ahukini near the southernmost point of Hawai'i exhibited a very high density of corals with many large colonies of Coralliidae. Based on these observations, a Coralliidae community with a mature size structure can fully develop or recover from major disturbance (e.g. precious coral harvesting) in ~143 yr under favorable conditions.

With enough time, the deep-water coral community showed a shift toward supporting a more diverse array of tall, slower-growing taxa. The oldest coral community at Keāhole (15 000 yr) exhibited the highest taxonomic diversity and largest colonies of all taxa. In contrast to all other sites, the relative abundance of Coralliidae colonies was low, and no small colonies (<50 cm²) were observed. Tall, thick, and fully mature colonies of the slow-growing, parasitic zoanthid *Kulamanamana haumea* (linear growth 2.2 ± 0.2 mm yr⁻¹ with a lifespan of 450–2742 yr; Roark et al. 2006, Parrish & Roark 2009), were common at Keāhole, but only small, recently recruited colonies of the taxon were present on the lava flows. Taking into consideration the rate of colonization observed on the lava flows and the growth rates of the slower-growing taxa, a community similar to that observed at Keāhole may take centuries to millennia to fully develop.

4.2. Re-initiation of prehistoric coral communities by recent lava events

The prehistoric lava substrates (400, 2000, 2330 yr) did not exhibit the predicted pattern of coral community structure relative to substrate age. Older substrate should mean that these coral communities had more time to mature and therefore, should be com-

prised of significantly larger colonies and more taxa, building on the trend seen across the younger flows. Instead, the species composition, diversity, and Coralliidae size structure of the prehistoric flows closely resembled that of the adjacent, historical lava flow. One plausible explanation for this pattern is that the older community was seriously disturbed by the newly emplaced lava flow, thereby reinitializing the community development process. This finding contrasts with the well-defined boundaries in shallow-water coral community structure observed between adjacent lava flows (Grigg & Maragos 1974). The difference may be due to the tropical and phototrophic nature of shallow-water corals versus suspension feeding deep-water corals living at cold, subphotic depths. The latter may be sensitive to elevated water temperatures and changes in the hydrodynamic regime (both macro- and micro-scale) caused by a change in geomorphology or displacement of zooplankton. Furthermore, for a lava flow to reach depths greater than 500 m, it must be a high-volume event that moves downslope rapidly, subsequently causing widespread impacts to adjacent areas, and will require several months to cool to ambient temperatures (Gosline et al. 1954, Holcomb et al. 1988, Gregg & Fink 2000). Although not previously studied, exposure to hot, turbid, mineral-rich water may have caused coral mortality either directly or indirectly by interrupting the food supply. Although the existing surveys of prehistoric lava substrates extended no more than 600 m from the edge of the younger historical lava flows, the increase in the size of Coralliidae colonies with distance away from the more recent flow is consistent with a disturbance-proximity effect.

The main difference between the growth pattern of the gold coral colonies, *K. haumea*, on the pair of flows at Wai'o'ahukini, i.e. that the historical flow (143 yrs) had only midas colonies, whereas the prehistoric flow had some colonies in the early stage of protein skeleton development, might also be due to disturbance from the historical lava flow. Bamboo and other coral colonies on the old flow may have been killed by the more recent adjacent historical flow, but their skeletons could have persisted and still served as a host for gold coral recruitment. Gold coral have been observed growing on dead or partially dead bamboo colonies (Parrish 2015), suggesting that gold coral could have colonized the prehistoric flow sooner given the presence of suitable host substrate, whereas on the historical flow, suitable bamboo host substrate would not become available for nearly 100 yr after the lava cooled. However, more exten-

sive surveys are required to characterize the extent of spatial and temporal impacts of this type of disturbance on the adjacent older coral community.

4.3. Environment, succession, and future work

Local environmental conditions, shaped by geomorphic parameters, influence the hydrodynamic regime and may explain the similarity between coral communities of adjacent lava flows (Grigg 2001, Parrish 2007, Dolan et al. 2008). In this study, there was a strong association between coral abundance with high relief features such as ridges, crests, and boulders indicated by positive values of BPI (Fig. 7). These areas are potential points of current acceleration, and as a result, locations with higher rates of food supply for the colonizing coral (Dolan et al. 2008). While the deep-water current regimes at these study sites are not known, there are well-established differences in the surface current flow velocities at the sites (Powell 2010). The Northeast Equatorial Current (NEC) and Northeast Trade Winds flowing past the southern point of Hawai'i cause predominantly westward surface currents across the Wai'o'ahukini site and generate an anticyclonic gyre farther north along the leeward Mauna Loa coast, causing a north to south flow of varying intensity at the Kealakekua and Ho'okena sites (Jia et al. 2011). Therefore, the higher density of coral communities observed at Wai'o'ahukini in comparison the 2 more northern sites, Ho'okena and Kealakekua, could be attributed to stronger bottom currents at Wai'o'ahukini.

Although the temporal resolution of this study was limited, the deep-water coral community in Hawai'i appears to undergo a pattern of ecological succession over time scales of centuries to millennia. The Coralliidae were both the first taxa to colonize and to accumulate in dense aggregations with an increase in size structure. This study validates the growth estimates for this taxon on a community scale. Pioneering Coralliidae colonies with calcite skeletons are the first to colonize, followed by taller, slower-growing corals (Isididae, Antipatharia) with skeletons made up of more robust proteinaceous components. Calcite skeletons are derived from ubiquitous elemental resources (calcium ions and dissolved inorganic carbon) and are brittle and easily broken. During the surveys, numerous partially damaged Coralliidae colonies were observed with fragments littering the sea floor, and 1 large fish (*Taractichthys steindachneri*) was seen shattering a large *Hemicorallium* colony. Proteinaceous nodes in Isididae skeletons make their

skeletons much more flexible, enabling the growth of larger colonies with lower incidents of mechanical damage. The fully proteinaceous skeletons of *Antipatharia* and *K. haumea* are robust, capable of supporting large colony size and withstand most mechanical stresses. This robust nature is consistent with their exceptional longevity (Roark et al. 2006, Parrish & Roark 2009). However, the formation of proteinaceous components requires organic nitrogen, a much more limiting resource in the deep sea (Karl 2007), thereby limiting growth rates to rates of nitrogen assimilation.

While the development of a Coralliidae community with a large size structure in Hawai'i may only take ~150 yr, the development of a 'mature' coral community requires far longer. None of the lava flow coral communities resembled the high-diversity community at Keāhole (15 000 yr). The absence of mature *K. haumea* colonies despite the availability of Isidiidae substrate on the lava flows confirms that this species is very slow (>100 yr) to recruit in considerable numbers (Parrish 2015). Although the data in this study are limited, the diversity trend with age of the communities studied with the highest diversity at Keāhole (15 000 yr) implies that community succession takes several millennia to run its course (per the intermediate disturbance hypothesis; Connell 1978, Parrish 2015). Alternatively, the coral community structure could be inherently different on carbonate substrate (vs. basalt), or the intermediate disturbance hypothesis may not apply to deep-water coral communities (Fox 2013, Sheil & Burslem 2013).

Future work comparing coral communities of known-age lava flows across millennia would benefit from *in situ* environmental sampling to evaluate the influence of covariates (e.g. temperature, flow, oxygen) on patterns of colonization, succession, and maturity. Also, as the Island of Hawai'i continues to have periodic eruptions producing very recent deep-water lava flows (most recently in May 2018), there is opportunity to study initial settlement patterns and appraise the impact that hot, turbid, mineral-rich water from new flows has on coral communities.

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