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Spatial and temporal patterns in Hawaiʻi's intertidal: decadal changes in benthic community composition

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Abstract

Spatially broad and long-term monitoring studies are lacking in tropical intertidal systems yet are necessary to test predictions regarding community assembly. To fill this gap, we examined spatial and decadal temporal patterns in benthic community structure at rocky intertidal sites along the main islands of Hawai'i. Quantitative community surveys done in 2017 across nine sites and five islands showed that organismal composition differed by site, substrate type, and island. Secondly, we leveraged an earlier dataset collected using the same methods and analyzed intertidal communities at five sites on three Hawaiian islands for temporal changes in organismal abundance and composition from 2006 and 2007 vs. 2016 and 2017. Overall community structure differed significantly across years and decades. Most decadal differences were site specific, such as the fivefold increase in turf algae at one site. Crustose coralline algae and *Turbinaria ornata* increased significantly across five sites; both are physically resilient algae and similar increases in their abundances have been observed in tropical systems worldwide. This increase in physically resilient macroalgal species is potentially caused by global drivers, such as rising temperatures and changing land uses. In conclusion, there is evidence that both local and regional factors contribute to structuring tropical intertidal communities.

Keywords

Crustose coralline algae
Decadal changes
Global and local factors
Physically resilient
Turbinaria ornata

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Electronic supplementary material

Introduction

Understanding ecological change and the factors that contribute to community maintenance and biodiversity are central tenets of marine ecology. Intertidal communities have a longer history of study compared to subtidal communities due to their accessibility. Since the pioneering work of Paine and Connell (e.g., Connell, 1961; Paine, 1966, 1974) the study of the intertidal has contributed to our understanding of cornerstone ecological concepts such as niche, competition, intermediate disturbance, and keystone species. Intertidal research has also emphasized the importance of physical factors, such wave action and tides, and their contribution to community variation (McQuaid & Branch, 1984; Underwood & Jernakoff, 1984; Hawkins & Hartnoll, 1985). Tropical intertidal zones, especially those on islands, have been studied less than their temperate counterparts and are likely structured differently than temperate zones (Macusi & Deepananda, 2013). For example, the importance of top-down control on sessile organisms is predicted to decrease with greater environmental stress (Menge & Sutherland, 1987); therefore, keystone species may be less important in structuring tropical intertidal systems compared to temperate intertidal systems (Macusi & Deepananda, 2013). Intertidal organisms may be more impacted by climate change than subtidal organisms because they are exposed to both rising air temperatures during low tides and rising ocean temperatures at high tides; in addition, intertidal organisms may be

impacted by freshwater floods during extreme rain events, which are predicted to increase in frequency/intensity (Emanuel & Sobel 2013).

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While some long-term studies of rocky intertidal zones have found few changes in species composition over time (Poloczanska et al., 2011; Zabin et al., 2013), other studies have found evidence of dramatic changes in richness and diversity (Smith et al., 2007). For example, researchers in California found that intertidal species ranges shifted northward over the span of 60 years in response to warming temperatures (Barry et al., 1995; Sagarin et al., 1999). Climate change is likely to cause complex chemical (e.g., ocean acidification) and physical (e.g., current patterns) changes in coastal marine ecosystems (Harley et al., 2006; Helmuth et al., 2006). Additionally, the accessibility of the intertidal environment and its position between the land and the sea make this ecosystem vulnerable to anthropogenic threats such as eutrophication (Lopez y Royo et al., 2009), species invasions (Smith et al., 2002), and overharvesting (Salomon et al., 2007). The degree to which these global and local threats will cause shifts at the species or community level is not clear.

Physical factors at different spatial and temporal scales can drive variation in community structure. Temperature is a primary abiotic factor driving species distributions from small (~ m) to regional (~ km) scales, and environmental temperature in the intertidal is influenced by tides, topography (Chapperon & Seuront, 2011), microhabitat (Seabra et al., 2011), vertical zonation, substrate type (Campbell et al., 2017), exposure (i.e., wave activity and prevailing wind direction), and latitude (Rivadeneira et al., 2002). Furthermore, temperature varies cyclically and linearly at tidal, daily, seasonal, yearly, and longer time spans. This study will focus on assessing the differences between intertidal communities on different islands and island regions as well as changes within these communities on longer temporal scales of years and decades. We predict that decadal changes in community structure will be greater than yearly differences because of shifting environmental baselines due to climate change, such as steadily increasing sea surface temperatures.

Hawai'i has a small tidal range, benign year-round air temperatures, and rocky intertidal shores that are often lush with diminutive macroalgal species—an area of high diversity and proportionally high degrees of endemism (Zabin et al., 2013). Recently, researchers have begun to identify spatial patterns in biological communities within Hawaiian intertidal zones and the factors that may shape or

maintain these communities (e.g., Smith, 1992; Cox & Smith, 2011; Cox & Foster, 2013; Bird et al., 2013). Smith (1992) compared intertidal communities on different Hawaiian Islands and found the age of the island was associated with community structure. Bird et al. (2013) identified wave activity to be an important factor in characterizing Hawaiian intertidal communities; intertidal communities in other regions have similarly been shown to differ between wave-sheltered and exposed shores (e.g., Bustamante & Branch, 1996). Cox et al. (2017) showed that shore topography and sand correspond with algal composition on the southwest shore of Oʻahu. Lastly, a 2004–2007 study of 13 sites on four islands concluded that Hawaiian intertidal communities exhibit a high degree of spatial variation that is likely driven by local factors (Cox et al., 2013). Studies examining long-term changes in Hawaiʻi's intertidal communities have been limited in part due to seasonal wave activity and a modest tidal range. To our knowledge, only one study on the Hawaiian intertidal has examined community change through time, from 2006 to 2015 along southwest Oʻahu; it found that rocky intertidal community composition shifted at sand-exposed sites after a heating event (Cox et al., 2017). Although there is a general anecdotal consensus on the decline of native edible seaweeds (Cox et al., 2012; Leone, 2004), the possible causes are numerous, and elucidating them is difficult without additional longitudinal quantitative data. The type of monitoring needed to detect changes, and provide insight into the cause of such changes, is difficult to implement and maintain long-term.

Citizen scientists can play a valuable role in collecting ecological research data that is costly, time-consuming, and labor-intensive (Silvertown, 2009). Involving citizens in the collection of data for research also has societal benefits, including increasing awareness and understanding of environmental issues, connectedness to the environment, and communication of scientific findings (Lovell et al., 2009). A state-wide educational and scientific program, Our Project in Hawaiʻi's Intertidal (OPIHI), was formed to describe Hawaiʻi's intertidal communities and engage teachers and students in citizen science (Baumgartner & Zabin, 2008). From 2004 to 2007 OPIHI monitored intertidal sites around the Hawaiian Islands, resulting in the first description of community-level patterns in this ecosystem (Cox et al., 2013). In this study we use past and current citizen science data from the OPIHI program to test the hypotheses: (1) tropical intertidal communities differ by site, island, substrate type, and wind/wave exposure and (2) tropical intertidal community structure has shifted more in the past decade compared to year-to-year variation.

Methods

Site descriptions

Eleven rocky intertidal sites located on 6 Hawaiian Islands (Kauaʻi, Oʻahu, Maui, Molokaʻi, Lānaʻi, and Hawaiʻi) were surveyed between March and May in 2016 and 2017. Five of these sites were surveyed in 2005 and 2006 and described in a previous publication (Cox et al., 2013); we re-analyzed these data with the newly collected 2016 and 2017 data to investigate community change over the past decade. For the purpose of this study, "site" is defined as a coastal area at least 15 m wide, consisting of a flat intertidal bench. Sites on the same island are spaced 1–35 km apart (Fig. 1); the substrate at each site was categorized as limestone, basalt, or mixed limestone and basalt. The Hawaiian Islands experience microtides (~ 1 m). Nonetheless, flora and fauna in these habitats can occupy distinct horizontal zones described as near, mid, and far from the subtidal habitat (see Cox et al., 2013).

Fig. 1

Survey locations on the main Hawaiian Islands. The symbol shapes refer to which analyzes the sites were included in—spatial, temporal or both analyses
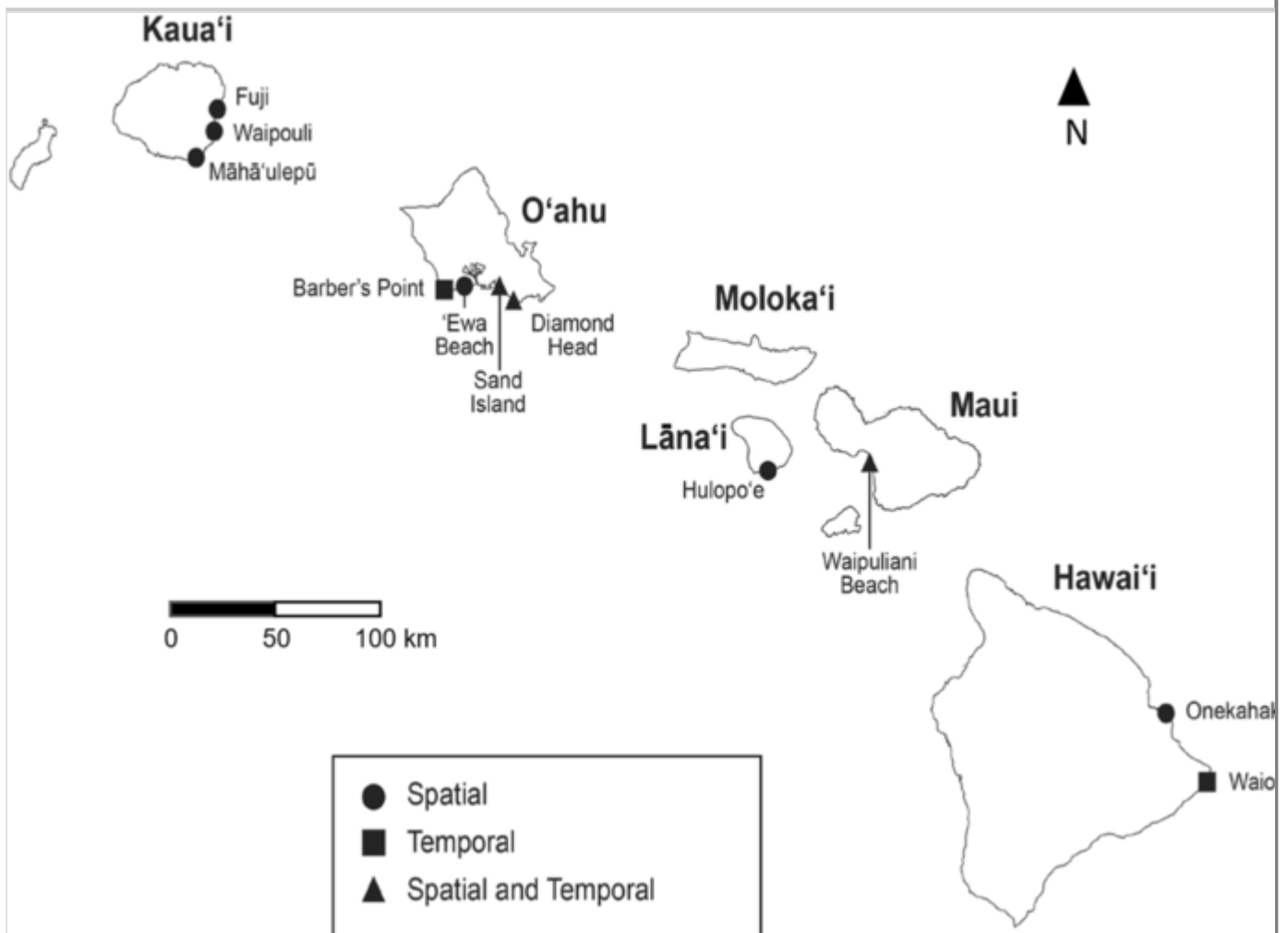
Benthic surveys of algal and invertebrate community composition

All benthic community data were collected by participants in a citizen science program called Our Project in Hawai'i's Intertidal (OPIHI). The citizen scientists were mostly secondary school students (grades 6–12) and their teachers; they were often aided by undergraduate and graduate students from the College of Natural Sciences at the University of Hawai'i as well as by other researchers from government and conservation agencies. All participants were trained in the OPIHI protocol. Community-level data generated by participants in OPIHI were previously shown to be robust and comparable to data collected by experienced researchers (Cox et al., 2012). All OPIHI citizen science data is publicly available in the OPIHI database, https://opihi.crdg.hawaii.edu/.

OPIHI participants used the point-intercept method described in Cox et al. (2013) to determine benthic algal and invertebrate community composition and abundances. Briefly, three to seven transects were laid a few meters apart and perpendicular to the shoreline. The location of transects were not fixed; GPS coordinates and photographs were used to ensure that the same locations were sampled each year. The number and spacing of transects were sufficient to cover the majority of each study site. Gridded quadrats (0.09 m^2) with 25 intercepts were set at regular intervals along the transect lines. The number and length of transects and the number of quadrats per transect varied depending on the number of survey participants and intertidal bench length and width. All surveys included at least 20 quadrats, except for one survey that had 10 quadrats and one survey that had 19 quadrats, which were included because they were representative of the communities at the sites surveyed. For each quadrat, the organism or substrate directly below each intercept in the grid was recorded. Because there are few large canopy-forming algal species in Hawai'i's intertidal, only organisms or substrate directly under the grid intercepts were recorded and layering was not considered. Organisms were identified in the field to the lowest possible taxonomic level or functional group given the expertise of the observers. Some species of algae and invertebrates are difficult to identify, particularly without a microscope; these species were identified to genus or a functional group (e.g., "turf algae" or "brown crust"). Organisms were identified using a project-developed identification guide (Philippoff et al., 2018) and reference books by Huisman et al. (2007) and Hoover (1998).

Prior to analysis of community-level patterns, data were subject to a rigorous screening process to ensure quality following the guidelines provided in Cox et al. (2012). Taxa were also pooled by genus or functional group in order to account for differences in identification expertise across different surveys. For example, citizen scientists recorded both *Laurencia majuscula* (Harvey) A.H.S.Lucas and *Laurencia mcdermidiae* I.A.Abbott, as well as the broader categorization *Laurencia* sp. Because *Laurencia* species are similar in appearance when small, and difficult for less-experienced researchers to distinguish, these three taxa were grouped and reclassified as *Laurencia* spp. Analyses were done at the taxa level with genus and functional groups treated similarly as species. Supplemental Tables 1–2 list all taxa included in community analyses and show how they were grouped. After grouping, we calculated the percent cover for each taxon identified on each survey. Percent cover is the number of quadrat points containing a given taxon divided by the total number of points per quadrat (25). We then took the average percent cover of all quadrats on one survey. This yielded one percent cover value per taxon for each survey.

Spatial analyses

To examine spatial variation among sites and to eliminate bias from yearly variation, only data collected in 2017 were used for the spatial analyses. We selected data collected in 2017 to maximize the number of comparisons made within the same time period. We constrained the analysis to sites surveyed more than once between March and May of 2017 (Table 1). These months were chosen because they were similar in temperature and rainfall amounts (Supp Table 3). Each survey was considered a replicate for the spatial analysis. Because we aimed to test for factors that contribute to spatial variation, sites were categorized by island, substrate type (limestone, basalt, or mixed limestone and basalt) and wind/wave exposure (leeward, windward, or bay). Percentages were square root transformed prior to analyses to down-weight abundant species and account for the patchy distribution of some species. We then used the Bray–Curtis index to build a similarity matrix comparing organism abundances from each survey. To visualize differences in community composition between sites, we used the metaMDS function in the vegan package (Oksanen et al., 2017) in R (version 1.0.44, R Core Team 2016) to create a nMDS plot with data grouped by site. We performed permutational multivariate analysis of variance (PERMANOVA) using the adonis function in the vegan package. A separate PERMANOVA was run for each factor including site, island, substrate type, and wind/wave exposure; the factors were tested separately rather than combining them in one PERMANOVA to maximize

degrees of freedom given limited replication. To avoid confounding site differences with island differences, data from only six of the nine spatial survey sites (Diamond Head, 'Ewa Beach, and Sand Island on O'ahu and Fuji, Waipouli, and Māhā'ulepū on Kaua'i) were included in the island PERMANOVA because the other three sites were the only survey sites on their respective islands. Similarly, data from Waipu'ilani was excluded from the PERMANOVA testing for differences in wind/wave exposure because this was the only site classified as a bay for wind/wave exposure. Diamond Head and 'Ewa Beach were excluded from the PERMANOVA testing for differences in substrate because these were the only sites with mixed basalt/limestone substrates and both were located on O'ahu. For the PERMANOVAs where significant differences in benthic assemblages were observed, an indicator species test was used to identify which taxa were most indicative of each subclass within a factor (e.g., O'ahu for island) using the function multipatt in the indicspecies package (Cáceres and Legendre 2009) with association function r.g and significance level < 0.05. The P values were controlled for false discovery rate ($\alpha = 0.05$) using the function p.adjust with the Benjamini–Hochberg–method in the R package stats.

Table 1

Intertidal sites in the spatial analysis and abiotic characteristics

Site	Island	GPS	Exposure	Substrate type	N field trips
Diamond Head	O'ahu	21.2554 N 157.8103 W	Leeward	Mixed	2
'Ewa Beach	O'ahu	21.3106 N 158.0044 W	Leeward	Mixed	6
Sand Island	O'ahu	21.3002 N 157.8826 W	Leeward	Basalt	3
Fuji	Kaua'i	22.0656 N 159.3177 W	Windward	Limestone	2
Waipouli	Kaua'i	22.0607 N 159.3185 W	Windward	Limestone	2
Māhā'ulepū	Kaua'i	21.8887 N 159.4164 W	Leeward	Basalt	2
Hulopo'e Bay	Lāna'i	20.7380 N 156.8950 W	Leeward	Basalt	2

Wind/wave exposure was classified as windward, leeward, channel, or bay after NOAA island region classification scheme; substrate was characterized as predominantly limestone, predominantly basalt, or mixed limestone and basalt

Site	Island	GPS	Exposure	Substrate type	N field trips
Onekahakaha	Hawaiʻi	19.7386 N 155.0389 W	Windward	Basalt	2
Waipuʻilani	Maui	20.7537 N 156.4609 W	Leeward	Limestone	2

Wind/wave exposure was classified as windward, leeward, channel, or bay after NOAA island region classification scheme; substrate was characterized as predominantly limestone, predominantly basalt, or mixed limestone and basalt

Temporal analyses

To examine the decadal change in Hawaiian intertidal communities, we compared community data collected by OPIHI citizen scientists in March through May of 2016–2017 with data from 2006 to 2007 using the same survey methods. Five sites were included in the temporal analysis. Waipuʻilani, Diamond Head, Sand Island, and Barber's Point were surveyed at least once in each of the 4 years, and Waiʻōpae was not surveyed in 2006 but was surveyed four times in 2007 (Table 2). Although Waiʻōpae was not surveyed in 2006, we included it in this analysis as an important historical record, since the shoreline where this site was located has been covered in lava from the Kīlauea Volcano eruption in 2018.

Table 2

Intertidal sites in the temporal analysis and number of times surveyed during 2006, 2007, 2016, and 2017

Site	Island	GPS	2006	2007	2016	2017
Diamond Head	Oʻahu	21.2554 N 157.8103 W	April (4)	April (9)	April (2)	March April
Sand Island	Oʻahu	21.3002 N 157.8826 W	April May	May (7)	March April	April (2) May
Barber's Point	Oʻahu	21.2958 N 158.1037 W	April May	May (5)	March	March
Waipuʻilani	Maui	22.0621 N 159.3189 W	April	April May	April	March May
Waiʻōpae	Hawaiʻi	19.4882 N 154.8193 W	NA	April May (3)	April	May

The number in parentheses following the month name indicates the number of times the site was surveyed in that month and year. NA refers to no surveys during the year indicated at the site indicated

To test the hypothesis that change in intertidal communities would be greater across decades than years, we used a PERMANOVA with site-specific yearly averages as the sampling unit. We took the mean percent cover values from site visits conducted in the same month within the same year (e.g., all site visits done in March 2006 were averaged) to obtain month-year averages for each site; then, we took the mean of the monthly averages from the same year (e.g., March 2006, April 2006, and May 2006 were averaged) to obtain site-year mean percent cover. This was repeated for each taxon at each site. Data were square root transformed and a Bray–Curtis similarity matrix was constructed comparing each site-specific yearly average. We used the metaMDS function in the vegan package to visualize community composition at each site and year. A PERMANOVA was run on the data with the factor year nested by site and a separate PERMANOVA was run with decade nested by site. The factors year and decade were each nested by site because previous analysis showed that benthic community composition differs significantly between sites, suggesting that any long-term change in community structure may be site-specific. The years 2006 and 2007 represent the same decade, and 2016 and 2017 were classified as a second decade. When significant decadal differences in benthic assemblages were found, we performed a SIMPER (similarity percentage analysis) to identify which taxa contributed to the observed differences in composition and abundance. The SIMPER was performed using month-year average abundances for each site (e.g., March 2017, April 2017, May 2017). To determine if there were taxon-specific decadal changes in individual taxa that may not be reflected in community-wide analyses, we performed a series of tests comparing the abundance of individual taxa between 2006–2007 and 2016–2017 for species that were relatively common or considered invasive. First, we checked the abundance data for normality using Shapiro–Wilk tests. Because data deviated significantly from a normal distribution and transformation did not improve normality, we utilized a non-parametric analysis, the Wilcoxon rank-sum test, to compare taxon abundances in 2006–2007 and 2016–2017 using survey as the sampling unit ($n = 2$–13 surveys per decade per site; see Table 2). We limited our testing to common taxa, defined as taxa with greater than 2% cover on at least one benthic survey of any site. Due to areas with bare rock as substrate, lack of large macroalgal canopies, and generally low total cover but high diversity of macroalgae in Hawai'i, taxa with greater than 2% cover are considered "common" in this system. We also performed tests on the abundance of taxa between decades (2006–2007 vs. 2016–2017) if they were considered invasive (i.e., fast-growing nuisance species) in Hawai'i regardless of their abundance. Wilcoxon rank-sum tests were performed in JMP Pro (version 13.1.0) for the 23 taxa that fit these requirements: *Acanthophora spicifera* (M.Vahl)

Børgesen, brown crust, *Cladophora* spp., *Codium* spp., crustose coralline algae (CCA), cyanobacteria, *Dictyosphaeria* spp., *Dictyota* spp., *Gracilaria salicornia* (Sonder) Durairatnam, *Halimeda discoidea* Decaisne, *Hypnea musciformis* J.Agardh, *Hypnea* spp., *Laurencia* spp., *Microdictyon setchellianum* M.Howe, *Montipora capitata* (Dana), *Padina* spp., *Porites lobata* (Dana), *Pterocladiella* spp., *Sargassum* spp., *Spyridia filamentosa* (Wulfen) Harvey, *Turbinaria ornata* (Turner) J.Agardh, turf algae, and *Ulva* spp. Because abundance differences could be driven by site-specific changes or by island-wide change, we first performed Wilcoxon tests on the abundances of common taxa for each of the five sites, followed by tests comparing the abundances of each taxon across the five sites in both decadal periods. *P* values were controlled for false discovery rate ($\alpha = 0.05$) using the function p.adjust with the Benjamini–Hochberg–method in the R package stats (R Core Team, 2016).
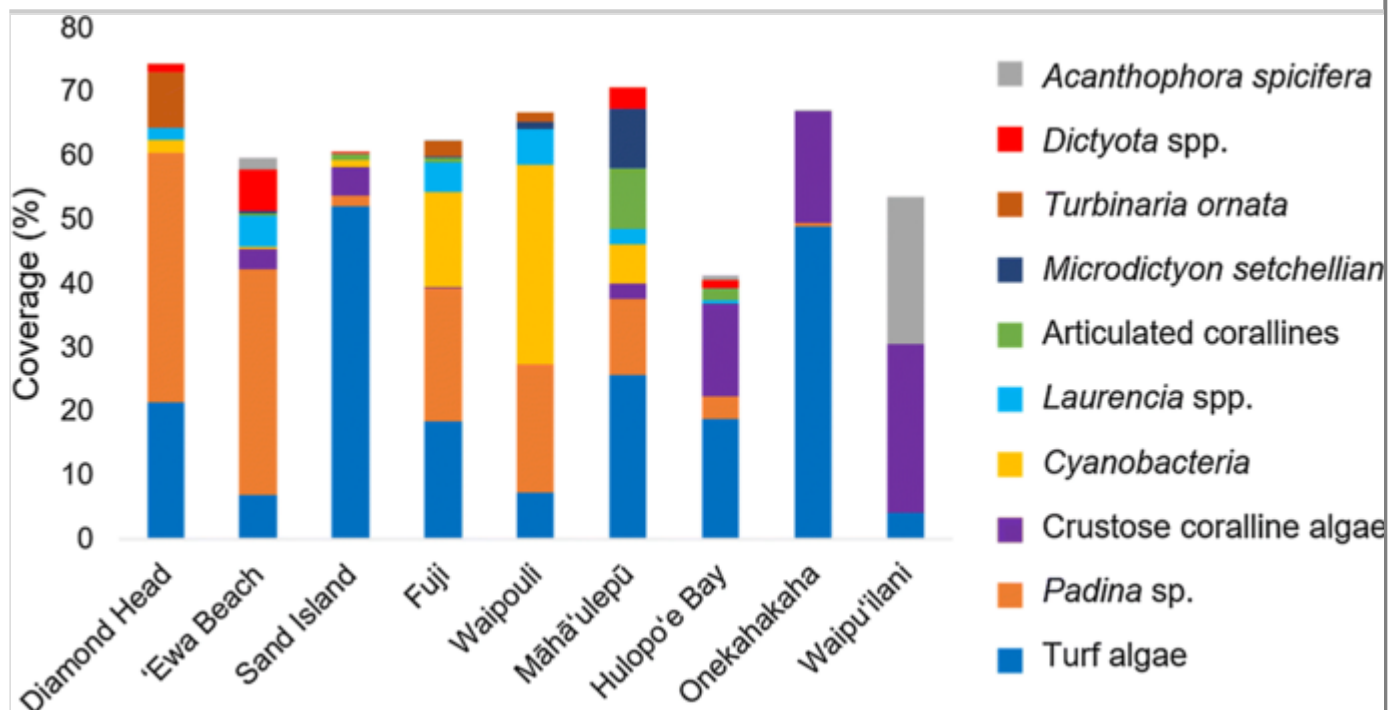
Results

Spatial variation in community assemblages

A total of 43 algal taxa, 24 invertebrate groups, and cyanobacteria were found at the nine sites included in the spatial analysis. Each site was surveyed between two to six times in 2017. The most common algal taxa across all sites were turf algal forms, *Padina* spp., and CCA. These three taxa occurred at abundances > 5% cover averaged over all sites. Figure 2 shows the ten most abundant taxa, which were present with higher than 5% cover at one or more sites. Among the ten most abundant species was *A. spicifera*, an invasive macroalgae, recorded at five out of the nine sites.

Fig. 2

Most abundant algal taxa across all sites. The ten taxa shown were recorded with > 5% cover at one or more sites used in the spatial analyses

Benthic community composition differed among sites, islands, and substrate types, as shown by the PERMANOVA results (Table 3). Community composition did not differ significantly by wind/wave exposure type. It is important to note that the factors site and island, followed by substrate type, appear to be driving the variation in assemblages (Table 3 and Fig. 3). This is evident in the high R-squared values for site and island and can be visually observed in the nMDS (Fig. 3).

Table 3

Single factor PERMANOVA results for spatial analysis of nine sites

Factor	df	SS	MS	Pseudo F	R^2	P
Site	8	3.234	0.404	5.249	0.750	0.0001*
Substrate	1	0.553	5.553	3.016	0.188	0.0216*
Island	1	0.336	0.336	2.400	0.138	0.0251*
Wind/wave exposure	1	0.264	0.264	1.533	0.075	0.1474

All PERMANOVAs were run with 9999 unique permutations; asterisks indicate P values < 0.05

Fig. 3

nMDS of sites in the spatial analysis. The gray polygons connect sites located on the same island; the gray polygon on the right represents Oʻahu and gray polygon on the

left represents Kaua'i. The shape of the points correspond to substrate type and color refers to wind/wave exposure type. Site codes are Diamond Head (DH), 'Ewa Beach (EB), Sand Island (SI), Fuji (FJ), Māhā'ulepū (MA), Waipouli (WP), Hulopo'e Bay (HB), Onekahakaha (ON), and Waipu'ilani (WL)
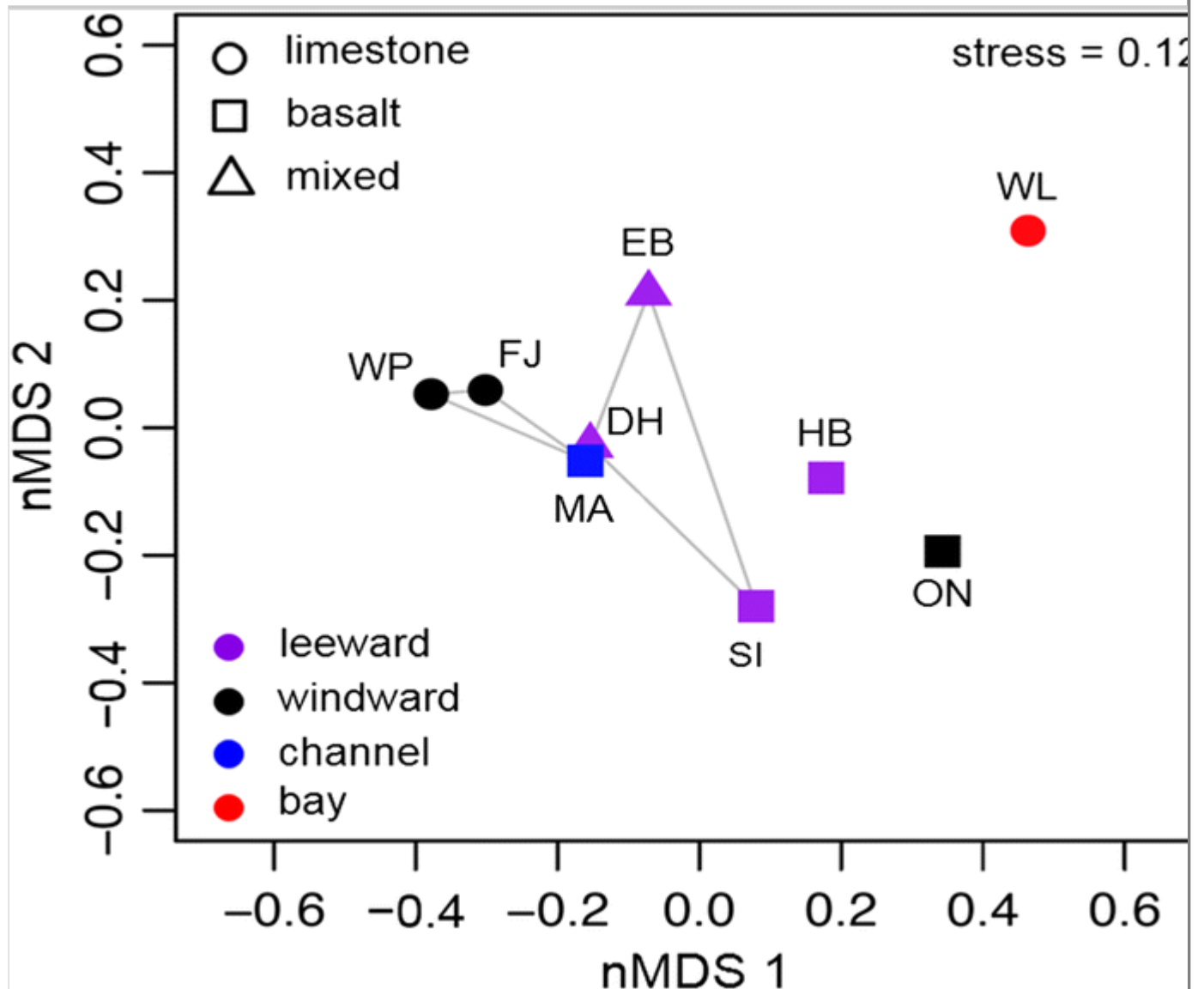
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The indicator species test pointed to specific taxa characterizing each subgroup of site, substrate type, and island (Table 4). Most indicator taxa were macroalgae; this reflects their greater coverage at sites relative to invertebrate taxa. Specific indicator taxa were identified for five out of nine sites and for the island of Kaua'i. Each substrate type had two indicator taxa.

Table 4

Indicator species for factors analyzed in the spatial data

Factor: level	Indicator species	Stat	P
Site			
Diamond Head	*Turbinaria ornata*	0.889	0.040*
ʻEwa Beach	*Avrainvillea amadelpha* (Montagne) A.Gepp & E.S.Gepp	0.861	0.021*
Māhāʻulepū	*Microdictyon setchellianum* M. Howe	0.990	0.028*
	Articulated corallines	0.866	0.032*
	Colpomenia sinuosa (Mertens ex Roth) Derbès & Solier	0.888	0.047*
Onekahakaha	Coral	0.979	0.017*
Waipuʻilani	*Acanthophora spicifera*	0.965	0.007**
	Gelidiales	0.744	0.049*
Fuji + Waipouli	Cyanobacteria	0.885	0.032*
Onekahakaha + Sand Island	Turf algae	0.879	0.008**
Hulopoʻe Bay + Onekahakaha + Waipuʻilani	CCA	0.788	0.049*
Diamond Head + ʻEwa Beach + Fuji + Waipouli	*Padina* spp.	0.848	0.007**
Island			
Kauaʻi	Cyanobacteria	0.653	0.015*
	Microdictyon setchellianum	0.558	0.015*
	Lyngbya majuscula Harvey ex Gomont	0.531	0.035*
Substrate type			
Basalt	Turf algae	0.782	0.010*
	Echinometra spp.	0.587	0.025*
Limestone	Cyanobacteria	0.647	0.015*
	Gelidiales	0.463	0.045*

Factors include site, island, substrate type, and wind/wave exposure type. For each factor, only the levels for which one or more significant indicator species were identified are listed. Asterisks indicate P values < 0.05 (*) and < 0.01 (**)

Although invertebrate taxa were seldom identified as indicator species, there were some similarities in invertebrate abundance and composition among sites. Sand Island, Onekahakaha, and Hulopoʻe Bay had high abundances of invertebrates and cluster together on the nMDS (Figs. 3, 4). The most abundant invertebrate species at Sand Island were urchins (*Echinometra* spp.) and vermetids. The coral species *Pocillopora damicornis* Linnaeus and *P. lobata* made up about 2% of the benthic cover at Onekahakaha. Nerites, urchins, and sea cucumbers (*Holothuria* spp.) were most abundant at Hulopoʻe Bay (Fig. 4).

Fig. 4

Most abundant invertebrate taxa across all sites. The five taxa shown were recorded with > 1% cover at one or more sites used in the spatial analyses
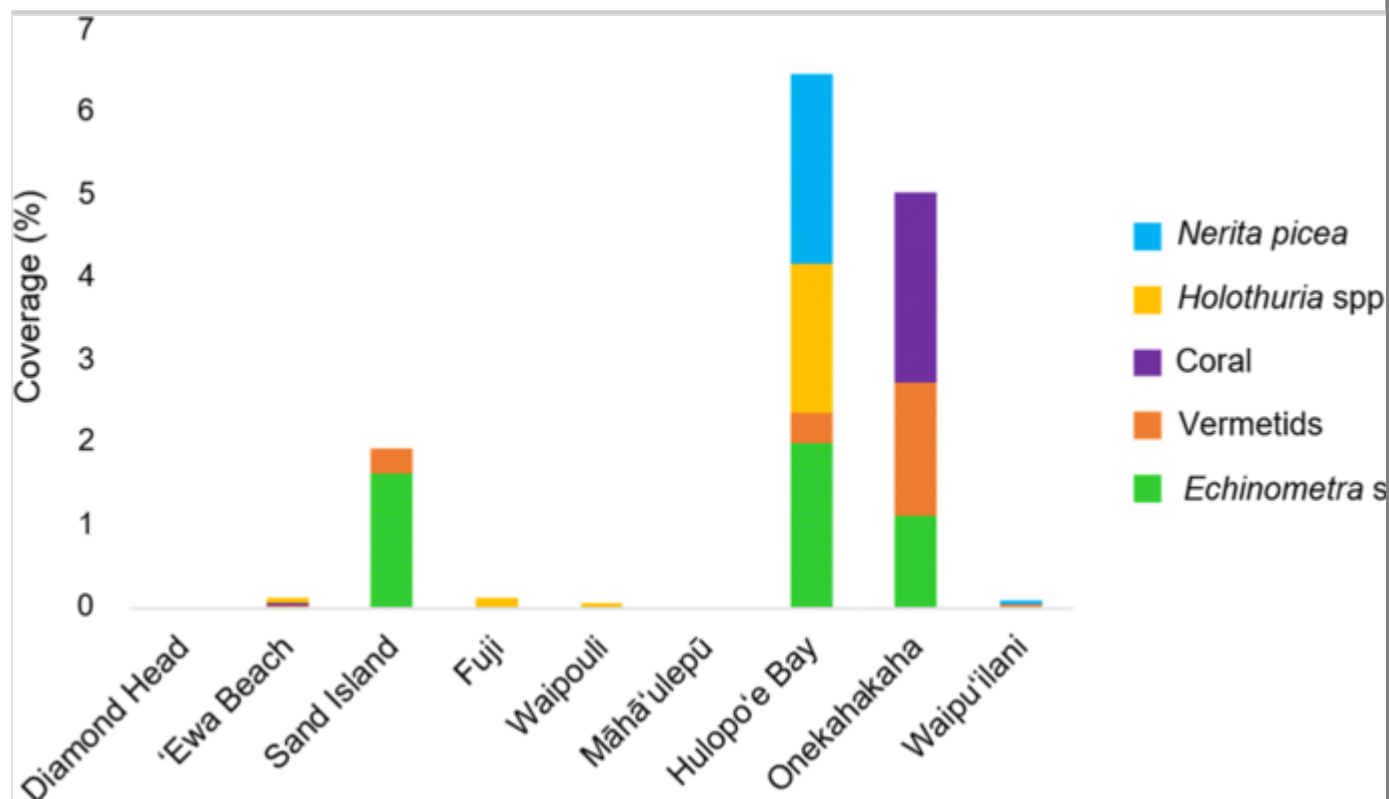
Decadal variation in community assemblages

The decadal dataset with grouped taxa showed high overall richness of benthic organisms, with a total of 55 algal taxa and 37 invertebrate taxa. Both year nested by site and decade nested by site were significant in the PERMANOVAs (single factor PERMANOVAs, Table 5). A visual assessment of community composition at Sand Island and Diamond Head suggested that communities vary more between

decades than between years in the same decade, although the other three sites did not follow this pattern (Supp. Figure 1).

Table 5

Single factor PERMANOVA results for temporal analysis

Factor	df	SS	MS	Pseudo F	R^2	P
Decade (site)	9	2.839	0.315	3.686	0.787	0.0001 *
Year (site)	5	2.256	0.451	4.332	0.625	0.0001 *

Each PERMANOVA was run with 9999t unique permutations; asterisks indicate P values < 0.05

In addition, we identified several taxa that changed abundance significantly between decades, either at one individual site or across the five sites. From averaged data of all sites (Table 6), turf algal forms were highly abundant in 2006 and 2007 ($\mu_{06-07} \approx 12\%$) and more than doubled by 2016 and 2017 ($\mu_{16-17} \approx 25\%$). This change was mainly driven by the high coverage of turf algae at Sand Island. The same pattern was observed for CCA ($\mu_{06-07} \approx 2\%$ to $\mu_{16-17} \approx 9\%$) (Fig. 5). *Padina* spp. was highly abundant in both decades ($\mu_{06-07} \approx 10\%$, $\mu_{16-17} \approx 13\%$). Among invertebrates, vermetids were abundant in both decades, averaging > 1%.

Table 6

Wilcoxon test results for taxa that changed abundance significantly between 2006–2007 and 2016–2017

| Taxon	Site	μ_{06-07} (± SD)	μ_{16-17} (± SD)	P
CCA	All sites	1.74 (± 3.44)	9.40 (± 14.6)	0.0437 *
Turbinaria ornata	All sites	0.0433 (± 0.149)	1.48 (± 2.97)	0.0491 *
	Diamond Head	0.133 (± 0.243)	5.30 (± 4.18)	0.0437 *
	Barber's Point	0 (± 0)	0.956 (± 0.482)	0.0437 *
Hypnea spp.	All sites	0.0235 (± 0.0806)	0.443 (± 0.649)	0.0138 *

Average abundances (μ) were calculated using surveys as replicates. The number of surveys conducted per site per decade ranged from 2 to 13, and P values are adjusted for false discovery rate. Classification "all sites" refers to a Wilcoxon test done on surveys from all five sites for 2006–2007 and 2016–2017. Asterisks indicate P values < 0.05

Taxon	Site	μ_{06-07} ($\pm$ SD)	μ_{16-17} ($\pm$ SD)	P
Turf algae	Sand Island	10.3 ($\pm$ 7.34)	50.3 ($\pm$ 5.68)	0.0437 *
Sargassum spp.	Diamond Head	9.31 ($\pm$ 4.18)	1.93 ($\pm$ 1.40)	0.0491 *
Acanthophora spicifera	Sand Island	0.816 ($\pm$ 0.800)	0 ($\pm$ 0)	0.0497 *
	Barber's Point	4.11 ($\pm$ 0.997)	1.68 ($\pm$ 1.01)	0.0593

Average abundances (μ) were calculated using surveys as replicates. The number of surveys conducted per site per decade ranged from 2 to 13, and P values are adjusted for false discovery rate. Classification "all sites" refers to a Wilcoxon test done on surveys from all five sites for 2006–2007 and 2016–2017. Asterisks indicate P values < 0.05

Fig. 5

Mean percent cover of CCA and *Turbinaria ornata* by site and year. Mean abundance of CCA (**a**) and *T. ornata* (**b**) surveyed at Diamond Head (DH), Barber's Point (BP), Sand Island (SI), Waipuʻilani (WL), and Waiʻōpae (WO) during 4 years spanning a decade (except for WO, which was not surveyed in 2006). The gray bars show the mean abundance of *T. ornata* and CCA averaged first by month, then by year within site, then averaged across the five sites. Symbols show the mean abundances at each site for that year
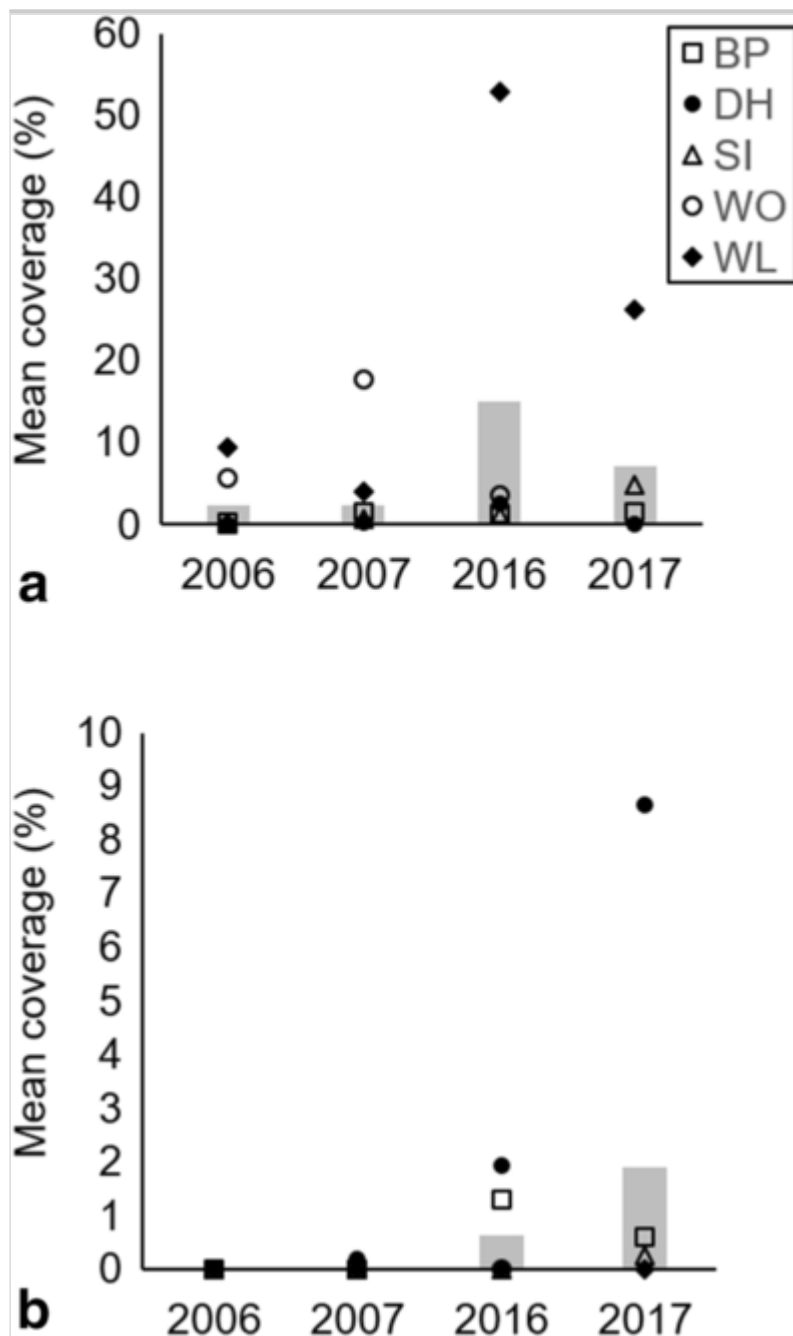
Three algal taxa (CCA, *T. ornata*, and *Hypnea* spp.) changed abundance significantly between 2006–2007 and 2016–2017 across the five sites. Four taxa changed abundance significantly at one or more individual sites (Table 6). In each case, the change in abundance in these taxa between decades was greater than within month variation, calculated by looking at ranges of relative abundance for data collected within the same month in the same year and by different observers (Supp Table 4). Most decadal changes appear to be site specific, which is in agreement with previous work (Cox et al., 2013) and the spatial analyses. *T.urbinaria ornata* increased from 2006–2007 to 2016–2017 when all sites were pooled together, as well as at Diamond Head and Barber's Point when site

abundances were examined separately. CCA increased in abundance from 2006–2007 to 2016–2017 across all sites (Fig. 5). The abundance of *Hypnea* spp. also changed significantly between 2006–2007 and 2016–2017, but its mean cover was < 1% in every year.

SIMPER analysis identified the taxa that contributed to the observed differences in composition and abundance of the benthic communities between 2006–2007 and 2016–2017 (Table 7). The increase in turf algae was responsible for 26% of the decadal difference between the assemblages, followed by increased abundances of *Padina* spp. (18%), and CCA (15%). The invasive algal species *A. spicifera* was responsible for 5% of the difference in assemblages between the two decades. Vermetids, the only invertebrates that were identified as contributing to community differences among decades, were responsible for 2% of the difference in assemblages. The top ten species listed in Table 7 are cumulatively responsible for over 85% of the differences in assemblages between 2006–2007 and 2016–2017.

Table 7

SIMPER results for temporal analysis (using year averages)

Taxa	Average	SD	Ratio	μ_{06-07}	μ_{16-17}	Cum. sum
Turf algae	0.1883	0.2006	0.9386	12.06	25.08	0.2620
Padina spp.	0.1326	0.1145	1.1580	10.44	12.78	0.4465
CCA	0.1046	0.1622	0.6452	2.402	11.17	0.5920
Brown crust	0.0506	0.1182	0.4279	0.4309	6.730	0.6624
Acanthophora spicifera	0.0346	0.06646	0.5204	1.026	3.168	0.7105
Laurencia spp.	0.0315	0.03593	0.8772	3.307	1.810	0.7543
Sargassum spp.	0.0297	0.02948	1.0084	3.352	1.747	0.7957
Vermetidae	0.0151	0.01489	1.0155	1.110	1.606	0.8167
Cyanobacteria	0.0150	0.01237	1.2152	8.192	1.805	0.8376
Turbinaria ornata	0.0111	0.02209	0.5043	0.043	1.476	0.8531

Taxa are ordered by contribution to between-group dissimilarity (Average). SD is the standard deviation of each taxon's contribution, ratio is the average to SD ratio, μ is the average relative abundance for 2006–2007 and 2016–2017, respectively, and Cum. sum is the cumulative sum of the taxa contributions to between-group similarity

Discussion

Spatial analysis

Spatially broad studies such as this are important for understanding the scales of variation in intertidal communities. In contrast, many intertidal studies have focused on a few species and their interactions (e.g., Menge et al., 1994 or have limited temporal coverage (e.g., Zabin et al., 2013. This study of tropical rocky intertidal communities increased spatial coverage compared to previous studies and reduced yearly and monthly bias. We found that benthic community composition in Hawaiʻi's intertidal is highly variable and differs significantly by site and island, in agreement with Cox et al. (2013. We identified substrate type as an additional, significant factor influencing intertidal communities.

One major result of our study is that Hawaiʻi exhibits distinct benthic intertidal communities at the scale of sites separated by 10 s to 100 s of kms, similar to patterns reported for other intertidal systems (Fraschetti et al., 2005; Valdivia et al., 2011; Watson & Barnes, 2004. Our results extend this finding in Hawaiʻi's tropical setting. The physical factors driving community site-specificity remain to be determined, although temperature (Blanchette et al., 2009, land-use (Groffman et al., 2004, nutrient availability (Larned, 1998, and groundwater (McCook, 1999; Lyons et al., 2014 are likely candidates. For example, local sea surface temperature was highly correlated with community structure in a study of 22 intertidal sites in the Channel Islands of California (Blanchette et al., 2009. Satellite data on sea surface temperature is readily available and could be combined with this citizen science data set to test additional hypotheses about intertidal community variation.

The observed variation across multiple spatial scales likely results from the biological processes and physical factors operating at these different scales (Martins et al., 2008. For example, dispersal may drive community assembly at both island and exposure type (i.e., island region scales (Palmer et al., 1996. In contrast, substrate is often site-specific and limestone and basalt differ in color and therefore retain heat differently, potentially affecting species vulnerable to warmer temperatures (Cox et al., 2011. Substrate can also influence local topography, which can, in turn, create physical refugia and structures that affect organisms' ability to persist in these areas (Green et al., 2012. In agreement with our study, substrate type was a significant indicator of algal and invertebrate community composition in Australian intertidal reefs (Bessey et al., 2019. Climate change will operate in different ways at all of these spatial scales; for example, thermal stress on intertidal organisms is not linearly related to latitude and is predicted to show complex spatial and temporal patterns of variation under climate change (Helmuth et al., 2006). Furthermore, the periodicity of high temperature

events has been linked to the spread of exotic species (Stachowicz et al., 2002), with potential to greatly alter intertidal community structure.

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Climatological, hydrodynamic, and oceanographic factors may affect the dispersal of organisms and their relative success in areas with different wind/wave exposure types (Bustamante & Branch, 1996; Morgan et al., 2009; Castorani et al., 2015). Despite broad climatological differences between windward and leeward sides of islands (e.g., rainfall, currents, wave action, wind), our results suggest that wind/wave exposure does not correspond with community composition in Hawaiian intertidal sites. It is likely that broad categories such as windward vs. leeward are too coarse and that benthic communities are more strongly impacted by local factors, such as substrate, or that the effects of wind and wave exposure on intertidal communities occur at smaller spatial scales.

Intertidal community composition differed between Oʻahu and Kauaʻi. This result agrees with the finding of Cox et al. (2013) that Hawaiian intertidal communities differ by island, although our spatial analysis is limited by the fact that only two islands, Oʻahu and Kauaʻi, were included in the analysis. Lānaʻi, Hawaiʻi, and Maui were each represented by a single site, so differences among islands would have been conflated with site differences. To characterize the intertidal communities of each island and region more generally, future studies should aim to sample additional sites on Lānaʻi, Hawaiʻi, and Maui within the same time period.

Finally, the importance of local factors in shaping benthic intertidal communities has implications for watershed management at the island level. As the Hawaiian archipelago contains numerous endemic species, including algae such as *Laurencia mcdermidiae* and *Wrangelia elegantissima* (Tsuda, 2014), it is important that state-level management empower local and regional authorities to protect these natural resources.

Temporal analysis

This study leveraged a long-term validated citizen science dataset to detect significant yearly and decadal shifts in Hawaiian intertidal communities, with notable significant changes in abundance of individual species over a decade. Most species-specific decadal changes appear to be site-specific, except for CCA and *T. ornata*, which exhibited significant changes in abundance across five sites. Our finding that most long-term changes are site specific agrees with our spatial analysis (Table 3) and Cox et al. (2013); this finding suggests that community

changes are strongly driven by local factors. It is also possible that the effects of global scale changes (e.g., ocean warming) are mediated by local factors, resulting in different changes across different communities (Gurney et al., 2013).

CCA increased significantly across the five sites, with the largest increase occurring at Waipuʻilani. Studies focused on tropical islands have shown that following warm water events there can be a drop in fleshy macroalgae abundance and an increase in CCA (Cox et al., 2017). The abundance of turf algae also increased across all sites and increased fivefold at Sand Island. Turf algae can be opportunistic species with high turnover rates, and they are highly stress tolerant compared to fleshy macrophytes (Airold, 1998). Filbee-Dexter & Wernberg (2018) showed that regime shifts from kelp forests to turf-dominated systems are widespread and mediated by biotic and abiotic (warming and eutrophication) processes. Both CCA and turf are understory algae and tend be resilient to physical disturbance (Micheli et al., 2016). It is possible that once fleshy perennial species are lost, they take longer to recover, leaving CCA and turf algae uncovered for long periods of time. In addition, Vermeij et al. (2011) found a negative relationship between CCA and macroalgal abundance on Hawaiian reefs. Our SIMPER analysis identified *Laurencia* spp. and *Sargassum* spp., both of which declined in abundance, as two of the top ten contributors to dissimilarity in intertidal communities between decades. Thus, a decline in fleshy species such as these may be related to the observed decadal increase in CCA and turf algae. According to the National Marine Fisheries Service (NOAA Fisheries), mean sea surface temperatures in Hawaiʻi have increased over the past five decades (Coles et al., 2018). It is possible that with an increased frequency of high temperature events, disturbances affecting fleshy macroalgae, as well as shifts in nutrient regimes caused by changing land cover, CCA and turf algae outcompeted macrophytes for space.

Turbinaria ornata increased in abundance across all sites; however, this trend was driven by large increases at Diamond Head and Barber's Point, both located on the south shore of Oʻahu. *Turbinaria ornata* is a fleshy and rigid macroalga that is also very resistant to high wave action and is usually found in wave exposed areas (Stiger and Payri 1999). In addition, *T. ornata* contains chemical deterrents in its thallus (Stiger et al., 2004) and becomes less susceptible to herbivory as it grows, with large stands of *T. ornata* experiencing low herbivory (Bittick et al., 2010; Davis, 2018). *T. ornata*'s resistance to herbivory combined with the depletion of herbivorous fish around Oʻahu (Helyer & Samhouri, 2017), may have contributed to its general increase at Barber's Point and Diamond Head. In French Polynesia, *T.*

ornata has been an established invader of reefs for the past three decades (Done, 1992; Payri & Stiger, 2001), suggesting that its presence and abundance on Hawaiian coastlines should be monitored. Among the multiple stressors currently impacting Hawaiian coastal marine communities are rising sea level and increased frequency of extreme tide events (Firing, 2004) and storms (Norton et al., 2011) as well as pulsed heating events resulting in coral bleaching (Jokiel & Brown, 2004). All of these stressors may have caused physical disturbances of fleshy macroalgae, creating space for hardier species, such as *T. ornata*, to continue to establish themselves.

Future work

Long-term monitoring studies are important in providing baseline data and to ground truth changes in community structure. Broad spatial and temporal studies can help us understand whether changes in benthic community patterns are cyclical, or due to local disturbances or climate change (Southward et al., 2005). Large scale disturbances can completely reset community structure, providing opportunities to study the assembly of new communities and succession dynamics; at Waiʻōpae, one of our sites on Hawaiʻi island, the volcanic eruption of Kīlauea covered the entire survey location, along with over 6 km of shoreline, with lava. The baseline community data collected at Waiʻōpae will allow future studies to compare the new community that develops with the community that was effaced. This study site could provide a rare opportunity to study primary succession at a spatial scale of kilometers, with the scale of disturbance being an important factor affecting alternative community states (Petraitis & Latham, 1999). Monitoring this site could elucidate the success of different types of recruits and their persistence over time.

The ability to correlate changes in Hawaiʻi's intertidal benthic communities with environmental variables is limited by the lack of coverage of environmental data and complexities associated with the many biological and physicochemical factors potentially affecting these systems (Helmuth et al., 2006; Cox & Smith, 2011). Future studies could monitor site-specific water and air temperatures as well as nutrient levels, particularly during dry periods and after rain events, to examine how community structure correlates with these abiotic factors. In addition, understanding the mechanisms driving temporal changes in species abundances is necessary in order to predict future changes, including the impacts of nutrient regimes, climate shifts, and coastal development on tropical intertidal systems. For example, experimental manipulation of fleshy macroalgal cover (e.g., by clearing these species from experimental plots in the intertidal) could be used to test the

hypothesis that disturbance and decline of fleshy macroalgae have allowed CCA and turf algae to increase in Hawai'i's intertidal, as documented across multiple sites in our study. Lab experiments could be used to investigate the effect of specific abiotic disturbances, such as pulsed heating events, on the competitive abilities of fleshy macroalgae compared to CCA and turf algae.

In conclusion, Hawaiian rocky intertidal sites are species rich and differ at local, regional, and island scales. Significant decadal changes in the abundance of intertidal algae, both site-specific and across sites, point to changes in the drivers of community structure at multiple spatial and temporal scales. Future studies with broad temporal and spatial coverage, facilitated by citizen scientists, should continue to monitor these community changes, as well as test mechanisms potentially driving them at relevant spatial scales.

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Electronic supplementary material

Below is the link to the electronic supplementary material.

Supplementary material 1 (DOCX 92 kb)

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