Coral Reefs
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REPORT

Environmental gradients drive physiological variation in Hawaiian corals

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Abstract To evaluate potential coral adaptive mechanisms, we investigated physiological traits (biomass, lipid, protein, chlorophyll, and isotopic proxies for trophic strategy) in eight Hawaiian corals species along an environmental gradient of significant wave height, sea surface temperature, and seawater chlorophyll *a* concentration around the island of Oʻahu, Hawaiʻi. We used the amount of physiological variation expressed in corals, and the proportion of this variation that could be explained by environmental variables, to construct hypotheses about the relative capacity for each species to adapt or acclimatize to differing conditions. Genus-level analyses indicated that *Montipora* and *Pocillopora* phenotypes are influenced more strongly by the environment than *Porites* corals. Species-level analyses revealed that *Montipora capitata* and *Pocillopora acuta* have the widest physiological niche boundaries, whereas *Porites evermanni* and *Pocillopora meandrina* are more physiologically restricted. Correlations between individual traits and the environmental gradient provided insight into potential adaptive mechanisms employed by each species that allow them to persist in reefs such as those within Kāne'ohe Bay, where water flow is lowest, and temperature, acidity, and nutrient concentrations are highest relative to other reefs around Oʻahu. Potential adaptive mechanisms included (a) increased surface-area-to-volume ratios to facilitate higher material flux across the diffusive boundary layer and/or to maximize light harvesting (*M. capitata* and *P. acuta*), (b) strategic investment of metabolic energy toward energy reserves (*Montipora* and *Pocillopora*), (c) changes in protein management likely via differential expression and function (*Porites*), and d) increased chlorophyll concentration per Symbiodiniaceae cell to maximize photosynthesis (*Porites compressa*). Comparison of our results with established patterns in the relative abundance of these species around Oʻahu suggests that species with wide physiological niche boundaries like *M. capitata* and *M. flabellata* might be expected to do better under predicted future ocean conditions and outcompete species such as *P. evermanni* and *P. meandrina*, making them potential candidates for coral conservation efforts.

Keywords Coral physiology · Environmental gradients · *Montipora* · *Pocillopora* · *Porites*

Introduction

Corals reefs are the most biologically diverse marine ecosystems on Earth (e.g., Fisher et al. 2015). They represent a substantial genetic library and provide raw material for new medicines (Moberg and Folke 1999). Through resources such as seafood provision, tourism, and shoreline

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protection from erosion and storm damage, coral reefs are essential for hundreds of billions of dollars of the global economy annually (Costanza et al. 2014; Hoegh-Guldberg 2015). However, the ecosystem and services that coral reefs provide are being degraded at an alarming rate due to the detrimental effects of global climate change, including ocean warming and acidification (e.g., Hughes et al. 2003). The responses of organisms to future increases in ocean temperature and reductions in pH will be determined by their abilities to alter their physiology through adaptation or acclimatization (e.g., Somero 2012). Thus, understanding the capacity for corals to alter their physiology following environmental changes is of great importance for predicting how these reef communities, and the ecological services they provide, may change under future climate change scenarios.

Physiological variation along natural environmental gradients can reveal the influence of the environment in driving adaptation or acclimatization of physiological traits within a species. For instance, decreases in light availability are associated with higher concentrations of photosynthetic pigments (i.e., chlorophyll) and changes in the number of reaction centers in light-harvesting photosystems in corals (reviewed by Brown 1997). This correlation between physiology and light gradients is not random and instead illustrates physiological adaptation or phenotypic plasticity to maximize photosynthetic yield under low-light conditions. Light, salinity, temperature, and pH gradients occur along latitudinal ranges of coral reefs (Veron 1995), but gradients in other seawater physico-chemical conditions also occur on smaller spatial scales (i.e., tens of kilometers or less; e.g., Smith et al. 2007; Guadayol et al. 2014; Silbiger et al. 2014; Jury and Toonen 2019; Jury et al. 2019). Around the island of O‘ahu, Hawai‘i, differences in local geography and bathymetry influence seawater residence times, causing gradients in sea surface temperature, pH, and water flow (Bathen 1968; Lowe et al. 2009a, b; Franklin et al. 2013; Jury and Toonen 2019). In areas with riverine input, differences in rainfall and run-off produce gradients in coastal nutrient concentrations (Ringuet and Mackenzie 2005; De Carlo et al. 2007).

In this study, we use the environmental gradients around the island of O‘ahu to investigate the capacity for the eight most dominant coral species in Hawai‘i to adapt or acclimatize to this suite of conditions. This approach provides insight into the complexities of native coral ecosystems, and allows for the investigation of the effect of chronic exposure to different environmental conditions. In addition, this approach encompasses the interactive effects of multiple environmental factors which account for a plethora of biotic interactions (e.g., competition and predation) that influence how coral communities, genera, and species likely respond to environmental change and are not feasible to replicate in controlled tank conditions. A limitation of such studies is the difficulty to identify which environmental parameter is primarily responsible for driving observed phenotypic changes as it is not possible to measure every abiotic variable. This study addresses two research questions:

(1) Is there a correlation between the seawater environment and coral physiological variation around O‘ahu? If so, does the nature of this relationship vary among genera and species?
(2) What physiological phenotypes do each species exhibit along the environmental gradients, and do they appear to be adaptive strategies that allow colonization and persistence among habitats?

This is the first study to utilize natural gradients in flow, temperature, and nutrients to investigate the physiological adaptation and acclimatization potential in Hawaiian corals around the island of O‘ahu. This is also the first study in Hawai‘i to investigate coral physiology in eight different species concurrently (McLachlan et al. 2020a), and thus offers unique insight into the role of species interactions in determining coral physiological phenotypes. This approach allows for the generation of hypotheses that integrate physiological and ecological aspects to explain the coral species composition of Hawaiian reefs, and for making predictions about how coral composition may change under global warming scenarios.

Materials and methods

Environmental data

Six sites surrounding the island of O‘ahu, Hawai‘i, USA were investigated in this study: Sampan, Moku o Lo‘e, Waimānalo, Magic Island, Electric Beach, and Hale‘iwa (Supplement 1 Fig. S1). The two sites within Kāne’ohe Bay were chosen to represent reefs with varying flow conditions and different seawater residence times (i.e., ~ 4 days at Sampan versus ~ 36 days at Moku o Lo‘e (Lowe et al. 2009a, b). In addition, as both Sampan and Moku o Lo‘e have similar temperature and pH conditions, using both sites allowed us to examine the role of flow and nutrients within Kāne’ohe Bay on the measured responses. Sea surface temperature (SST), seawater chlorophyll *a* concentration (SW Chl), and significant wave height (SWH) were obtained from buoy and satellite data archives for the geographic coordinates of each site in 2015, the year the corals were collected. Daily average SST values were obtained using quality-controlled buoy data available from NOAA’s National Data Buoy Center and the National Center for Environmental Information (Supplement 1

Table S1). As both Sampan and Moku o Loʻe were near each other in Kāne'ohe Bay (1000–3000 m apart, Supplement 1 Fig. S1b i–ii), we used the same buoy data for both sites. Weekly spatiotemporally composited SW Chl data (here used as a proxy for seawater nutrients) was retrieved from NOAA Coral Reef Watch's Ocean Color at a resolution of 750 m via the Virtual Infrared Imaging Radiometer Suite (VIIRS) aboard the Suomi National Polar-orbiting Partnership (S-NPP) satellite. Values for SWH were collected at weekly intervals from a Simulated Waves Nearshore (SWAN) hindcast regional model for Oʻahu (Arinaga and Cheung 2012) and used as a proxy for near-bed shear stress (Storlazzi et al. 2005), as large amplitude waves generate higher bottom friction and thus increase water flow. Daily (SST) and weekly (SW Chl and SWH) values were used to calculate annual (January 1–December 25, 2015) and summer (June 20–October 10, 2015) mean values for each of the environmental variables. Summer mean values were calculated as thermal gradients are most pronounced during summer months (this study). Likewise, water flow patterns around Oʻahu vary annually and seasonally due to winter swells and summer storms (Fletcher et al. 2008). Thus, the annual and summer mean values allowed us to evaluate a range of conditions at each reef. A strong pH gradient is also present around the island of Oʻahu with Kāne'ohe Bay experiencing lowest pH and Waimānalo experiencing the highest (Jury et al. 2019). However, the available pH data either did not correspond with the exact locations where we collected corals, were unavailable for the temporal period used in this study, and/or were only single timepoint measurements thus preventing the calculation of annual and summertime averages. Therefore, pH was not included as an abiotic factor in this study.

Coral collection

Corals were collected in 2015 from each of the six study sites (Supplement 1 Fig. S1a). Unsafe weather conditions led to several delays during sampling which caused coral collection to span an 11-week period (between 17 August and 13 November, Supplement 2 Fig. S1). Eight species of coral from three genera were sampled: *Montipora capitata* (branching and encrusting), *Montipora flabellata* (encrusting), *Montipora patula* (encrusting), *Porites compressa* (branching), *Porites lobata* (massive), *Porites evermanni* (massive), *Pocillopora meandrina* (branching), and *Pocillopora acuta* (branching) (Fig. 1). Corals were identified morphologically in the field followed by close inspection of the corallite structure of the live corals upon returning to the lab to confirm species identification (Supplement 1 Text 1). The Y and B morphs of *P. damicornis* that were historically common in Kāne'ohe Bay (Richmond and Jokiel 1984) appear to correspond to the cryptic species *P. damicornis* and *P. acuta* (Johnston et al. 2018). Recent studies have found that *P. acuta* has become the dominant species and that *P. damicornis* is now rare in Kāne'ohe Bay (Gorospe et al. 2015; Johnston et al. 2018), so we focus on *P. acuta* in this study. Due to the natural zonation in coral species distributions, not all eight species were found in all six locations. To minimize the impact of collection, only the most commonly available species were sampled at each site, and spread across a wide area (see yellow polygons in Supplement 1 Fig. S1b–f). From each site, between nine and fifteen coral ramets (each from a different parent colony, with all parent colonies representing a distinct genet) of each commonly available species were collected from 2 ± 1 m depth yielding a total of 422 samples (Table 1). Genetic distinctiveness among parent colonies were confirmed by genotyping about half of the colonies (232 of the 422 colonies sampled) using available microsatellite markers (Concepcion et al. 2010; Gorospe and Karl 2013), and no identical multilocus genotypes were found within a site, suggesting very low probability that any were clonally derived and that each parent colony was likely a unique genet. Each coral ramet was 5–10 cm in size and was removed from larger parent genets using a hammer and chisel. None of the coral ramets included in this study were visibly pale or severely bleached. Samples were immediately frozen at − 20 °C, stored at the Hawaiʻi Institute of Marine Biology, and later shipped to The Ohio State University, Ohio, USA on dry ice, where they were stored at − 80 °C.

Physiological data

Encrusting algae and boring organisms were removed from the surface of each coral ramet using a Dremel tool fitted with a diamond tipped bit (Dremel Inc., Racine, WI). Each coral ramet was split into two pieces: one for biochemical and one for isotopic analysis.

The coral pieces designated for biochemical physiological analyses were photographed from all sides and the photographs processed in the software ImageJ (Rasband 1997) to estimate surface area using the geometric method (Naumann et al. 2009). Each coral piece was then individually ground into a fine homogenous paste using a chilled mortar and pestle, partitioned into subsamples designated for each biochemical analysis, and stored at − 80 °C. Analyses of total tissue biomass, total soluble lipid, total soluble protein, and total chlorophyll *a* and *c2* concentration (henceforth referred to as biomass, lipid, protein, and chlorophyll, respectively) were conducted based on methods modified from Grottoli et al. (2004), Rodrigues and Grottoli (2007), Bradford (1976), and Jeffrey and Humphrey (1975), respectively. Total carbohydrate was

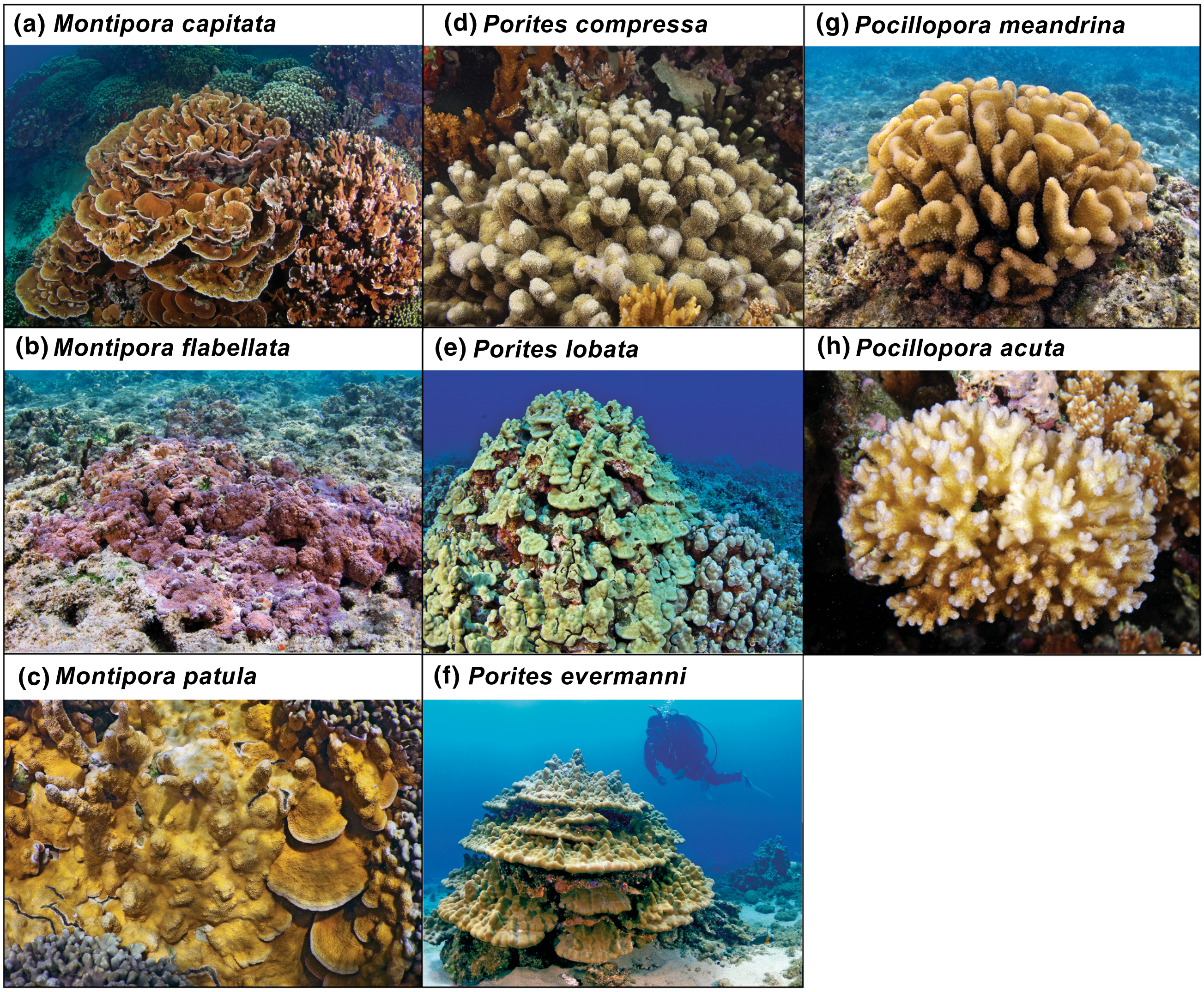

Fig. 1 Photographs of **a** *Montipora capitata*, **b** *Montipora flabellata*, **c** *Montipora patula*, **d** *Porites compressa*, **e** *Porites lobata*, **f** *Porites evermanni*, **g** *Pocillopora meandrina*, and **h** *Pocillopora acuta* around the island of O‘ahu, Hawai‘i. Photographs courtesy of Keoki Stender

not quantified as carbohydrate molecules are used for the active metabolism of energy, and our goal was to quantify long-term stored energy reserves. Briefly, biomass ash-free dry weight was quantified by drying ground coral subsamples to a constant weight (60 °C for 24 h) and burning it (450 °C for 6 h). Lipids were extracted using 2:1 chloroform methanol. Protein was quantified using the Bradford method (Bradford 1976). Chlorophyll was extracted from ground coral samples using a double extraction in 100% acetone, and the absorbance at 630, 663, and 750 nm wavelengths was measured using a spectrophotometer. Detailed protocols for the analysis of biomass, lipid, protein, and the estimation of surface area are deposited in *Protocols.io* (McLachlan et al. 2020b, c, d; McLachlan and Grottoli 2021).

The coral pieces designated for stable isotope analyses were prepared using methods modified from Hughes et al. (2010) and a detailed protocol is deposited in *Protocols.io* (Price et al. 2020). All isotope samples were combusted using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK) at the University of California Davis Stable Isotope Facility. The carbon isotopic signature of the animal host ($\delta^{13}C_h$), and algal endosymbiont ($\delta^{13}C_e$), were reported as the per mil deviation of the stable isotopes ^{13}C:^{12}C relative to Vienna Peedee Belemnite Limestone Standard. The nitrogen isotopic signature of the animal host ($\delta^{15}N_h$), and algal endosymbiont ($\delta^{15}N_e$), were reported as the per mil deviation of the stable isotopes ^{14} N:^{15} N relative to air. At least 10% of all sample measurements were made in duplicate (n = 59 host fraction, 27 algae fraction), and the standard deviations of duplicate sample analyses were ± 0.09 ‰ for $\delta^{13}C_h$, ± 0.21 ‰ for $\delta^{13}C_e$, ± 0.06 ‰ for

Table 1 Number of coral ramets collected (each from a different parent colony) per species at each collection site from Fig. 2a

Species	Collection Site						Total # ramets
	Sampan	Moku o Lo‘e	Waimānalo	Magic Island	Electric Beach	Hale‘iwa	
Montipora capitata †	12	12	12	–	12	12	60
Montipora flabellata	6	–	2	–	–	13	21
Montipora patula	10	–	10	–	12	15	47
Porites compressa	12	12	12	11	–	12	59
Porites lobata	12	–	12	12	12	12	60
Porites evermanni	12	–	12	12	10	12	58
Pocillopora meandrina	12	–	12	12	12	12	60
Pocillopora acuta ‡	12	12	9	12	–	12	57
Grand Total							422

†Morphological variation among sites: Sampan, Moku o Lo‘e, and Waimānalo = branching, Electric Beach and Hale‘iwa = encrusting

‡Morphological variation among sites: Sampan and Moku o Lo‘e = finely branching, Waimānalo, Magic Island, and Hale‘iwa = densely branching

$\delta^{15}N_h$, and ± 0.12 ‰ for $\delta^{15}N_e$. Differences between $\delta^{13}C_h$ and $\delta^{13}C_e$ (i.e., $\delta^{13}C_{h\text{-}e}$) of each ramet were used to assess the relative contribution of photosynthetically and heterotrophically derived C in coral tissues [sensu Muscatine et al. (1989) and Rodrigues and Grottoli (2006)]. The lower the $\delta^{13}C_{h\text{-}e}$ value, the greater the relative contribution of heterotrophically versus photoautotrophically derived carbon to coral tissues (Muscatine et al. 1989; Rodrigues and Grottoli 2006; Levas et al. 2013; Schoepf et al. 2015; Grottoli et al. 2017). Conversely, the lower the differences between $\delta^{15}N_h$ and $\delta^{15}N_e$ (i.e., $\delta^{15}N_{h\text{-}e}$), the lower the relative contribution of heterotrophically derived nitrogen to coral tissues (Conti-Jerpe et al. 2020).

Data analysis

All multivariate statistical analyses were performed using PERMANOVA + for PRIMER v6 (Anderson, 2008). To investigate if unintended temporal biases were present in our physiological data, we used one-way analysis of similarities (ANOSIM) to (1) compare the physiological profiles of corals sampled in close temporal proximity (e.g., within 0–4 weeks) to the physiological profiles of corals sampled across the entire 11-week period for each species, and (2) to compare the physiological profiles of corals from the same site collected up to five weeks apart for two species (*M. flabellata* from Hale‘iwa and *M. patula* corals from Sampan, Supplement 2). Covariance among environmental variables was investigated using draftsman plots and Pearson's correlation coefficient. If two or more environmental variables are highly co-linear (i.e., correlation $|r| \geq 0.95$), then they are effectively redundant for the purpose of distance-based linear modelling (DISTLM) (Legendre and Anderson 1999; Anderson 2008) and the redundant variable(s) should be removed before proceeding (Anderson et al. 2008). However, caution is warranted when interpreting results as the variable which is retained may in fact just be a proxy for the variable(s) which were dropped (Anderson et al. 2008). To start with, physiological data were standardized (normalized function in PRIMER) and separate Euclidean distance dissimilarity matrices were constructed for all samples initially (community level analysis), and then for each genus and species individually. The six measured physiological traits (biomass, lipid, protein, chlorophyll, $\delta^{13}C_{h\text{-}e}$ and $\delta^{15}N_{h\text{-}e}$) when considered together are henceforth referred to as the "physiological profile" of each coral. Differences in physiological profiles among sites were tested using one-way ANOSIMs at the community, genus, and species level, and were visualized using non-metric multidimensional scaling (NMDS) plots. The amount of variance in the physiological profiles exhibited by each species across all sites, and the relative influence of the environment in driving that variation, was investigated using homogeneity of multivariate dispersion analysis (PERMDISP, Anderson 2006) and DISTLM (Legendre and Anderson 1999; Anderson 2008), respectively. PERMDISP was used to identify differences in multivariate dispersion among species across sites, using 9999 permutations. DISTLM was used to test for significant relationships between physiological and environmental data at the community, genus, and species level. The relative contribution of each environmental variable in explaining physiological variation was investigated using marginal tests with 9999 permutations. Pearson's correlation coefficients were calculated between individual physiological traits and environmental data. Differences in physiological traits among sites were investigated for each species individually using one-way analysis of variance (ANOVA) and Tukey's test for post hoc analysis. When ANOVA assumptions could not be met, Kruskal Wallis one-way analysis of variance and Pairwise Wilcoxon Rank Sum tests were used. The Bonferroni correction was used to control the familywise error rate. All univariate statistics were performed using R v3.6.2 (R Core Team 2020).

Results

Environmental characterization of collection sites

While annual mean SST varied only by 0.5 °C among sites, summer mean SST varied by 1.4 °C (Table S2). The sites within Kāne'ohe Bay (Moku o Lo'e and Sampan) experienced the highest mean seawater temperatures in the summer of 2015, whereas Hale'iwa experienced the lowest mean temperature (Table S2). SW Chl concentration was highest within Kāne'ohe Bay, intermediate at Waimānalo and Hale'iwa, and lowest at Magic Island and Electric Beach, both in summer and annually (Table S2). Finally, annual mean SWH was lowest at Moku o Lo'e and Sampan, and greatest at Hale'iwa on the North Shore, while Magic Island on the South Shore had the greatest mean SWH during the summer (Table S2).

All environmental variables were highly covarying (Table S3), and sites with higher SWH concurrently experienced lower SST and SW Chl (Fig. 2). We hypothesize that SWH is one of the dominant drivers of this environmental gradient, as wave-induced mixing of the surface ocean is known to disrupt thermo- and pycnoclines (e.g., Garrison 2013). Henceforth, we shall refer to the concurrent gradients in SWH, SST, and SW Chl as simply "the environmental gradient" around O'ahu (Fig. 2b). When SWH, SST, and SW Chl are considered together, the sites around O'ahu fall into three groups: (1) Hale'iwa, (2) Waimānalo, Magic Island, and Electric Beach, and (3) Sampan and Moku o Lo'e (Fig. 2b). Due to the covarying nature of the environmental variables, only SWH was selected for inclusion in the Pearson's correlation analyses.

Physiological profiles were not biased by the extended sampling duration

We found significant differences in coral physiological profiles among sites regardless of whether they were sampled within a 4-week or an 11-week period, although not all differences were considered strong based on the R-statistics (Supplement 2 Table S1a). We also compared the physiology of corals from the same site collected up to five weeks apart and found no significant differences, although this test was only possible for two species (Supplement 2 Table S1b). These results provide some evidence that differences in coral physiological profiles presented here are likely due to differences in environmental conditions among sites rather than temporal biases in the sampling design.

Physiological characterization among and across collection sites

We found significant differences in coral physiological profiles among sites at the coral community level (Table 2a), genus level (Table 2b), and species level (Table 2c). At the community level, the strength of dissimilarity in physiological profiles among sites was weak (small R-values, Table 2a) and not all sites differed from each other (Supplement 1 Table S4a) as illustrated by the highly overlapping nature of samples in multivariate space (Fig. 3). At the genus level, differences in coral physiology among sites were largest for *Pocillopora* [$R = 0.29$] followed by *Montipora* [$R = 0.11$], and smallest for *Porites* [$R = 0.08$] (Fig. 4a–c, Table 2b) and the sites that differed from each other varied among genera (Supplement 1 Table S4b). At the species level, physiological profiles differed among sites and differences were most pronounced (i.e., largest R-statistics) in *P. acuta*, *M. capitata*, and *M. flabellata* (Fig. 5a, b, h, Table 2c). Conversely, differences in physiological profiles among sites were smallest for *M. patula* and *P. meandrina* (Fig. 5c, g, Table 2c). In addition, *P. acuta* and *M. capitata* varied morphologically among sites (Table 1). At Waimānalo and within Kāne'ohe Bay *M. capitata* was branching, whereas the individuals from Electric Beach and Hale'iwa were encrusting. For *P. acuta*, colonies within Kāne'ohe Bay were finely branching compared to conspecifics elsewhere around O'ahu which were denser with thicker branches. Finally, the amount of multivariate dispersion (analogous to univariate variance) in physiological profiles exhibited by each species across sites in O'ahu was not consistent. Homogeneity of multivariate dispersion (PERMDISP) analysis revealed that overall physiological dispersion was largest in the three *Montipora* species and *P. acuta*, and smallest in *P. compressa*, *P. evermanni*, and *P. meandrina* (Fig. 6, Supplement 1 Table S5).

Relationship between physiological profiles and the environment at different ecological scales

Community level

Each environmental variable tested was correlated with multivariate physiological profiles of corals at the

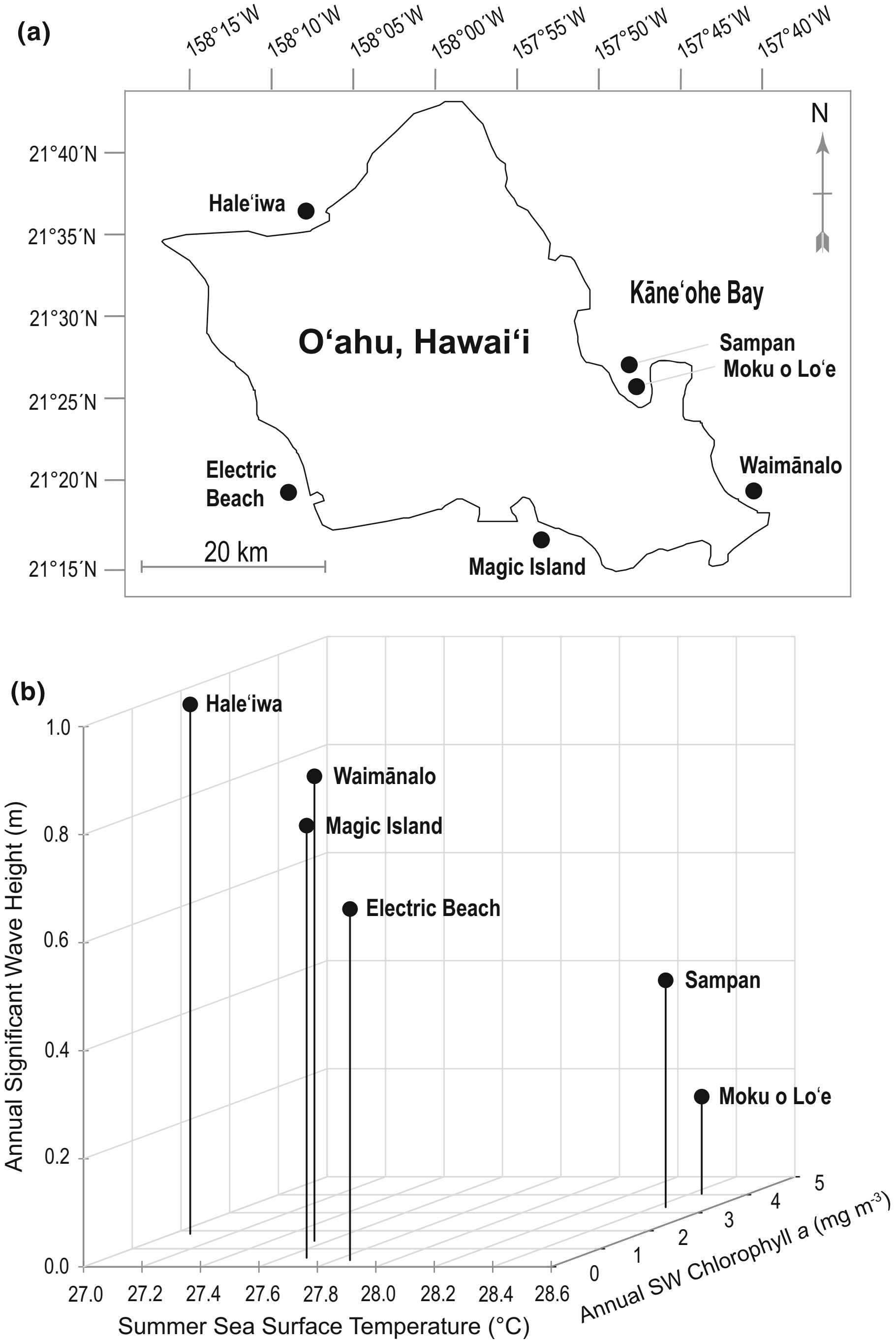

Fig. 2 **a** Map of coral sampling locations around the island of Oʻahu, Hawaiʻi. **b** 3-D plot of the summer mean sea surface temperature, annual mean seawater chlorophyll concentration, and annual mean significant wave height at each site. Values and sources listed in Supplement 1 Table S1 and S2, respectively. SW = seawater

community level (Table 3). However, the proportion of the physiological variance which was explained by the environmental variables was small, ranging from 1.9 to 3.1% (Table 3). We did not focus on which specific environmental variables explained the largest proportion of the physiological variation, as all environmental variables were strongly covarying (Supplement 1 Table S3), and therefore not independent. Given our prediction that the gradients in SST and SW Chl are strongly determined by the gradient in water flow, and that wave height is the dominant environmental variable determining the abundance and distribution of these species in Hawaiʻi (Franklin et al. 2013), we selected the single variable of annual mean SWH to investigate patterns of individual physiological traits.

Table 2 One-way ANOSIM analyses of coral physiological profiles among collection sites at the (a) community, (b) genus, and (c) individual species level

Ecological Scale	Factor	Global R	P-value
a) Coral community level	Site	0.029	**0.0030**
b) Genus level			
Montipora	Site	0.112	**0.0001**
Porites	Site	0.083	**0.0001**
Pocillopora	Site	0.290	**0.0001**
c) Species level			
Montipora capitata	Site	0.447	**0.0001**
Montipora flabellata	Site	0.314	**0.0070**
Montipora patula	Site	0.151	**0.0005**
Porites compressa	Site	0.287	**0.0001**
Porites lobata	Site	0.276	**0.0001**
Porites evermanni	Site	0.215	**0.0001**
Pocillopora meandrina	Site	0.171	**0.0001**
Pocillopora acuta	Site	0.770	**0.0001**

R-statistics are highest when physiological dissimilarity among sites is large and lowest when physiological dissimilarity among sites is small. The strength of physiological dissimilarity among sites is categorized here as: very strong (R between 0.750 and 1), strong (R between 0.500 and 0.749), moderate (R between 0.250 and 0.499), and weak (R between 0 and 0.249). Bolded P-values are significant. All models were run with 9999 permutations. Details of pairwise comparisons are provided in Supplement 1 Table S5

Pearson's correlation between individual physiological traits and annual mean SWH revealed significant correlations in 5 of the 6 traits (Table 4). Decreases in SWH (and thus, increases in SST and SW Chl) were correlated with decreased tissue biomass and chlorophyll, increased energy reserves, and a higher contribution of heterotrophically derived carbon to the diet at the community level (Table 4).

Genus level

Physiological profiles were correlated with the environmental gradient at the genus level, but to varying degrees (Table 5). Specifically, environmental variables explained between 6.4 and 12.0% of the physiological profile variance of *Montipora* corals (Table 5a). This was almost threefold higher than the explanatory power of the environment on the physiological profiles of *Porites* (2.9–4.4%, Table 5b). In *Pocillopora*, environmental variables explained between 9.8 and 10.1% of the physiological variance (Table 5c). Looking at individual physiological traits, decreases in annual mean SWH were associated with decreased tissue biomass and increased energy reserves (lipids, proteins, or both) in all three genera (Table 6). For *Montipora* and *Pocillopora*, decreasing SWH was also associated with an increase in lipids (Table 6a, c). Coral chlorophyll was higher at lower flow in *Porites* (Table 6b), and lower at lower flow for *Montipora* and *Pocillopora* (Table 6a, c). *Montipora* was the only genus to show an increase in the relative contribution of heterotrophic carbon to the diet under low flow conditions (Table 6a). Conversely, the relative contribution of heterotrophic nitrogen to the diet was higher in *Porites* and lower in *Montipora* and *Pocillopora* at reduced flow (Table 6).

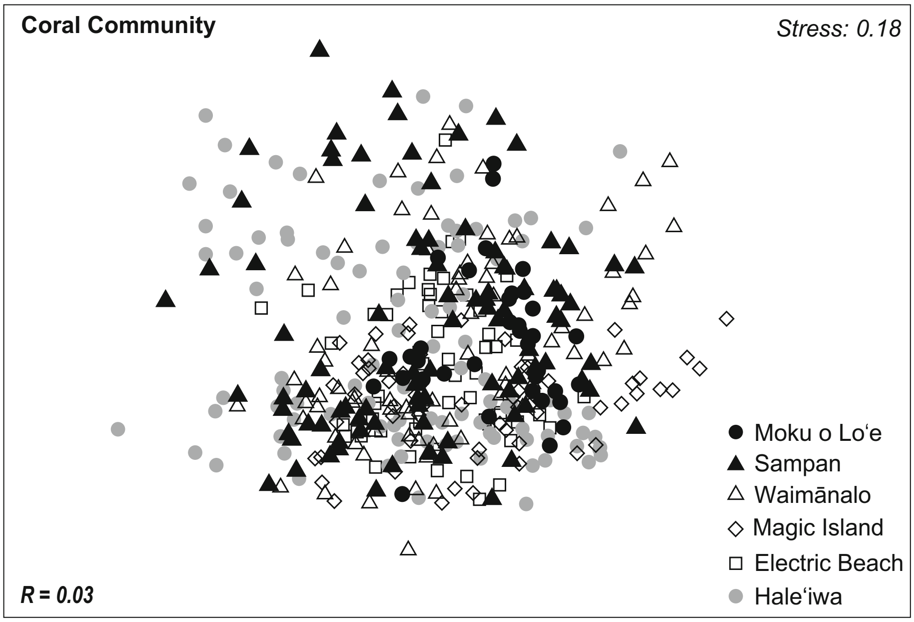

Fig. 3 NMDS plot of corals sampled in 2015 around the island of O'ahu, Hawai'i with attention given to corals from three site groupings: (1) Sampan and Moku o Lo'e within Kāne'ohe Bay (black filled shapes), (2) Waimānalo, Magic Island, and Electric Beach (black open shapes), and (3) Hale'iwa (gray filled circles)

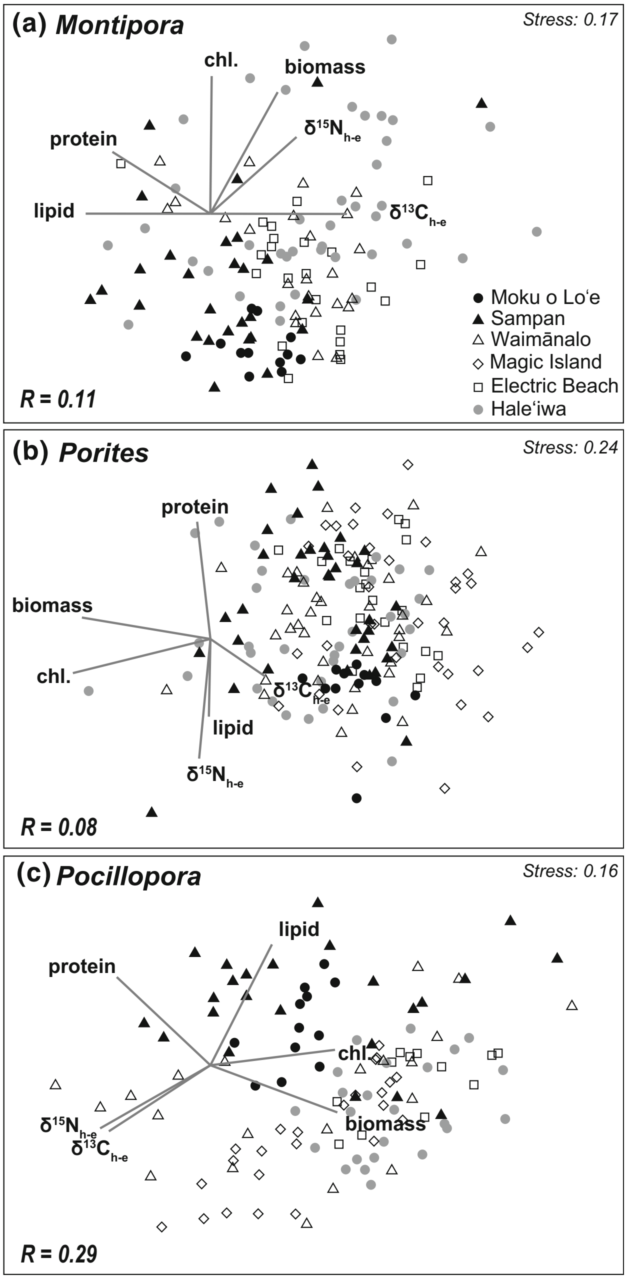

Fig. 4 NMDS plot of **a** *Montipora*, **b** *Porites*, and **c** *Pocillopora* corals sampled in 2015 around the island of O‘ahu, Hawai‘i with attention given to corals from three site groupings: (1) Sampan and Moku o Lo‘e within Kāne’ohe Bay (black filled shapes), (2) Waimānalo, Magic Island, and Electric Beach (black open shapes), and (3) Hale‘iwa (gray filled circles). Grey vectors indicate strength and direction of the relative contribution of each physiological trait to the sample distribution as determined by Pearson’s correlation analysis. chl. = chlorophyll

Species level

Physiological profiles were correlated with the environmental gradient at the species level (Table 7). However, the strength of correlation varied considerably, especially among congeners (Table 7). Environmental variables explained physiological profile variance the most in *M. capitata* and *P. acuta* (31% and 26%, respectively), at an intermediate level in *M. flabellata, P. compressa,* and *M. patula* (between 15 and 20%), and the least in *P. lobata, P. evermanni,* and *P. meandrina* (between 6 and 12%) (Table 7).

For all three *Montipora* species, decreases in annual mean SWH (and thus, increases in SST and SW Chl) were correlated with decreased biomass, a larger accumulation of energy reserves (lipids, proteins, or both) and a higher incorporation of heterotrophic carbon, (Table 8a–c). In addition, SWH was positively correlated with chlorophyll and $\delta^{15}N_{h-e}$ in *M. capitata* and *M. patula* (Table 8a, c). One-way ANOVAs and Tukey HSD post hoc tests confirmed that biomass was lower at Moku o Lo‘e and Sampan compared to the higher flow Hale‘iwa site for *M. capitata* (Supplement 1 Fig. S2A). Conversely, *Montipora* corals at Hale‘iwa had lower lipids, proteins, or both compared to conspecifics in Kāne’ohe Bay (Supplement 1 Fig. S2I, K, R, S). *M. capitata* chlorophyll was lowest at Moku o Lo‘e and Sampan (Supplement 1 Fig. S2Y). Finally, $\delta^{13}C_{h-e}$, $\delta^{15}N_{h-e}$, or both were significantly lower at Moku o Lo‘e and Sampan relative to *Montipora* corals from Hale‘iwa (Supplement 2 Fig. S2AG, AH, AO, AQ).

For all three *Porites* species, protein concentration was negatively correlated with annual mean SWH (although not significantly for *P. evermanni,* Table 8d–f). In addition, a negative correlation was found between SWH and the physiological variables chlorophyll and $\delta^{15}N_{h-e}$ in *Porites compressa* (Table 8d), but not in *P. lobata* or *P. evermanni* (Table 8e, f). Interestingly, *P. evermanni* was the only species which displayed positive correlations between SWH and lipid reserves (Table 8f). One-way ANOVAs and Tukey HSD post hoc tests confirmed that *P. evermanni* had lower lipids at Sampan than at Hale‘iwa (Supplement 1 Fig. S2N), whereas protein was higher for both *P. lobata* and *P. evermanni* (Supplement 1 Table S2U, V). Finally, *P. compressa* from Moku o Lo‘e had significantly higher chlorophyll concentrations and $\delta^{15}N_{h-e}$ values relative to conspecifics located at Hale‘iwa (Supplement 1 Fig. S2AB, AR).

Both species of *Pocillopora* exhibited a negative correlation between SWH and lipids (Table 3, 8 g, h). In *P. acuta,* SWH was also positively correlated with biomass and $\delta^{15}N_{h-e}$, and negatively correlated with protein (Table 8h). One-way ANOVAs and Tukey HSD post hoc tests confirmed that for both *Pocillopora* species, lipids were higher at the Kāne’ohe Bay sites relative to Hale‘iwa (Supplement 1 Fig. S2O, P). For *P. acuta*, biomass, chlorophyll, and $\delta^{15}N_{h-e}$ were lower and protein higher at Moku o Lo‘e, Sampan, or both compared to conspecifics at

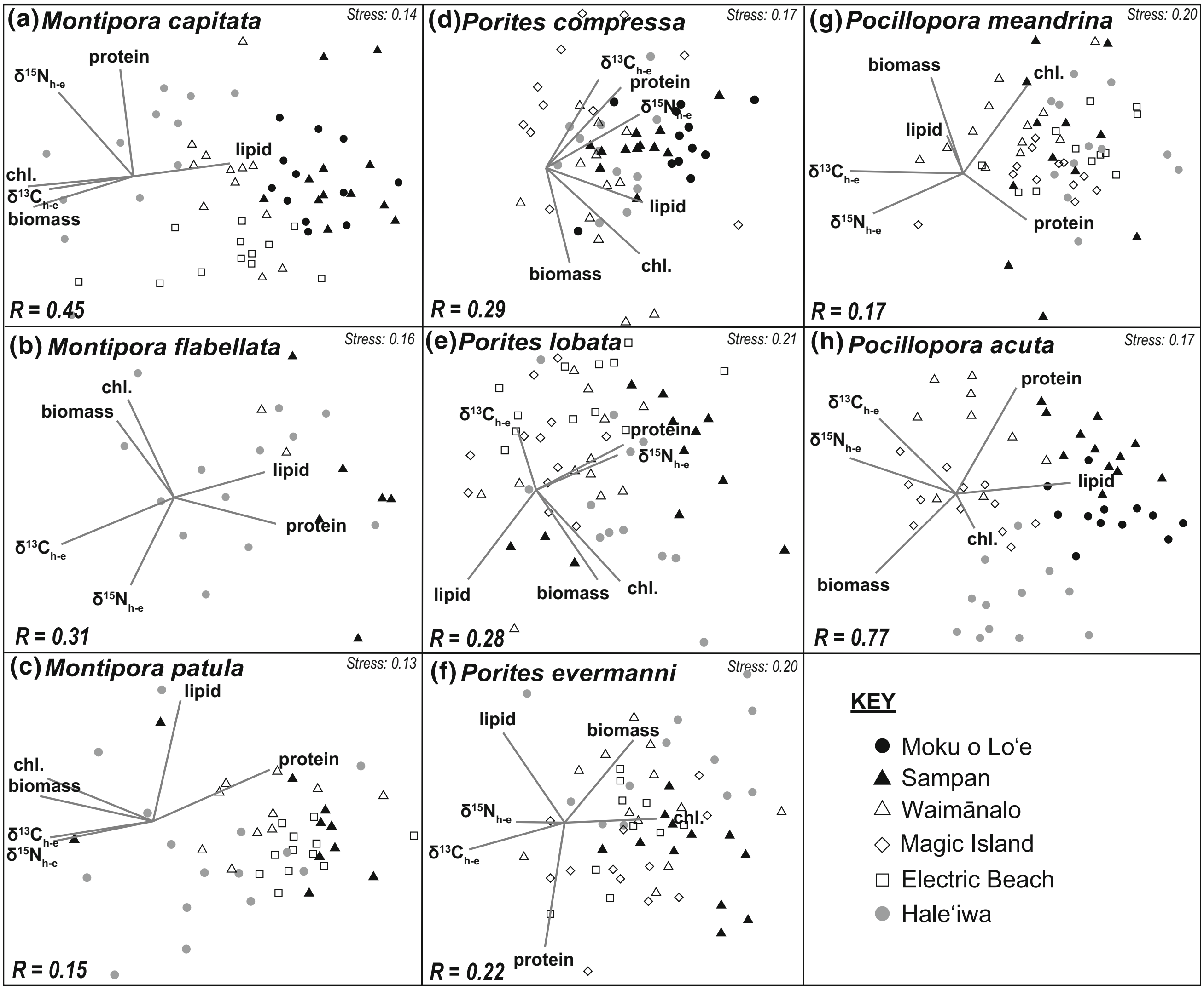

Fig. 5 NMDS plots of **a** *Montipora capitata*, **b** *Montipora flabellata*, **c** *Montipora patula*, **d** *Porites compressa*, **e** *Porites lobata*, **f** *Porites evermanni*, **g** *Pocillopora meandrina*, and **h** *Pocillopora acuta* sampled in 2015 around the island of O'ahu, Hawai'i, with attention given to corals from three site groupings: (1) Sampan and Moku o Lo'e within Kāne'ohe Bay (black filled shapes), (2) Waimānalo, Magic Island, and Electric Beach (black open shapes), and (3) Hale'iwa (gray filled circles). Grey vectors indicate strength and direction of the relative contribution of each physiological trait to the sample distribution as determined by Pearson's correlation analysis. chl. = chlorophyll

the higher flow Hale'iwa site (Supplement 1 Fig. S2H, X, AF, AR).

Discussion

In this study, we quantified the phenotypic diversity of physiological traits in corals around the island of O'ahu, Hawai'i. We found that significant wave height, sea surface temperature, and seawater chlorophyll concentration were significantly correlated with coral physiological profiles at all ecological scales (Table 2). Correlations between coral physiology and natural environmental gradients have been found in reef locations worldwide, including the Red Sea (Sawall et al. 2014, 2015; Ziegler et al. 2015a, 2015b), the South China Sea (Qin et al. 2019), the Caribbean (Thornhill et al. 2011), and the Great Barrier Reef (Cooper et al. 2008; Cooper and Ulstrup 2009; Fabricius et al. 2012). Although correlative in nature, taken together these results imply that phenotypic variation is not random, and instead environmental gradients appear to drive changes in coral physiological traits through adaptation and/or acclimatization. As all three environmental variables measured in this study were highly covarying (Supplement 1 Table S3), we cannot differentiate which (if any) variable has the strongest influence on aspects of coral physiology measured in this study. Instead, the interactive influence of these abiotic variables (and others not measured in this

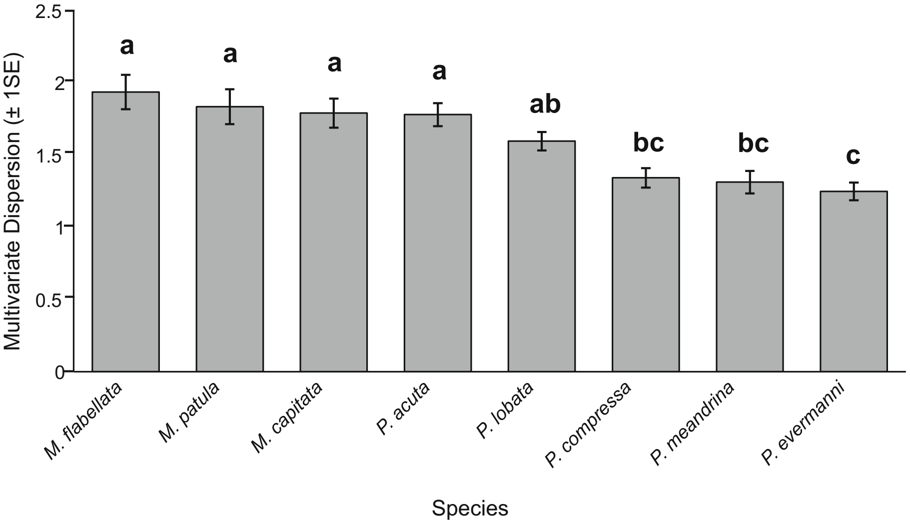

Fig. 6 Multivariate dispersion (analogous to univariate variance) of physiological profiles for the eight Hawaiian coral species collected around the island of O'ahu, Hawai'i. Species with different letters indicate significant differences in mean distance from group centroid among species. Statistical details in Supplement 1 Table S6

Table 3 Distance-based linear modelling (DISTLM) results showing relationship between environmental variables and coral physiological profiles at the coral community level

Environmental variables	Marginal tests		
	Pseudo-F	*p* value	Percent variation explained
Community-level (all species)			
SST_{annual}	8.2029	**0.001**	1.92
SST_{summer}	13.1030	**0.001**	3.03
SW Chl_{annual}	12.1960	**0.001**	2.82
SW Chl_{summer}	12.3140	**0.001**	2.84
SWH_{annual}	13.6180	**0.001**	3.14
SWH_{summer}	9.2998	**0.001**	2.17

Bolded P-values are significant. SST = sea surface temperature. SW Chl = seawater chlorophyll *a* concentration. SWH = significant wave height

Table 4 Pearson's correlation coefficients and associated P-values (in parentheses) between annual mean significant wave height (SWH) and individual physiological traits for the coral community

Coral community	Environmental variable	Biomass	Lipid	Protein	Chl	$\delta^{13}C_{h-e}$	$\delta^{15}N_{h-e}$
	SWH annual	0.33 (**< 0.001**)	-0.18 (**< 0.001**)	-0.15 (**0.0027**)	0.10 (**0.0407**)	0.12 (**0.0167**)	0.02 (0.682)

Bolded P-values are significant. Chl. = chlorophyll

study) is likely responsible for the physiological patterns we observed. It has been suggested that SWH is the primary driver of the distribution in Hawai'i of the eight species investigated here (Franklin et al. 2013). However, Franklin et al. (2013) did not measure SST, and given the highly covarying nature of these two variables (Supplement 1 Table S3), it is currently impossible to determine whether SWH or SST has a stronger or equal influence. Although not included in this study, a strong pH gradient exists around O'ahu (Jury et al. 2019) that corresponds to the SWH, SST, and SW Chl gradient shown here (Supplement 1 Table S2). Differences in pH are known to elicit physiological changes in corals (e.g., Schoepf et al. 2013; Levas et al. 2015) and are associated with shifts in community composition (e.g., Barkley et al. 2015). We were not able to reliably include pH as an abiotic factor in this study due to a lack of sufficient or appropriate pH data. However, the correlation between pH, SWH, SST, and SW Chl enabled us to infer possible underlying physiological strategies that allow corals to persist along abiotic gradients, which appear to influence their local abundance around O'ahu under current ocean conditions and shed light on how future ocean conditions might influence coral distribution.

Table 5 Genus level distance-based linear modelling (DISTLM) results showing relationship between environmental variables and physiological profiles for **a)** *Montipora*, **b)** *Porites*, and **c)** *Pocillopora*

Environmental variables	Marginal tests		
	Pseudo-F	*p* value	Percent variation explained
a) *Montipora*			
SST $_{\text{annual}}$	9.0807	**0.001**	6.72
SST $_{\text{summer}}$	16.8660	**0.001**	11.81
SW Chl $_{\text{annual}}$	9.5632	**0.001**	7.05
SW Chl $_{\text{summer}}$	10.0280	**0.001**	7.37
SWH $_{\text{annual}}$	17.1210	**0.001**	11.96
SWH $_{\text{summer}}$	8.6545	**0.001**	6.43
b) *Porites*			
SST $_{\text{annual}}$	7.1034	**0.001**	3.90
SST $_{\text{summer}}$	5.2049	**0.003**	2.89
SW Chl $_{\text{annual}}$	8.0931	**0.001**	4.42
SW Chl $_{\text{summer}}$	8.0708	**0.001**	4.41
SWH $_{\text{annual}}$	6.0991	**0.001**	3.37
SWH $_{\text{summer}}$	6.7847	**0.001**	3.73
c) *Pocillopora*			
SST $_{\text{annual}}$	1.9852	0.104	1.70
SST $_{\text{summer}}$	12.7760	**0.001**	10.00
SW Chl $_{\text{annual}}$	12.5030	**0.001**	9.81
SW Chl $_{\text{summer}}$	12.6040	**0.001**	9.88
SWH $_{\text{annual}}$	12.9410	**0.001**	10.12
SWH $_{\text{summer}}$	12.5730	**0.001**	9.86

Bolded P-values are significant. SST = sea surface temperature. SW Chl = seawater chlorophyll *a* concentration. SWH = significant wave height

Table 6 Pearson's correlation coefficients and associated *p* values (in parentheses) between annual mean significant wave height (SWH) and individual physiological traits for (a) *Montipora*, (b) *Porites*, and (c) *Pocillopora*

Genus	Environmental variable	Biomass	Lipid	Protein	Chl	$\delta^{13}C_{h\text{-}e}$	$\delta^{15}N_{h\text{-}e}$
Montipora	SWH annual	0.50 (**< 0.001**)	-0.25 (**0.0043**)	0.01 (0.914)	0.43 (**< 0.001**)	0.34 (**< 0.001**)	0.33 (**< 0.001**)
Porites	SWH annual	0.27 (**< 0.001**)	0.07 (0.322)	-0.19 (**0.0094**)	-0.18 (**0.015**)	0.02 (0.765)	-0.22 (**0.0031**)
Pocillopora	SWH annual	0.47 (**< 0.001**)	-0.38 (**< 0.001**)	-0.37 (**< 0.001**)	0.23 (**0.0108**)	0.12 (0.193)	0.19 (**0.0382**)

Bolded *p* values are significant. Chl. = chlorophyll

Morphological variation and tissue growth

In this survey, *M. capitata* and *P. acuta* were the only species to exhibit noticeable differences in morphology among sites, with branching or more finely branching individuals inhabiting the lower flow Kāne'ohe Bay sites and plating or thicker branches inhabiting the higher flow sites elsewhere (Table 1). Morphological plasticity to increase the surface areas to volume ratio is common in scleractinian corals in response to reductions in water flow (e.g., Jokiel 1978) and light (e.g., Willis 1985). This strategy of shifting toward a more complex morphology changes the thickness of the diffusive boundary layer around the coral colony, and as a result facilitates an increased exchange of nutrients and waste with the surrounding seawater (Jokiel et al. 1978) and alters pH and dissolved oxygen gradients, which influence skeletal growth rates (Chan et al. 2016; Schoepf et al. 2018). Decreasing the thickness of the diffusive boundary layer due to increased flow has been linked to increased bleaching tolerance and decreased post-bleaching mortality in corals (Nakamura and van Woesik 2001). The change in surface area to volume ratio likely explains the patterns of lower biomass and chlorophyll (both normalized to surface area) in Kāne'ohe Bay for these two species (Supplement 1 Fig. S2A, H). However, for *M. flabellata*, *M. patula*, *P. evermanni*, and *P. meandrina*, there was also a positive correlation between biomass and SWH, but no concurrent

Table 7 Species level distance-based linear modelling (DISTLM) results showing relationship between environmental variables and coral physiological profiles for (a) *Montipora capitata*, (b) *Montipora flabellata*, (c) *Montipora patula*, (d) *Porites compressa*, (e) *Porites lobata*, (f) *Porites evermanni*, (g) *Pocillopora meandrina*, and (h) *Pocillopora acuta*. SST = sea surface temperature

Environmental variables	Marginal tests		
	Pseudo-F	*p* value	Percent variation explained
(a) *Montipora capitata*			
SST$_{\text{annual}}$	12.3070	**0.001**	17.51
SST$_{\text{summer}}$	25.5340	**0.001**	30.57
SW Chl$_{\text{annual}}$	12.1470	**0.001**	17.32
SW Chl$_{\text{summer}}$	12.4350	**0.001**	17.66
SWH$_{\text{annual}}$	20.5310	**0.001**	26.14
SWH$_{\text{summer}}$	9.1526	**0.001**	13.63
(b) *Montipora flabellata*			
SST$_{\text{annual}}$	4.2753	**0.002**	18.37
SST$_{\text{summer}}$	4.6310	**0.001**	19.60
SW Chl$_{\text{annual}}$	4.4560	**0.002**	19.00
SW Chl$_{\text{summer}}$	4.5962	**0.001**	19.48
SWH$_{\text{annual}}$	4.7221	**0.001**	19.91
SWH$_{\text{summer}}$	3.0844	**0.004**	13.97
(c) *Montipora patula*			
SST$_{\text{annual}}$	7.8678	**0.001**	14.88
SST$_{\text{summer}}$	6.1467	**0.001**	12.02
SW Chl$_{\text{annual}}$	0.7484	0.545	1.64
SW Chl$_{\text{summer}}$	0.7354	0.530	1.61
SWH$_{\text{annual}}$	5.6980	**0.004**	11.24
SWH$_{\text{summer}}$	0.8318	0.488	1.81
(d) *Porites compressa*			
SST$_{\text{annual}}$	1.9167	0.083	3.25
SST$_{\text{summer}}$	5.3298	**0.001**	8.55
SW Chl$_{\text{annual}}$	10.5120	**0.001**	15.57
SW Chl$_{\text{summer}}$	10.5700	**0.001**	15.64
SWH$_{\text{annual}}$	8.0557	**0.001**	12.38
SWH$_{\text{summer}}$	10.7530	**0.001**	15.87
(e) *Porites lobata*			
SST$_{\text{annual}}$	7.5578	**0.001**	11.53
SS $_{\text{summer}}$	4.4798	**0.001**	7.17
SW Chl$_{\text{annual}}$	7.2573	**0.001**	11.12
SW Chl$_{\text{summer}}$	7.1316	**0.001**	10.95
SWH$_{\text{annual}}$	4.7191	**0.001**	7.52
SWH$_{\text{summer}}$	4.6613	**0.001**	7.44
(f) *Porites evermanni*			
SST$_{\text{annual}}$	6.6265	**0.001**	10.58
SST$_{\text{summer}}$	5.4335	**0.001**	8.84
SW Chl$_{\text{annual}}$	3.8805	**0.003**	6.48
SW Chl$_{\text{summer}}$	3.7210	**0.002**	6.23
SWH$_{\text{annual}}$	5.0603	**0.002**	8.29
SWH$_{\text{summer}}$	3.0885	**0.004**	5.23
(g) *Pocillopora meandrina*			
SST$_{\text{annual}}$	0.9357	0.457	1.59
SST$_{\text{summer}}$	2.2861	**0.034**	3.79
SW Chl$_{\text{annual}}$	3.4985	**0.006**	5.69
SW Chl$_{\text{summer}}$	3.6293	**0.006**	5.89
SWH$_{\text{annual}}$	2.1064	0.068	3.50

Table 7 continued

Environmental variables	Marginal tests		
	Pseudo-F	p value	Percent variation explained
$\mathrm{SWH}_{\mathrm{summer}}$	3.9055	**0.001**	6.31
(h) *Pocillopora acuta*			
$\mathrm{SST}_{\mathrm{annual}}$	11.7760	**0.001**	17.64
$\mathrm{SST}_{\mathrm{summer}}$	19.4110	**0.001**	26.09
SW $\mathrm{Chl}_{\mathrm{annual}}$	19.6160	**0.001**	26.29
SW $\mathrm{Chl}_{\mathrm{summer}}$	19.1320	**0.001**	25.81
$\mathrm{SWH}_{\mathrm{annual}}$	18.5320	**0.001**	25.20
$\mathrm{SWH}_{\mathrm{summer}}$	18.9640	**0.001**	25.64

SW Chl = seawater chlorophyll *a* concentration. SWH = significant wave height. Bolded *p* values are significant

change in morphology (i.e., surface-area-to-volume ratio). This suggests that somatic growth of these latter species is reduced within Kāne'ohe Bay due to reduced SWH and/or other abiotic variables. Reductions in tissue biomass can be associated with stress (Loya et al. 2001; Rodrigues and Grottoli 2007; Thornhill et al. 2011) or may reflect an adaptive strategy whereby corals divert energy from somatic growth toward other processes such as reproduction or calcification. As neither reproduction nor calcification were measured in this study, further research is required to investigate this potential trade-off.

Effective management of lipids and proteins

Pearson's correlations indicate that the montiporids and pocilloporids increased their lipid and/or protein reserves along the gradient of decreasing flow and increasing SST and SW Chl to varying degrees (Table 8a–d, g, h). A previous study from the Red Sea found a positive correlation between lipids, proteins, and SST in the coral *Pocillopora verrucosa* (Sawall et al. 2015). Maintenance of energy reserves is also associated with higher resistance to, and faster recovery from, bleaching in Hawaiian corals (Rodrigues and Grottoli 2007) and corals from the Great Barrier Reef (Anthony et al. 2009). Overall, these results suggest that the increased energy reserves in the montiporids and pocilloporids might be an adaptive strategy to counteract the metabolic strain and energy deficits associated with living in habitats at the lower flow (and higher temperature and nutrients) end of the environmental gradient within Kāne'ohe Bay.

The poritids also had a negative correlation between protein and SWH, but their lipids did not follow this same pattern (Table 8e, f). However, it is unlikely that increases in protein under lower flow conditions reflect a general change in energy reserves but rather suggests a change in the type and function of proteins being expressed and synthesized at this end of the environmental gradient (e.g., Barshis et al. 2010; Kenkel and Matz 2017). These observations imply that the effective management of proteins in the poritids is an adaptive strategy which allows them to persist in the lower flow, higher temperature and nutrient environment of Kāne'ohe Bay.

Trophic strategies

Porites compressa was the only species with a significant negative correlation between chlorophyll content and SWH (Table 8d) and may reflect a compensating mechanism to maximize photosynthetic yields under reduced downwelling irradiance caused by high turbidity within Kāne'ohe Bay (Bahr et al. 2015). This was not the case in *M. capitata* and *M. patula* where chlorophyll was positively correlated with SWH (Table 8a, c), indicating a potential reduction in photosynthetic carbon acquisition within Kāne'ohe Bay relative to other sites.

We found a positive correlation between $\delta^{13}C_{\text{h-e}}$ and SWH in the montiporids, which is interpreted as a higher proportionate contribution of heterotrophically derived carbon to animal tissue relative to photosynthetically derived carbon in lower flow environments (e.g., Muscatine et al. 1989; Rodrigues and Grottoli 2006; Grottoli et al. 2017; Fox et al. 2019). However, the $\delta^{15}N_{\text{h-e}}$ values for two of the montiporid species also showed a positive correlation with SWH, which suggests either a lower proportionate contribution of heterotrophically derived nitrogen to animal tissue relative to photosynthetically derived nitrogen in lower flow environments (Conti-Jerpe et al. 2020; Price et al. 2021) or no relationship with trophic status (Fox et al. 2019). While our results indicate that there are different trophic strategies across the environmental gradient, interpreting the bulk $\delta^{13}C$ and $\delta^{15}N$ values

Table 8 Pearson's correlation coefficients and associated P-values (in parentheses) between annual mean significant wave height (SWH) and individual physiological traits for (a) *Montipora capitata*, (b) *Montipora flabellata*, (c) *Montipora patula*, (d) *Porites compressa*, (e) *Porites lobata*, (f) *Porites evermanni*, (g) *Pocillopora meandrina*, and (h) *Pocillopora acuta*

Species	Environmental variable	Biomass	Lipid	Protein	Chl	$\delta^{13}C_{h\text{-}e}$	$\delta^{15}N_{h\text{-}e}$
(a) *Montipora capitata*	SWH annual	0.59 **(< 0.001)**	− 0.56 **(< 0.001)**	0.19 (0.156)	0.54 **(< 0.001)**	0.59 **(< 0.001)**	0.47 **(< 0.001)**
(b) *Montipora flabellata*	SWH annual	0.46 **(0.035)**	− 0.33 (0.147)	− 0.65 **(0.0015)**	0.06 (0.805)	0.59 **(0.005)**	− 0.32 (0.156)
(c) *Montipora patula*	SWH annual	0.29 **(0.048)**	− 0.22 (0.146)	− 0.29 **(0.047)**	0.30 **(0.044)**	0.41 **(0.004)**	0.45 **(0.002)**
(d) *Porites compressa*	SWH annual	0.09 (0.450)	− 0.20 (0.123)	− 0.38 **(0.003)**	− 0.46 **(< 0.001)**	− 0.04 (0.769)	− 0.58 **(< 0.001)**
(e) *Porites lobata*	SWH annual	0.25 (0.057)	0.19 (0.139)	− 0.55 **(< 0.001)**	− 0.08 (0.553)	0.17 (0.196)	0.10 (0.443)
(f) *Porites evermanni*	SWH annual	0.32 **(0.013)**	0.55 **(< 0.001)**	− 0.23 (0.076)	− 0.17 (0.194)	− 0.03 (0.826)	0.08 (0.564)
(g) *Pocillopora meandrina*	SWH annual	0.11 (0.423)	− 0.39 **(0.002)**	− 0.15 (0.261)	0.10 (0.434)	0.12 (0.357)	− 0.02 (0.901)
(h) *Pocillopora acuta*	SWH annual	0.69 **(< 0.001)**	− 0.66 **(< 0.001)**	− 0.38 **(0.003)**	0.21 (0.122)	0.23 (0.079)	0.59 **(< 0.001)**

Bolded *p* values are significant. Chl. = chlorophyll of naturally occurring corals remains complicated (Price et al. 2021). Further research with direct evaluations of heterotrophy and bulk isotopic analyses is needed to differentiate the correlations between the Oʻahu environmental gradient and heterotrophy in naturally occurring healthy corals.

Relationship between local abundance and physiological phenotype

It has been long recognized that the degree to which animals adjust their physiological phenotypes to the biotic and abiotic conditions of the environment, either through acclimatization, adaptation, or both, is important for understanding ecological processes and patterns (e.g., Pearse 1923; Spicer and Gaston 1999). The expression of physiological phenotypes in the eight species of Hawaiian corals across environmental gradients correlates with patterns in local abundance and dominance (this study; Franklin et al. 2013; Guest et al. 2018). Thus, the patterns in coral community composition around Oʻahu can be explained with a combination of physiological and ecological processes and their interactions. For example, *M. capitata* has acclimated and/or is better adapted to live in the low flow environment of Kāne'ohe Bay where it is one of the most dominant species (Bahr et al. 2015). As flow increases, the percent cover of *M. capitata* decreases (Guest et al. 2018). Conversely, the percent cover of *M. patula* and *M. flabellata* increases with increasing water flow (Franklin et al. 2013; Guest et al. 2018). When all three *Montipora* species exist at the same site, one typically dominates over the others (e.g., *M. capitata* dominates over *M. flabellata* and *M. patula* at Electric Beach, but *M. flabellata* dominates over *M. capitata* and *M. patula* at Haleʻiwa (Guest et al. 2018)), possibly a result of competitive interactions.

P. lobata is the dominant species of coral at intermediate to high flow environments like Haleʻiwa or Electric Beach, but it is completely absent from extremely low flow environments like Moku o Loʻe (Franklin et al. 2013; Guest et al. 2018),where it is replaced entirely by *P. compressa* (Forsman et al. 2020). In this study, *P. compressa* was the only poritid with higher heterotrophically derived nitrogen and chlorophyll at lower flow (Table 8d–f). Thus, the absence of *P. lobata* and *P. evermanni* in habitats with extremely low flow could be due to a lack of physiological plasticity to increase heterotrophy (Palardy et al. 2008) or chlorophyll content to increase photosynthetic yields and tolerate these environments, or because they are outcompeted by other species. In fact, even within the species there is evidence for selection driving genetic divergence between those *P. lobata* individuals that can persist in lower energy nearshore habitats and those individuals that can only survive in more oceanic offshore waters (Forsman et al. 2020; Tisthammer et al. 2020). Consistent genetic differences resolved between nearshore and offshore groups of *Porites* indicate that the host, Symbiodiniaceae, and microbiome all show concordant genetic divergence among habitats suggesting strong selection and co-evolution for habitat specialization in the *P. lobata* species complex (Forsman et al. 2020).

Predicting how the composition of Hawaiian reefs may change under future global climate change

Differences in physiological diversity and environmental correlations suggest that Hawaiian corals vary in their capacity to adapt or acclimatize to environmental heterogeneity. Our species level analyses suggest that *M. capitata* and *P. acuta* have the widest physiological niche boundaries, whereas *P. evermanni* and *P. meandrina* have the narrowest. Such differences in physiological niches are important to understand for their role in structuring community composition under stressful environmental conditions (e.g., Anthony and Connolly 2004; Emery et al. 2001). If future global or local stressors alter the abiotic marine environment beyond the tolerance ranges of species with narrow niches, they might be replaced by those with broader niches. Overall, we propose that the composition of Hawaiian reefs under ocean warming and local stressors (e.g., nutrient pollution and changes in circulation/water flow) will favor species capable of adaptively adjusting their physiological phenotype such as those species with broader niches. Though not included in our analyses, pH and dissolved oxygen concentrations will also likely play an important role in determining how the composition of reefs may change in the future. Semi-enclosed bays such as Kāne'ohe Bay with long residence times and reduced surface mixing are at greater risk from acidification and hypoxia relative to higher flow, well mixed sites. Regardless of the environmental stressor(s) present, species capable of maximizing their fixed carbon acquisition through heterotrophy, photoautotrophy, or both will likely increase in relative abundance. Likewise, species capable of adaptively managing their energy reserves (e.g., building larger lipid and protein reserves) under elevated temperature conditions will likely eventually outcompete phenotypically inflexible species with limited physiological ranges. Based on our results, corals with flexible physiological traits and broad niche boundaries best suited for future conditions are species like *M. capitata* and *M. flabellata* which might be expected to do better under predicted future ocean conditions, compared to species with narrower physiological niche boundaries such as *P. evermanni* and *P. meandrina*. Overall, this study provides insight into how coral species persist across a spatially heterogenous environment, suggests strategies that may allow them to cope with future environmental change, and identifies which Hawaiian species should be targeted for coral conservation management in the face of changing ocean conditions.

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Authors' contributions AGG, CPJ, and RJT conceived of the study, wrote proposals, and secured funding. AGG and RJT supervised the study; CPJ collected samples; RHM and JTP performed the laboratory analyses; JTP performed stable isotope analyses; NW and AMG assisted with method development and facilitated use of laboratory equipment; RHM conducted the data analysis and wrote the manuscript. All authors contributed critically to drafts and gave final approval for publication.

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Data availability The data analyzed for this study are deposited at BCO-DMO https://www.bco-dmo.org/project/546273

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval Samples were collected under State of Hawai‘i Department of Land & Natural Resources Division of Aquatic Resources Special Activity Permit (SAP) #2015–48.

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