scientific reports

Cryptobenthic crab assemblages are more distinct across a 90 m depth gradient than 2500 km of shallow marine habitat in the Hawaiian archipelago

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Despite high biodiversity and the recognized importance of mesophotic habitats, most studies of coral reef community structure have focused on conspicuous taxa such as fishes and corals in shallow habitat <30 m. Here, we examined the variability of crab assemblages from Autonomous Reef Monitoring Structures deployed on shallow reefs across the Hawaiian Islands and a mesophotic depth gradient on O'ahu. We tested the effects of environmental, ecological, and anthropogenic factors on shallow (8–17 m) crab assemblages. These assemblages were significantly different between the densely inhabited high islands (Main Hawaiian Islands) and the relatively pristine uninhabited atolls of the Northwestern Hawaiian Islands. Drivers of these differences include sea-surface temperature, chlorophyll-A, depth, island slope, potential larval immigration, and human impacts. We then compared shallow assemblages to those sampled along a depth gradient (12–90 m) on O'ahu. Despite considerable variability among sites distributed across nearly 10 degrees of latitude, differences along the depth gradient on O'ahu alone were greater than among the shallow assemblages across the entire archipelago. This finding suggests that 90 m of depth is a stronger driver of brachyuran assemblage structure than the latitudinal, environmental, and anthropogenic gradients across the entire ~2500 km span of the Hawaiian Islands.

Keywords Mesophotic coral ecosystems, Community structure, Depth gradient, Environmental drivers, Hawaii, Autonomous reef monitoring structures

Coral reefs are among the most diverse habitats in the world, and they face increasing threats of degradation, including climate-driven bleaching and phase shifts to alternate ecological regimes[1–3]. In the face of these threats, understanding drivers of metazoan community structure in coral reef ecosystems is critically important[4,5], particularly as the search for criteria to prioritize climate refugia such as upwelling zones or deep water reefs intensifies. While the structure and composition of coral reef communities is influenced by a suite of environmental and anthropogenic factors, the nature and makeup of those factors remain poorly resolved[6–8]. One aspect of coral reef community structure thought to be important that remains under-investigated is depth (although interest in this area has grown substantially in recent years[9]). Many studies to date have focused on the upper ~30 m of the water column, yet coral reefs and associated communities are known to extend beyond 150 m[10,11], with photosymbiotic corals reported to 170 m[12]. As much as two thirds of coral reef ecosystems lie below typical scuba depths in this under-explored zone[13]. These habitats, known as mesophotic coral ecosystems (MCEs), are typically defined as extending from ~30 to 150 m depth[13,14]. They have been proposed as possible refugia from climate change impacts on shallow reefs[15–19], although a growing number of studies have found evidence that MCEs are unique and uniquely threatened, challenging this notion[20–27].

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The Hawaiian Archipelago, spanning ~2500 km in the North Pacific Ocean, provides a natural laboratory to examine drivers of metazoan community structure. This chain of islands comprises two regions, the inhabited high islands of the main Hawaiian Islands (MHI) and the uninhabited low islands, atolls, and banks of the Northwestern Hawaiian Islands (NWHI) which reside within one of the world's largest marine protected areas—Papahānaumokuākea Marine National Monument. The island chain is subject to various anthropogenic and physical gradients driving differences in temperature, coral cover, human population, and anthropogenic impact, among others, all of which influence coral reefs and associated communities[28]. Nearshore drop-offs along the island chain also allow access to deeper reef habitat, enabling the examination of depth influences on community structure.

To date, the majority of studies that have examined community structure across the Hawaiian archipelago and/or along a depth gradient have focused on conspicuous taxa such as corals and fishes [e.g.,[29–33]]. One previous study[23] found a significant depth gradient on the island of O'ahu for brachyuran crabs. However, the most conspicuous and frequently-studied taxa make up a minority of coral reef biodiversity and thus may not be indicative of community patterns overall[34]. Furthermore, some studies examining environmental effects on reef assemblages have been criticized for confounding multiple potentially covarying factors (such as habitat area and/or complexity) across the measured gradients[35–39]. Here, we used autonomous reef monitoring structures (ARMS)—standardized collection devices designed to mimic reef structural complexity—to sample cryptic brachyuran crab communities while controlling for habitat[40,41]. Such standardization can reduce variability in recovered communities that may arise due to local variation in habitat composition and availability[42]. This study builds on previous work targeting brachyuran crabs[23], a ubiquitous group often used as an exemplar to assess coral reef biodiversity[43–46] and comprising a notable proportion of the Hawaiian coral reef cryptofauna (284 reported species[47]). We used crab assemblages recovered from ARMS units to examine drivers of community composition across the Hawaiian Archipelago. We compared assemblages among islands and regions (MHI vs. NWHI), among major depth zones (shallow vs. mesophotic), and examined the effects of a suite of possible environmental and anthropogenic drivers of community structure on shallow reefs (including fine-scale depth differences), to test hypotheses about their relative importance.

Given the strong reported differences between deep and shallow reefs across taxa and the paucity of research on drivers of cryptic coral reef community variation, we sought to answer the following four research questions: (1) How do shallow reef brachyuran crab assemblages vary in response to the natural and anthropogenic gradients of the Hawaiian Archipelago? (2) Do shallow reef brachyuran crab assemblages differ between the Main and Northwestern Hawaiian Islands? (3) What environmental and anthropogenic factors drive crab assemblage structure in shallow coral reefs across the Hawaiian Archipelago? (4) What are the relative contributions of depth (shallow vs. mesophotic) and island region to crab community variation across the Hawaiian Archipelago?

Results

Brachyuran diversity summary

All ARMS

The 116 ARMS units deployed across the Hawaiian Islands (in 8–90 m depth) yielded a total of 2283 adult crabs. Units contained 19.7 ± 13.1 (mean ± SD) individuals, and abundance ranged from 3 to 75 individuals per unit. Crabs were identified to 89 distinct taxa (71 species-level identifications, 11 genus, 7 family) encompassing 59 genera in 22 families, which accounted for ~25.0% of the known crab diversity reported from Hawaiian waters for species-level IDs[47]. The four most abundant species were: *Chlorodiella* cf. *laevissima* (Dana, 1852) (610 individuals from 59 units; Fig. 1a), *Perinia* cf. *tumida* Dana, 1851 (268 individuals from 67 units; Fig. 1b), *Percnon abbreviatum* (Dana, 1851) (121 individuals from 47 units; Fig. 1c), and *Dynomene hispida* (Latreille in Milbert, 1812) (114 individuals from 49 units; Fig. 1d). There were 14 singleton taxa (taxa occurring in a single unit across all sites), accounting for ~15.7% of total recovered crab taxa. For a breakdown of specific crab taxa recovered by island and deployment depth, see Supplementary Table S1.

Mesophotic ARMS

The 18 units deployed at mesophotic depths ≥ 30 m on O'ahu contained 271 crabs overall, 37 distinct taxa (28 species-level identifications, 7 genus, 2 family), 15.1 ± 6.2 individuals per unit, and abundance ranging from 7 to 31. The four most abundant taxa in the deep ARMS did not overlap with the most abundant taxa from the complete dataset: *Chlorodiella* spp. (46 individuals from 16 units), *Epiactaea nodulosa* (White, 1848) (40 individuals from 10 units), *Catoptrus inaequalis* (Rathbun, 1906) (17 individuals from 8 units), and *Pilumnus* spp. (14 individuals from 7 units). There were 10 singletons, which proportionally accounted for ~27.0% of species found on deep ARMS.

Comparisons

Out of the 22 families recovered, 10 were exclusive to shallow ARMS recovered from 8 to 17 m and 2 were exclusive to units ≥ 30 m (Acidopsidae and Inachidae; Supplementary Table S2). Thirty-two genera were found exclusively shallow and 2 exclusively deep (*Achaeus* and *Parapilumnus*; Supplementary Table S3). Fifty-two distinct taxa (including those collapsed to genus or family) were exclusive to shallow ARMS units and 5 were found only deep (*Achaeus* spp., Dromiidae spp., *Parapilumnus* spp., *Thalamita bevisi*, and *Thalamita seurati*; Supplementary Table S4). Out of the 89 total taxa, 10 were found across all 4 depth zones (shallow, 30 m, 60 m, and 90 m; *Catoptrus inaequalis*, *Chlorodiella* cf. *laevissima*, *Chlorodiella* spp., *Epiactaea nodulosa*, *Exopalicus maculatus*, *Hyastenus* spp., *Laleonectes nipponensis*, *Liomera bella*, *Liomera medipacifica*, and *Pilumnus* spp.). For a more in-depth taxonomic treatment of the assemblage composition of mesophotic vs. shallow ARMS units, see[23].

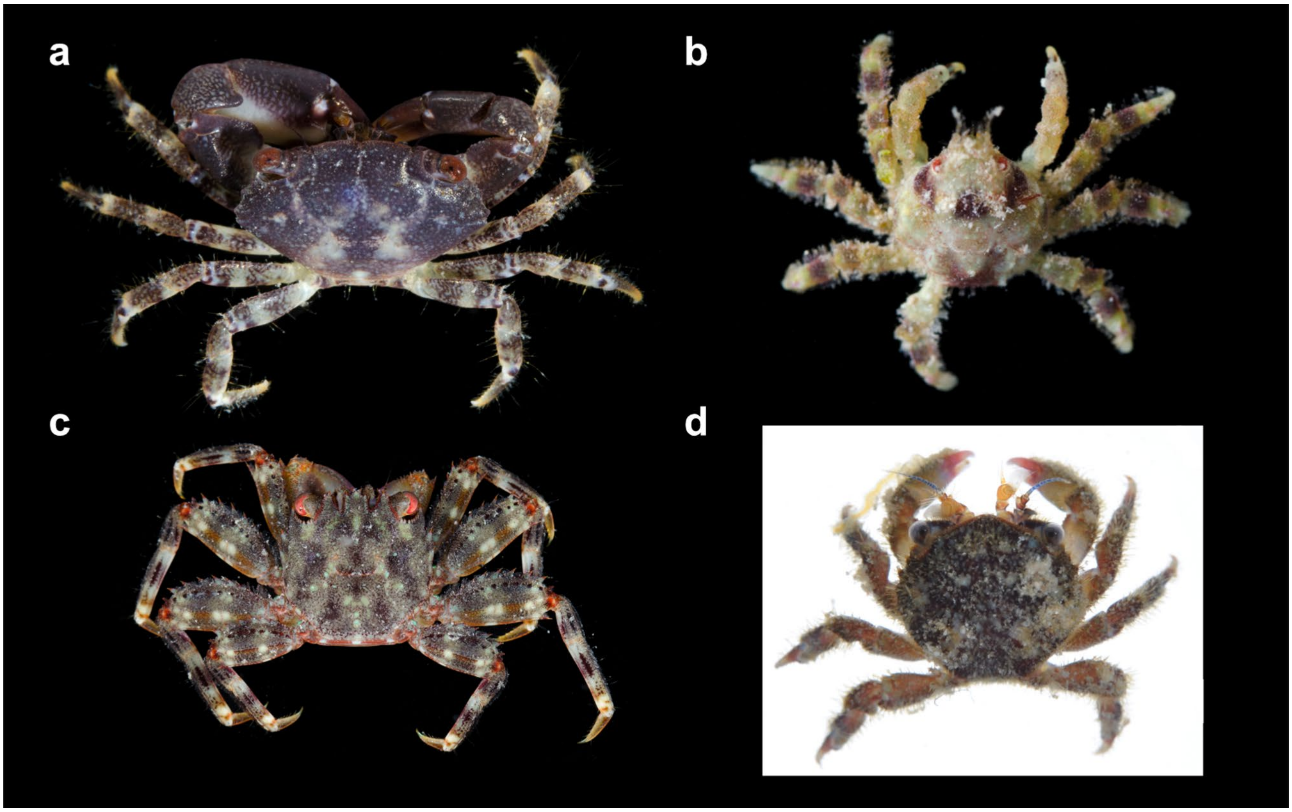

Fig. 1. Photographs of the four most abundant crab species found across all deployed ARMS units (pictured are representative museum specimens from Hawai'i, not collected for this study). Specimen size data was not retained, but all individuals were < 3.5 cm in carapace width. (**a**) *Chlorodiella* cf. *laevissima* (FLMNH 45,490, Kāne'ohe, Hawai'i). (**b**) *Perinia* cf. *tumida* (FLMNH 45,652, Kāne'ohe, Hawai'i). (**c**) *Percnon abbreviatum* (FLMNH 45,628, Kāne'ohe, Hawai'i). (**d**) *Dynomene hispida* (FLMNH 69,204, Manawai, Hawai'i). Photo credits: Florida Museum of Natural History, licensed CC BY-NC 3.0

Brachyuran community structure

Environmental drivers

The PCA of environmental variables indicated strong clustering according to island group (Supplementary Fig. S1), with orthogonal variation in variables associated with the MHI vs the NWHI. The best dbRDA model (Model: DF = 6.00, SS = 5.65, F = 3.78, $p < 0.01$) explained 14.26% (adjusted R^2) of the variability in crab communities across the archipelago (Fig. 2). Six of the nine environmental variables tested were significant and sufficiently uncorrelated. The two drivers contributing most to explained variation were sea-surface temperature (F = 6.94) and chlorophyll-A (F = 4.35) (Table 1). These factors also produced the longest effect vectors in the dbRDA plot (Fig. 2).

Regional & depth comparisons

Shallow crab assemblages were significantly different between island groups (MHI vs. NWHI; $p < 0.01$) and among individual islands ($p < 0.01$; see Supplementary Fig. S2 for results of pairwise comparisons). There was no significant difference in community dispersion between the MHI and NWHI ($p = 0.39$) for shallow crab assemblages. Crab assemblages were significantly different among depth zones (< 30 m, 30 m, 60 m, 90 m) both when comparing shallow assemblages at all islands to deep assemblages on O'ahu ($p < 0.01$) and when comparing assemblages on O'ahu alone ($p < 0.01$). Community dispersion was significantly different among depth zones for comparison among all islands ($p < 0.001$), however community dispersion was not different among depth zones $\geq$ 30 m ($p = 0.79$). Crab assemblages were significantly different among both depth zones ($p < 0.01$) and island groups ($p < 0.01$) in a combined model of the complete dataset. Although cumulative explanatory power was low (combined R^2: 0.20), depth ($R^2 = 0.144$) explained 2.6 times more variability than island group ($R^2 = 0.055$). For detailed statistical results, see Supplementary Table S5.

In the CAP analysis of island group and depth zone, ARMS units were correctly reassigned to sample groups 81.9% of the time. The first two linear discriminant axes explained 63.3% and 24.4% of the variation, respectively. Mesophotic samples (30–90 m) from O'ahu were grouped separately in ordination space from shallow samples across the archipelago (including O'ahu; Fig. 3). Shallow samples from O'ahu primarily clustered with shallow samples from other islands (Fig. 3). A CAP ordination limited to O'ahu shows similar patterns of depth zonation (Supplementary Fig. S3). Variability in canonical space was significantly greater among deep (30–90 m) than among shallow samples ($\leq$ 30 m) (Welch two-sample t-test of mean Euclidean distances: $t = 2.76$, DF = 156.25,

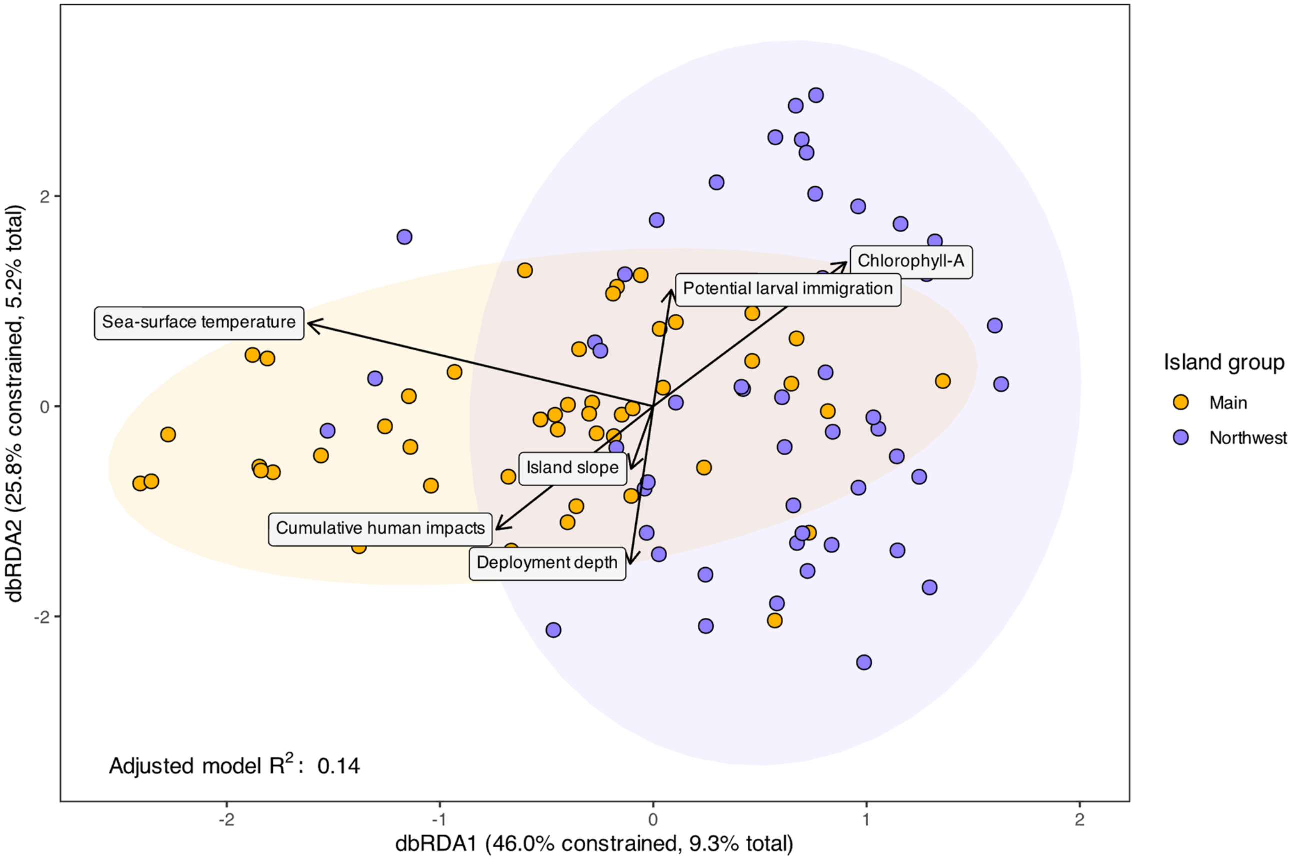

Fig. 2. dbRDA plot showing significant drivers of crab community variation among shallow-water (8–17 m) sites across the Hawaiian Archipelago. Colored ellipses represent 95% confidence intervals around island groups (Main Hawaiian Islands vs. Northwestern Hawaiian Islands).

Term	DF	Sum of squares	F-statistic	*p*-value
Sea-surface temperature	1.000	1.727	6.935	0.001
Chlorophyll-A	1.000	1.082	4.347	0.001
Deployment depth	1.000	0.945	3.794	0.001
Island slope	1.000	0.788	3.166	0.002
Potential larval immigration	1.000	0.572	2.296	0.012
Cumulative human impacts	1.000	0.536	2.151	0.019

Table 1. Significant terms in the dbRDA analysis of crab community variation across the Hawaiian Archipelago.

$p < 0.01$; Fig. 3, Supplementary Fig. S4). Similarly, variability within O'ahu alone (when mesophotic samples were included) exceeded the variability among all shallow samples combined ($t = 20.94$, DF = 803.83, $p < 0.001$).

Discussion

The Hawaiian Archipelago is among the most remote oceanic island chains on the planet and encompasses a range of gradients (anthropogenic, biotic, abiotic), making it an ideal natural laboratory to study the impacts of various drivers of species assemblages across space. We investigated the effects of a suite of factors on shallow brachyuran assemblage structure across the Hawaiian Archipelago and compared shallow assemblages to those sampled along a mesophotic depth gradient on O'ahu. We found that crab assemblages were more distinct across 90 m of depth on O'ahu alone than across the ~2500 km archipelago and the influence of diverse significant environmental, anthropogenic, and ecological drivers.

Three of the factors we found to be significantly associated with shallow crab assemblage variation correspond to well-known gradients across the islands: sea-surface temperature, chlorophyll-A, and human impacts. While few studies have examined the role of sea-surface temperature (SST) in structuring reef communities across the span of the Hawaiian Islands, it was found to be an important factor influencing intertidal communities

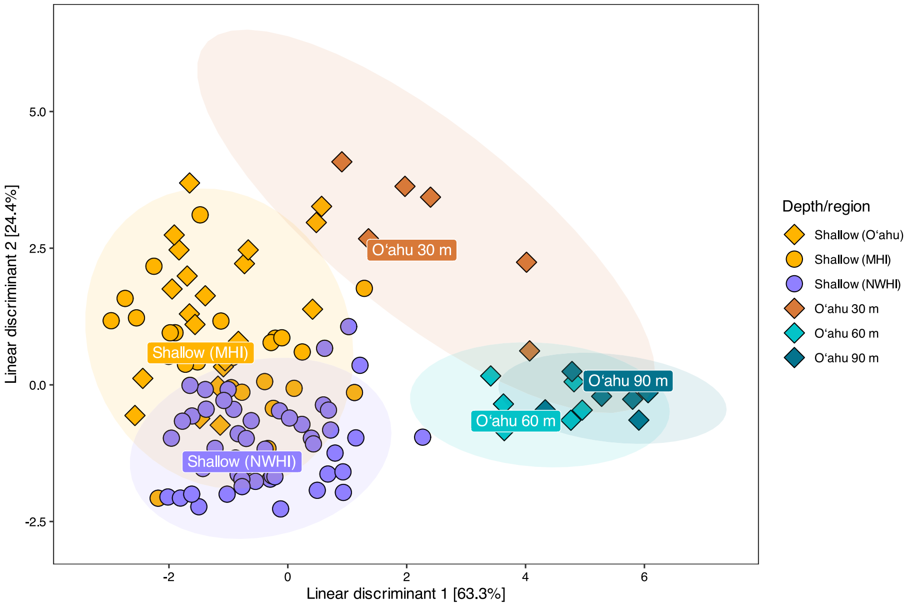

Fig. 3. Canonical analysis of principal coordinates (CAP) ordination of crab assemblages by island group and depth zone. Shallow samples are the same as those plotted with environmental drivers in Fig. 2, to which the mesophotic samples (30 m, 60 m, and 90 m) are added here for comparison. Depth transect samples collected on the island of O'ahu are plotted with a diamond (and separately as Supplementary Fig. S3) for direct comparison relative to archipelago-wide shallow samples represented by a circle.

within the MHI[48]. Chlorophyll-A can be used as a proxy for primary productivity. Productivity gradients across the Hawaiian Archipelago coincide with differences in coral reef community composition[49], endemic reef fish dominance[50], survival rates of top predators[51], and island geomorphology[52]. Human activities are considerably higher in the populated MHI than in the protected and remote NWHI[28,49,53]. Although we did not consider the effects of individual anthropogenic impacts here, an index representing cumulative impacts was a significant driver of shallow brachyuran community structure, similar to findings in previous work examining the relationships of genetic diversity to species richness and habitat area, quality, and stability across the archipelago[49]. Thus, given the prevalence in our model of significant factors known to be important influencers of marine communities in Hawai'i, it is not surprising that we find the same top drivers of community structure for brachyuran crabs, one of the primary taxonomic groups inhabiting coral reefs. What is surprising, given the 9 m maximum depth difference among shallow ARMS, is the consistent significance of depth as a driver of community composition across these gradients.

Depth consistently emerged as a significant driver of brachyuran assemblage variation among shallow-water ARMS units, despite the narrow depth range (8–17 m) within which they were deployed. Fine-scale depth patterns have been found in previous studies, both using molecular[54,55] and traditional survey methods[56,57], but we recovered them despite numerous other latitudinal and environmental gradients and across a broad spatial scale. Depth in and of itself is unlikely to affect marine community composition and oceanographic factors with well-known depth profiles (e.g., temperature, oxygen, nutrients, etc.) are not expected to vary dramatically across such a narrow depth range (<10 m) in Hawai'i, although internal waves can deliver variable temperatures across shallow reefs[58,59] and fine-scale habitat variability may also exert an influence[60]. Unfortunately, we lack high resolution environmental data at depth for individual deployments, and thus cannot unravel the co-varying factor(s) associated with the depth effects we observed for shallow assemblages. Regardless, given its significance across both narrow (<10 m) and wider (90 m) depth ranges sampled here, a factor associated with depth is clearly an important driver for cryptobenthic crab communities across the Hawaiian Archipelago. As brachyurans are a ubiquitous and important component of coral reef communities[61–63], these findings may apply more broadly as well.

While depth was a significant driver of community composition among shallow-water ARMS units (Fig. 2, Table 1), its influence was considerably more striking when comparing shallow to mesophotic habitat. In the CAP ordination, shallow assemblages spanning the archipelago clustered separately from the deep assemblages $\geq$ 30 m at the single island of O'ahu (Fig. 3). Further, the average distance among O'ahu samples (including 30–90 m) in canonical space was significantly greater than among all shallow samples (MHI and NWHI). Thus, there was more variation (both visually and statistically) among assemblages spanning 90 m of depth on a single island than across ~2500 km of shallow habitat experiencing multiple gradients of environmental, ecological, and anthropogenic influence. The CAP ordination also revealed two groups within the mesophotic samples: one at 30 m and the other encompassing the 60–90 m depths. These depth zones correspond with the upper and lower mesophotic zones, respectively [14, 26, but see 11]. The upper mesophotic zone has been found to constitute an extension of shallow reefs (with beta diversity patterns largely driven by nestedness), while the lower mesophotic harbors unique communities (with beta diversity driven primarily by turnover)[14,26,35,64]. Groupings in ordination space match these trends, with 30 m samples lying closer to shallow O'ahu samples and 60–90 m samples forming a distinct cluster. This pattern of community transition from shallow to mesophotic reefs is consistent with what has been shown for various other taxonomic groups[26,65,66] and subsets of entire communities[22], supporting the possibility that there may be broad-scale depth-based assembly rules for coral reef communities.

Since we lack environmental data at mesophotic depths, we cannot make conclusions about the specific influences driving the differences we found. However, light and temperature have been proposed as important bottom-up drivers of depth zonation in benthic communities[11,14,65,67]. Oceanographic conditions may be inconsistent close to shore, but the average mixed-layer depth (calculated using the 0.8 °C ΔT criterion[68]) based on CTD casts taken at station ALOHA (22.75°N, 158.00°W; within the latitudinal expanse of the MHI) was 84.6 ± 26 m over the course of the year (based on monthly averages from casts taken across the duration of ARMS unit deployments[69]). Thus, given the assumption of similar temperature profiles near the O'ahu shoreline, temperature alone appears insufficient to explain the zonation patterns we observed—although due to its significant role as a driver of shallow community variation, it cannot be ruled out. In contrast, the lower depth boundaries of mesophotic ecosystems are largely defined by surface irradiance[13,14], so light may exert a bottom-up influence on community structure across depths. Crab assemblage structure overall is unlikely to be directly affected by light variability (diurnal behavior patterns of individual species notwithstanding). However, habitat-building species such as corals, algae, and sponges are frequently subject to light requirements[14,64], and may in turn affect the structure of the communities dependent upon them[70–72]. If patterns of community structure are driven primarily from the bottom up by light, that may contribute to our observation of a significant depth effect over less than 10 m in our shallow samples.

Two potential weaknesses of our dataset are the time periods over which ARMS units were deployed and the fact that mesophotic samples were only available from O'ahu. Our ARMS units were deployed across a broad range of years, but the majority were deployed during 2010–2012 or 2010–2013 (an overlap of two years) (Table 2). A reduced version of the CAP ordination filtered to include only ARMS units deployed during these overlapping time periods retains the same (if not more pronounced) overall patterns as the full version (Supplementary Fig. S5), suggesting that the inclusion of prior or subsequent soaking periods did not adversely skew our analyses. Soak time differed by one year between O'ahu mesophotic ARMS units and those deployed across the rest of the archipelago. This difference may potentially bias results, but due to the distinct clustering in the CAP ordination despite the extra year that shallow units spent in the water, we feel that the patterns we observed reflect a true separation. The limitation of our depth transect to O'ahu means that we cannot make broad-scale conclusions about biodiversity patterns on deep reefs across the Hawaiian Islands. However, it remains the case that differences among depth zones at that single island outpace differences among shallow-water coral reef habitat across the archipelago and depth appears to be the strongest organizing factor in canonical space regardless of where or when the communities were sampled. Similar patterns were found at a local scale (tens of kilometers) on Hawai'i Island using environmental DNA (eDNA)[22]. In that study, communities were found to have more affinity within depth zones across sites than among depth zones within sites. Despite the limitations in our dataset, the patterns we observed suggest that factors associated with the shallow-to-mesophotic depth gradient exert stronger ecological influence than those that vary across the latitudinal, physical, and anthropogenic gradients throughout the Hawaiian Archipelago.

Further work to investigate drivers of depth zonation could take advantage of established gradients across the Hawaiian Archipelago by sampling depth transects across the archipelago. Coral reef biodiversity is generally thought to be structured at depth by a combination of the attenuation of light, a decrease in temperature, increasing salinity, and a reduction in trophic resources[14,64,73]. If mesophotic communities are found to be different from their shallow counterparts across multiple islands (ideally comparing sites experiencing similar irradiance), this suggests that they are vertically structured by a factor (e.g., light) outside of the numerous natural gradients that exist across the Hawaiian Islands. In contrast, other factors (such as temperature, dissolved inorganic nitrogen, particulate organic carbon, or productivity) expected to have more strongly-defined gradients across the regions[64], would lead to variable zonation patterns that should be detected in a spatial comparison of the MHI & NWHI. Such differences should be tested in future studies to understand the specific physical and

Island	Depth range (m)	2009–2011	2010–2012	2010–2013	2013–2016
Hōlanikū (Kure Atoll)	10–14	0	0	3	0
Manawai (Pearl and Hermes Reef)	14–15	0	0	7	12
Kapou (Lisianski)	8–15	0	0	7	0
Lalo (French Frigate Shoals)	8–17	0	0	15	7
Kaua'i	12–14	0	0	6	0
O'ahu (shallow)	12–15	9	0	3	9
O'ahu (deep)	**30–90**	**0**	**18**	**0**	**0**
Maui	12–12	0	0	3	0
Hawai'i Island	12–15	0	0	6	11

Table 2. ARMS unit deployment schedule by island (number of units). Mesophotic deployments appear in bold.

ecological drivers of coral reef depth zonation. The cost, logistical complexity, and time investment required for ARMS deployments (particularly at mesophotic depths) make this challenging, but emerging approaches such as environmental DNA (eDNA) may offer a suitable alternative.

Marine communities are structured by a suite of factors, but there remains no consensus for either generalized mechanisms or the relative importance of drivers of community structure for coral reefs. Our best knowledge of the role of depth in structuring marine communities comes from the intertidal, and points to biotic factors (e.g., predation, competition) determining lower limits and abiotic factors (e.g., desiccation, thermal stress) setting upper limits of vertical species distributions[74–77]. There are numerous examples from other study systems in which the relative contributions of biotic versus abiotic factors to structuring communities run in opposing directions across some habitat gradient (e.g., climate, soil type, elevation, etc.[78–80]). However, abiotic stressors on intertidal communities are obviously different from those on coral reefs, and generalizations about the mechanisms and ecological processes that structure coral reef communities remain a subject of considerable debate[81–87]. In the Hawaiian archipelago, we found significant differences in the composition of shallow coral reef crab communities between the populated high islands of the MHI and the uninhabited atolls of the NWHI. Moreover, these differences were driven by a combination of environmental (sea-surface temperature, chlorophyll-A concentration, depth, island slope), biotic (potential larval immigration), and anthropogenic (cumulative human impacts) factors. Despite the significance of these factors in driving shallow community variation across the archipelago, mesophotic assemblages were found to be distinct (Fig. 3). Although there were variables we did not consider in our model, this suggests that vertical distributions are influenced by factors other than those driving spatial variation across the island chain. Our data was collected using ARMS, which in mimicking the reef matrix are biased toward recruiting a specific subset of fauna that prefer cryptic habitats. However, the depth zonation patterns that we observed match those observed for other taxa and communities[20–27]. In light of this, and since mesophotic communities are generally less biodiverse than shallow reefs[14,67,73], it may be possible that the gradients driving depth distributions on coral reefs run opposite to those in the intertidal. Given the rapid changes in important factors like temperature, nutrients, and light throughout the upper ~100 to 150 m of the water column (particularly the diminishment of photosynthetically active radiation below 100 m), the *lower* limits of the coral reef mesophotic zone (the transition from reef-associated to slope habitat) may be determined by abiotic factors that correlate with depth. Conversely, the *upper* limits of the mesophotic zone (the transition from shallow reef to mesophotic habitat), which occur at the higher end of the depth-biodiversity gradient[14,73] may be driven by ecological interactions[88].

By comparing shallow-water ARMS across the latitudinal, physical and anthropogenic gradients of the Hawaiian Archipelago, we were able to test the relative importance of these factors in driving shallow crab assemblage structure. We additionally find that assemblages along a 90 m depth transect at a single island show greater divergence in canonical space than across the full ~2500 km gradient of the Hawaiian Archipelago on shallow reefs. Our analyses corroborate previous work and show that depth is among the strongest drivers of community structure, highlighting the fact that mesophotic ecosystems constitute distinct habitats and should be considered as such when formulating management and conservation strategies. We conclude that some factor(s) covarying with depth exert more influence on cryptobenthic coral reef community structure than those biotic and abiotic gradients that span the entire Hawaiian Archipelago in shallow-water environments.

Methods

Sample collection

Brachyuran crab assemblages were sampled from benthic coral reef habitat in the Hawaiian Archipelago using Autonomous Reef Monitoring Structures (ARMS) collected by NOAA's Ecosystem Science Division as part of its Pacific Reef Assessment and Monitoring Program. ARMS are standardized collection devices designed to mimic coral reef structural complexity to attract settlement of reef cryptofauna[40,41]. They are constructed from 10 grey type 1 PVC plates (23 cm × 23 cm) stacked in an alternating series of open and semi-enclosed layers (Fig. 4). The stack is fastened to a larger base plate (35 cm × 45 cm) which can be attached to the benthos upon deployment[23,40,41,43].

A total of 89 ARMS units were deployed over the course of six years (2010–2016) in shallow (8–17 m depth) coral reefs in both the Main (MHI) and Northwest Hawaiian Islands (NWHI) (Fig. 5, Table 2). All shallow units included in this study were deployed in forereef habitat and had a soaking period of three years (2010–2013 or 2013–2016). To explore the effects of depth, we also present data from an earlier study by Hurley et al.[23], in which 27 units were deployed off O'ahu from 2009 to 2012 in 12–90 m depth; nine shallow units were deployed at 12 m, and six each at depths of 30 m, 60 m, and 90 m (Table 2). Shallow units were deployed according to NOAA-RAMP methodology, whereas units $\geq$ 30 m were deployed and recovered using technical mixed gas closed-circuit rebreather diving (see[23]). Units from this study soaked for two years during 2009–2011 or 2010–2012. When discussing assemblage depths, we will refer either to one of four specific depth zones (< 30 m or "shallow", 30 m, 60 m, 90 m) or units deployed at 8–17 m as "shallow" and $\geq$ 30 m as "deep".

ARMS units were retrieved by encapsulating them in-situ in a 100 µm mesh-lined crate to prevent escape of motile organisms. Once returned to the surface, they were placed in containers of aerated, filtered seawater, crates were removed, and units were systematically disassembled plate-by-plate (see[89] for processing details). All adult brachyuran crabs ($\geq$ 2 mm) were photographed, identified, preserved in 95% ethanol, and retained in a specimen archive at the Hawai'i Institute of Marine Biology. Specimens were initially identified to family or genus using Poore & Ahyong[90] and additionally to species where possible according to expert advice from Scott Godwin (former curator of invertebrate zoology, Bishop Museum) and Gustav Paulay (curator of invertebrate zoology, Florida Museum of Natural History). Where species-level identifications were not possible, taxa were collapsed to family or genus (depending on individual identification). We recognize that the species-level taxonomy of Indo-Pacific brachyurans remains poorly resolved, particularly for abundant groups like the Chlorodiellinae[62,91],

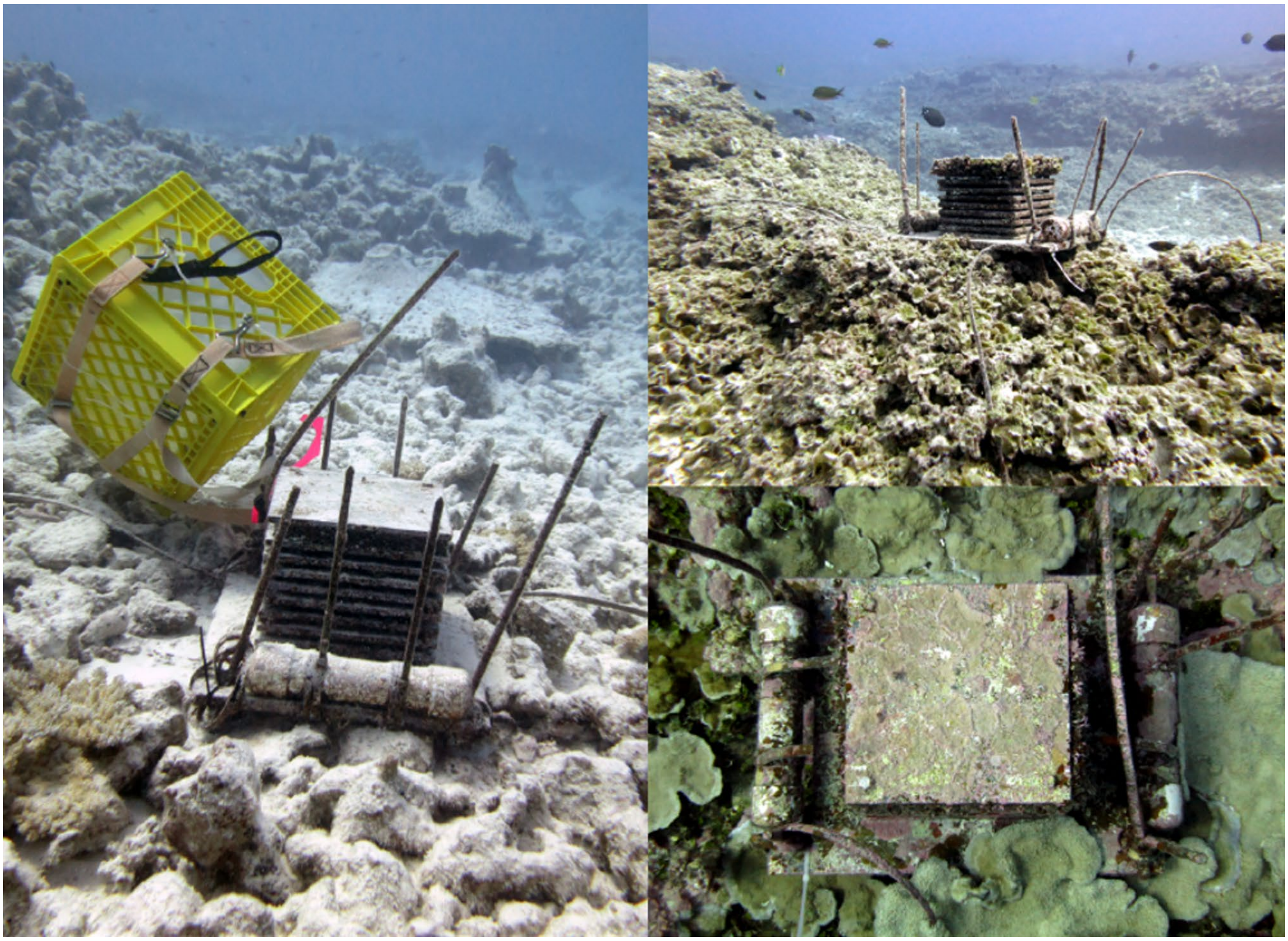

Fig. 4. Example photographs of autonomous reef monitoring structures (ARMS) deployed in the Hawaiian Archipelago. Photo credits: the authors and NOAA (uncopyrighted).

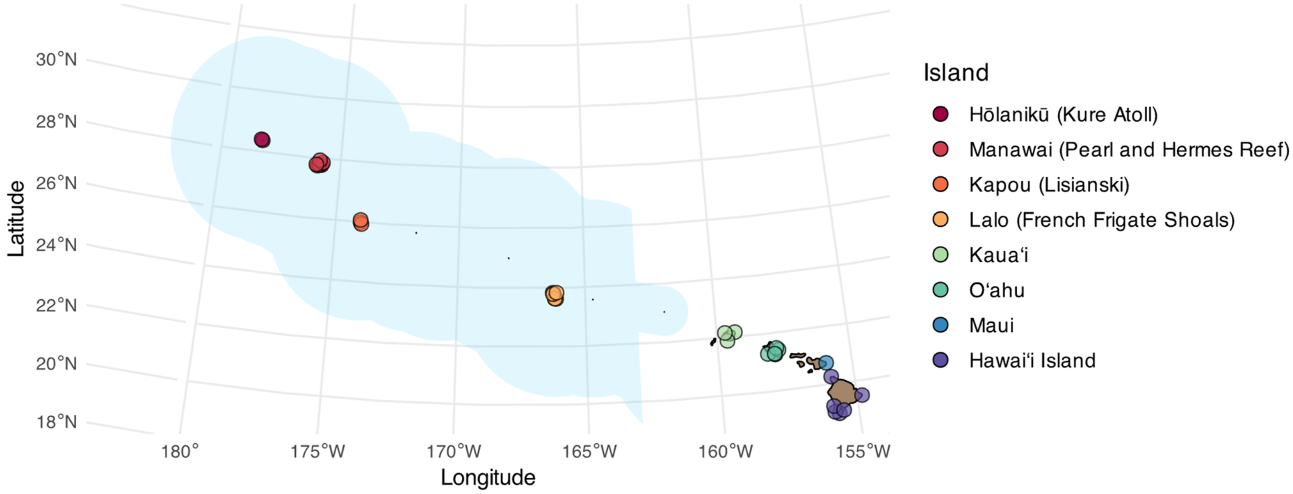

Fig. 5. Map of ARMS deployment sites across the Hawaiian Archipelago (Papahānaumokuākea Marine National Monument (NWHI) is shaded in light blue).

Environmental driver	Description	Source	Data resolution
Deployment depth	ARMS unit deployment depths	NOAA NCRMP	Site
Latitude	ARMS unit deployment latitude	NOAA NCRMP	Site
Longitude	ARMS unit deployment longitude	NOAA NCRMP	Site
Chlorophyll-A	Satellite-derived sea surface chlorophyll-A (4 km resolution), based on monthly means averaged over deployment years	OB.DAAC[100]	Site/Years
Sea-surface temperature	Satellite-derived sea surface temparature (4 km resolution), based on monthly means averaged over deployment years	PO.DAAC[101]	Site/Years
Island slope	Bathymetric slope index, 1000 × deployment depth (m) divided by the average horizontal distance from shore to the 50 m isobath (m)	PacIOOS	Site
Coral cover (%)	Satellite-derived coral cover. Defined as the number of pixels with more than 10% cover in IKONOS satellite imagery within the 0–30 m isobaths. Expressed as a percentage of the total number of pixels analyzed for each island in the study	Published literature[49]	Island
Potential larval immigration	Incoming centrality metric calculated from modelled larval connectivity derived from a biophysical oceanographic model parameterized for a broad selection of Hawaiian marine species	Published literature[49]	Island
Cumulative human impacts	Dimensionless index of cumulative human impacts to marine ecosystems based on high resolution, annual data on the intensity of 14 human stressors and their impact on 21 marine ecosystems globally over 11 years (2003–2013)	Published literature[99,102,103]	Island/ Years

Table 3. Potential environmental drivers of crab community structure across the Hawaiian Archipelago.

and some "species" are known to comprise complexes [e.g. *Perinia* cf. *tumida*, 45, 46]. However, the prevalence of species complexes and cryptic diversity suggests that our assignments are likely to under- rather than overrepresent the true number of taxa. Thus, any significant patterns we detected likely persist in spite of the potential presence of cryptic diversity. Since our primary concern was categorical diversity of assemblages rather than accurate naming, we have retained species names in cases where complexes are suspected.

Data analysis

Unless otherwise specified, all analyses were performed using R version 4.4.1[92]. Community matrices were loaded and encapsulated into data objects using the R package phyloseq[93] and multivariate community analyses were performed using the package vegan[94] on Bray–Curtis dissimilarities of Hellinger-transformed species abundance matrices[95,96].

To visualize how potential environmental drivers varied across the archipelago, we used a principal components analysis (PCA), plotting the results with points colored by island group (MHI or NWHI). We used distance-based redundancy analysis (dbRDA; a form of multivariate multiple regression) with dbrda to examine the relative contribution of environmental variables (Table 3) to shallow crab community variation across the islands, conditioning the ARMS unit soak time as a random effect. From a model incorporating all potential drivers, we sequentially removed variables with the largest variance inflation factors (VIF; calculated using vif.cca) until all values were < 3, indicating variables were sufficiently uncorrelated. Model significance was assessed using permutation tests with 999 permutations with the function anova. Continuous variables were scaled to unit variance. dbRDA analyses were conducted only for communities sampled from shallow (< 30 m) ARMS units, since detailed environmental/ecological drivers were not available for deep (≥ 30 m) samples.

We assessed variation among groups using betadisper and adonis2. These functions implement analysis of multivariate homogeneity of group dispersions (PERMDISP) and multivariate permutational analysis of variance (PERMANOVA) respectively. PERMDISP is used to assess variability within groups and PERMANOVA is used to assess differences among groups. Significance was assessed with permutation tests in both cases. We used PERMANOVA to make the following comparisons: island group (MHI vs NWHI, shallow samples only), island (shallow samples only), depth zone only (all samples), depth zone only (O'ahu samples), island group and depth zone (all samples). Variation among island groups and sampling depths was further examined and visualized using canonical analysis of principal coordinates (CAP) based on discriminant analysis[97] as implemented in the CAPdiscrim function from BiodiversityR[98]. To explore differences in community variability among groups (shallow/deep, O'ahu/all shallow samples), we compared Euclidean distances among assemblage points in canonical space (from the CAP analysis) using Welch two-sample t-tests, assuming unequal variances.

Environmental variables

We assembled potential drivers of brachyuran crab community structure from previous studies[49,99], NOAA's National Coral Reef Monitoring Program (NCRMP), the Pacific Islands Ocean Observing System (PacIOOS), and MODIS satellite data products compiled by NASA's Physical Oceanography/Ocean Biology Distributed Active Archive Centers[100,101]. Variables were either intrinsic (site depth, latitude, longitude, island slope) or derived from remote sensing and/or modeling (chlorophyll-A, sea-surface temperature, coral cover, potential larval immigration, cumulative human impacts) (Table 3, Supplementary Table S6). Sea-surface temperature (SST) and chlorophyll-A values were calculated by averaging monthly means across the duration of the soaking period for each deployment using AQUA MODIS 4 km-resolution gridded datasets. The cumulative human impacts index, a dimensionless numerical value representing spatially-explicit cumulative anthropogenic impacts on various marine ecosystems, is based on a synthesis of a combination of "high resolution, annual data on the intensity of 14 human stressors and their impact on 21 marine ecosystems over 11 years (2003–2013)"[99,102]. The index of potential larval immigration was imported from[49] and represents the potential of a given island to act as a destination for larval settlement. It is an "estimate of in-closeness centrality" from a biophysical model simulating larval dispersal in the Hawaiian Islands [49 supp. mat.]. For details regarding data import, preparation, and synthesis, see Supplementary Information. Due to logistical and dataset limitations, environmental/ecological drivers were only available for shallow (< 30 m) samples.

Data availability

All data and code used to generate this manuscript and its accompanying figures and tables can be found on github at https://github.com/mhoban/arms_crabs.

Received: 24 March 2025; Accepted: 2 July 2025

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Acknowledgements

We thank the NOAA Coral Reef Conservation Program for supporting the deployment and recovery of the shallow ARMS. We thank the UH Mānoa Dive Safety Office (D. Pence, K. Stender, J. Jones, and C.J. Bradley) for installation and retrieval of the mesophotic ARMS. We specially thank K. Flanagan from the UH dive program, whose support was instrumental in the development of the mesophotic ARMS project, and J. Copus, who provided expert mesophotic field support; both were taken too soon. May their memories be a blessing. We thank the members of the ToBo lab, particularly M. Iacchei, C. Kaʻapu-Lyons, and Z. Hee, for discussion, support, and their efforts in the disassembly and sorting of ARMS samples on retrieval. This is contribution #2002 from the Hawaiʻi Institute of Marine Biology and #11972 from the School of Ocean and Earth Science and Technology at the University of Hawaiʻi.

Author contributions

Conceptualization: MLH, KKH, DJS, RJT; Data curation: MLH; Formal Analysis: MLH, KKH; Funding acquisition: KKH, DJS, RJT; Investigation: MLH, KKH, KR, DJS, RJT; Methodology: MLH, KKH, DJS, MAT, RJT; Project administration: KKH, DJS, RJT; Resources: KR, MAT, RJT; Software: MLH; Supervision: DJS, RJT; Validation: MLH, MAT, RJT; Visualization: MLH, KR; Writing—original draft: MLH, KKH, RJT; Writing—review & editing: MLH, KKH, KR, DJS, MAT, RJT

Funding

This work was funded through a combination of grants including NSF OCE-1260169, NSF GRFP DGE-1329626, and NSF OCE-2048457. In addition, the NOAA Coral Reef Conservation Program funded the Pacific Reef Assessment and Monitoring Program, which included the shallow ARMS deployment in the Hawaiian Archipelago.

Declarations

Competing interests

The authors declare that they have no competing interests.

Additional information

Supplementary Information The online version contains supplementary material available at https://doi.org/1

0.1038/s41598-025-10232-6.

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