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Community structure of southern California's subtidal rocky reefs and implications for artificial reef design

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ABSTRACT: With the rapid growth of the blue economy worldwide, the footprint of marine infrastructure is expanding. In highly developed coastal regions such as southern California (USA), novel human-made structures can help compensate for the loss of nearshore hard-bottom habitats. However, it is critical to establish a baseline understanding of how natural rocky reef communities vary across habitat gradients to inform marine infrastructure design. Here, we used an extensive biodiversity survey of the Southern California Bight between 2016 and 2023 to investigate patterns in species abundance, diversity, and community zonation across depths accessible to SCUBA (≤25 m) at both mainland and island habitats across 25 artificial and 66 natural reefs. Overall, artificial reefs supported higher fish densities and similar macroinvertebrate densities compared to natural reefs, but had lower macroalgae densities. While fish species richness on artificial reefs was similar to that observed on natural reefs, the diversity of macroinvertebrates and macroalgae was lower. Community composition also differed by reef type: artificial reefs constructed far from natural reefs, and on soft bottom habitat with high turbidity, supported different communities than those established on artificial reefs adjacent to natural reef habitat in cooler waters. Fish communities were more consistent across artificial and natural reefs than other taxa and were consistently dominated by blacksmith *Chromis punctipinnis*. Patterns of community zonation also differed between mainland and island reef contexts. Together, these findings provide key ecological insights to inform the design and placement of future marine infrastructure to enhance populations of rocky reef species.

KEY WORDS: Artificial reefs · Fish · Macroalgae · Macroinvertebrates · Rocky reefs · Diversity · Depth zonation · PERMANOVA

1. INTRODUCTION

The blue economy is expanding globally (Organization for Economic Cooperation and Development 2016), leading to a rapid increase in human-made structures in the ocean. The worldwide physical footprint of marine construction is projected to increase at least 23% by 2030 compared to 2018 levels (Bugnot et al. 2021). As nearshore hard-bottom habitat is declining in coastal regions worldwide, hard materials associated with marine infrastructure (e.g. pipelines, wind farms, breakwaters) could compensate for lost habitat area (Airoldi et al. 2009). Artificial reefs can promote the development of productive and robust ecosystems in nearshore marine environments where hard substrate and nutrient availability are limited (Layman & Allgeier 2020). For example, in southern California (USA), structures built to process and produce oil and gas support highly productive communities of rocky reef fish and invertebrates (Froeschke et al. 2005, Claisse et al. 2014, Love et al. 2019, Meyer-Gutbrod et al. 2019, 2021, Nishimoto et al. 2023).

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However, engineering designs rarely integrate ecological principles (Dafforn et al. 2015). Improving our understanding of how rocky reef species assemblages vary across space, depth, and habitat type can aid in the intentional design of marine infrastructure to provide novel habitat for species of high ecological and economic value (Perkol-Finkel et al. 2006).

Rapid turnover in environmental gradients on marine reefs results in distinct community zonation (Konar et al. 2009, Twist et al. 2020). In comparison to coral reefs, relatively less is known about how patterns in species abundance, diversity, and community structure vary across depth and other gradients in temperate rocky reefs (Lazarus & Belmaker 2021). Light, substrate, rugosity, temperature, and wave action change with depth, and shape vertical distributions of marine species (Hixon 2006 and references therein, and see Larson 1980, Fulton et al. 2005, Brokovich et al. 2008, Konar et al. 2009, Reed et al. 2011, Magalhães et al. 2015, Parsons et al. 2016). Habitat-forming species (i.e. oysters, coral, and kelp) subsequently create biotic gradients (Wernberg et al. 2011, Beaton et al. 2020). Variable distributions of other reef species across depth influence competition, herbivory, and predation (Bell 1983, Bay et al. 2001, Pedersen et al. 2012, Vergés et al. 2012, Carr & Reed 2016). Despite the high turnover of conditions and resultant communities in the coastal ocean, the effect of depth on subtidal species abundance, diversity, and community composition is still relatively unexplored because of the challenges associated with multi-taxa, underwater surveys (Parsons et al. 2016).

The Southern California Bight (SCB) provides an ideal context for integrating knowledge of rocky reef species distributions into infrastructure design. Future development of aquaculture, oil and gas, renewable energy, and mining projects in this region will require the construction of new marine infrastructure (Institute for Applied Economics 2020). Already, the SCB has experienced extensive human disturbance, especially along the coast of the mainland, that has directly impacted the availability of hard substrate and subsequently the composition of nearshore aquatic communities (Murray & Littler 1981, Foster & Schiel 2010). Recently, coastal landslides, marine heatwaves, and food-web modifications have further highlighted the vulnerability of these critical ecosystems (Pondella et al. 2018, Cavanaugh et al. 2019).

Located at the intersection of cold and warm biogeographical provinces, southern California's rocky reefs also offer a unique opportunity to investigate variability in subtidal zonation across an ecotone. These provinces are further divided into island and mainland habitats that differ in bathymetry, habitat diversity, oceanography, and extent of coastal development (Ebeling & Larson 1980, Pondella et al. 2015, Claisse et al. 2018, Gamble 2025). In this transitional zone, northward-flowing warm waters of the Davidson Countercurrent intersect with southward-flowing cold waters of the California Current (Emery 1960, Dailey et al. 1993, Hickey 1993). This confluence leads to the presence of both warm- and cool-water species, with dynamic distributions through both space and time (Murray & Littler 1981, McClatchie et al. 2016, Zahn et al. 2016). Dependent on hard substrate, giant kelp *Macrocystis pyrifera* functions as a fast-growing foundational species (Carr & Reed 2016). Kelp forests provide diverse ecosystem goods and services including harvesting opportunities, wave attenuation and nutrient cycling (Carr & Reed 2016, Teagle et al. 2017). California's reefs support recreational and commercial fisheries for kelp, urchin, abalone, lobster, and finfish (Tegner et al. 1996). The Chumash, Gabrieleño-Tongva, Acjachemen, and Kumeyaay Peoples of what is now California have historically maintained deep relationships with these rocky reef ecosystems (Steneck et al. 2002, Learn 2021, Gabrielino-Tongva Indian Tribe, https://gabrielinotribe.org/; Northern Chumash Tribal Council, https://chumashsanctuary.org/; Juaneño Band of Mission Indians Acjachemen Nation, https://www.jbmian.com/).

Despite the prevalence of long-term monitoring in this region (Pondella et al. 2019, Caselle et al. 2022), depth zonation of subtidal rocky reef species has not previously been described. Here, we used 8 years of subtidal (≤25 m) biodiversity surveys across mainland and island biogeographic provinces to examine (1) whether artificial reefs in southern California support similar communities to natural rocky reefs; (2) how species abundance, diversity, and community composition vary with depth; and (3) whether these patterns are consistent across mainland and island reefs. Our findings establish a baseline to guide proactive and ecologically informed designs for future introductions of hard substrate into temperate coastal waters.

2. MATERIALS AND METHODS

2.1. Biodiversity surveys

We used self-contained underwater breathing apparatus (SCUBA) to conduct biodiversity surveys of reefs in the warm temperate region of the SCB (Table S1 in the Supplement at www.int-res.com/articles/suppl/m774p091_supp.pdf; Zahn et al. 2016, Pondella et al.

2019, Williams et al. 2021). Data for these analyses were from surveys conducted by the Vantuna Research Group between 2016 and 2023 of sites with at least 3 years of observations (Fig. 1; Table S1). Fish, macroinvertebrates, and brown macroalgae (referred to as macroalgae hereafter) were surveyed along benthic (all) and midwater (only fish) set-length transects using standardized survey methodologies that have been previously described (for further details, see Text S1, Table S2 both in the Supplement, and MME 2011, Claisse et al. 2012, Pondella et al. 2015). To maximize consistency between years, each site was surveyed either during summer (peak upwelling) or during the fall (waning upwelling). We surveyed artificial reefs across 4 complexes with unique characteristics (Fig. S1 in the Supplement). Three complexes were located in Santa Monica Bay (SMB): (1) Santa Monica Artificial Reef (n = 3 biodiversity survey sites), (2) Marina del Rey Artificial Reef (n = 3), and (3) Hermosa Beach Artificial Reef (n = 1), and the fourth was built adjacent to natural reef along the Palos Verdes Peninsula: (4) Palos Verdes Restoration Reef (PVR) (n = 18). The SMB reefs surveyed for this study were primarily designed to improve sport fishing opportunities and were constructed between the 1960s and 1980s using predominantly quarry rock, with 2 of the sites also including concrete shelters or the degraded steel baseframes of streetcars (Lewis & McKee 1989, D. J. Pondella II & J. P. Williams pers. obs.) (Table S1). PVR was constructed in 2020 using quarry rock to restore rocky reef communities by replacing hard substrate that had been lost or degraded through sedimentation and scour (Williams et al. 2022). Artificial reef sites had relatively small footprints (average size: SMB = 371 m^2, PVR = 1787 m^2) and were therefore each surveyed with the same effort as a single natural reef depth zone. Artificial reefs were all located off the mainland between 13 and 23 m deep and were therefore compared to mainland natural reefs at similar depths (outer and deep depth zones).

For comparison and to describe trends across depth and location, we also surveyed natural rocky reef sites. These reefs consisted of at least 250 m of continuous reef and were distributed across 200+ km between Malibu and San Diego. Unlike artificial reefs, natural reefs exist and therefore were surveyed off the mainland and islands (i.e. Santa Barbara, Santa Catalina, and San Clemente Islands; Fig. 1). Natural reef sites were surveyed within 4 depth zones that encompassed the majority of hard subtidal habitat. Moving perpendicular from the shore, these zones were (with target depths) inner: ~5 m, middle: ~10 m, outer: ~15 m, and deep: ~25 m. Some sites were missing one or multiple depth zones where only soft sediment substrates were present (n = inner: 65 biodiversity survey sites, middle: 64, outer: 56, deep: 26; Fig. 1; Table S1).

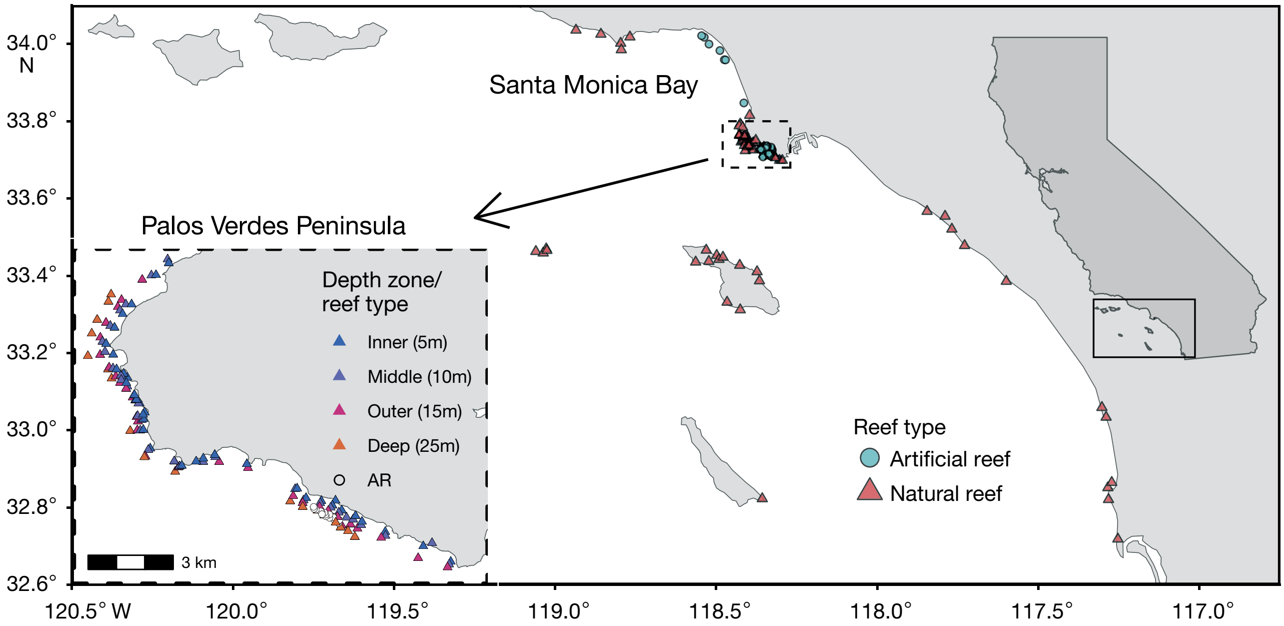

Fig. 1. Study sites across the Southern California Bight, highlighting artificial (circles; n = 25) and natural (triangles; n = 66) reefs. A slight positional jitter was applied to improve visibility of adjacent sites. Inset: close-up of the Palos Verdes Peninsula, a region of dense sites, showing the arrangement of individual depth zones (inner, middle, outer, deep) surveyed within natural reef sites, as well as the location of the Palos Verdes Restoration Reef (artificial reef, AR; open circles)

2.2. Species abundance and diversity

We examined patterns in abundance and alpha diversity (richness and evenness) of fish, invertebrates, and macroalgae across site type (artificial versus natural), depth, and site location (island versus mainland). Comparisons between island and mainland were only made for natural reefs due to the lack of subtidal artificial reefs near islands in the region. For each artificial reef site and depth zone of natural reef sites, count densities (all taxa) and biomass densities (fish only) were averaged across the time series (between 3 and 8 yr, depending on site, Table S1). Averages included zeros in the case where a species was once observed at a site but not in a given transect. We then used multi-year density averages to calculate 2 metrics of alpha diversity: (1) species richness and (2) Simpson's diversity index. We used the nonparametric Kruskal-Wallis test to compare the SMB and PVR artificial reef complexes to mainland natural reefs at similar depths, followed by Dunn's post hoc test using the Holm method for multiple comparisons. Additionally, for natural reefs, we tested for significant differences in mean density or biomass between depth zones, and between mainland and island habitats using the same statistical testing framework. While marine protected areas (MPAs) were not the focus of this study, we compared patterns in abundance and diversity for sites within and outside of MPAs because human activity can impact depth zonation observed in reef ecosystems (Richardson et al. 2023).

2.3. Multivariate community analyses

We used principal coordinates analysis (PCoA) to visualize and interpret differences in community composition among artificial reef sites and depth zones of natural reef sites. PCoA maximizes the similarity between true dissimilarities and how these dissimilarities are displayed in ordination space (Anderson & Willis 2003). For multivariate visualizations and statistical analyses, we took the square root of all density values to reduce the weight of highly abundant species, and used Bray-Curtis dissimilarity to measure distance between sites (artificial reefs) and depth zones (natural reef sites). Bray-Curtis dissimilarity calculates percent difference in community composition, is robust to sampling error, and is commonly used in multivariate ecological studies (Barwell et al. 2015, Schroeder & Jenkins 2018). To compare differences between artificial reefs and natural reefs at comparable depths, we conducted permutational multivariate analysis of variance (PERMANOVA; Anderson 2017) using the 'adonis2' function of the 'vegan' package in R, version 4.2.1 (Oksanen et al. 2022, R Core Team 2022). We estimated the marginal effect of each term, therefore accounting for the contribution of other covariates when estimating coefficients and significance. PERMANOVAs were performed with 9999 permutations, and results were considered significant when $p < 0.05$. We also performed permutational multivariate analysis of dispersion (PERMDISP) to compare variance between site types (Anderson & Walsh 2013). We repeated these analyses for natural reefs alone to compare communities across the full range of depth zones and locations, and to compare natural reef sites within MPAs to those outside of MPAs. When PERMANOVAs revealed significant differences across depths of natural reefs, we conducted additional pairwise PERMANOVAs to compare each pair of depth zones. Finally, we calculated the average density of each taxon at each depth zone to identify the most abundant species at each depth and provide a high-level illustration of community zonation across reef locations and types.

3. RESULTS

Across 25 artificial reef sites, we identified many of the same taxa present on natural reefs in addition to 3 only observed during the study period on the artificial structures (44 fish [2 unique to artificial reefs], 50 macroinvertebrates [1 unique to artificial reefs], and 7 macroalgae) (Figs. 1 & 2b,c). Both SMB and PVR artificial reefs were dominated by blacksmith *Chromis punctipinnis*, and this damselfish was recorded at higher densities than at mainland natural reefs at similar depths (Fig. S2a). Additionally, PVR supported densities of kelp perch *Brachyistius frenatus*, and SMB reefs supported densities of barred sand bass *Paralabrax nebulifer* higher than those found on similarly positioned natural reefs. Fish biomass in SMB was dominated by barred sand bass, while opaleye *Girella nigricans* was most abundant on PVR. Giant sea bass *Stereolepis gigas*, kelp bass *Paralabrax clathratus*, blacksmith, and California sheephead *Bodianus pulcher* had consistently high biomass on both artificial and natural reefs (Fig. S2b). In general, artificial reefs across individual complexes supported similar species assemblages (Fig. S3). However, average biomass of fish at Hermosa Beach Artificial Reef was more than double that of other complexes due to the presence of a few high-biomass species (broomtail

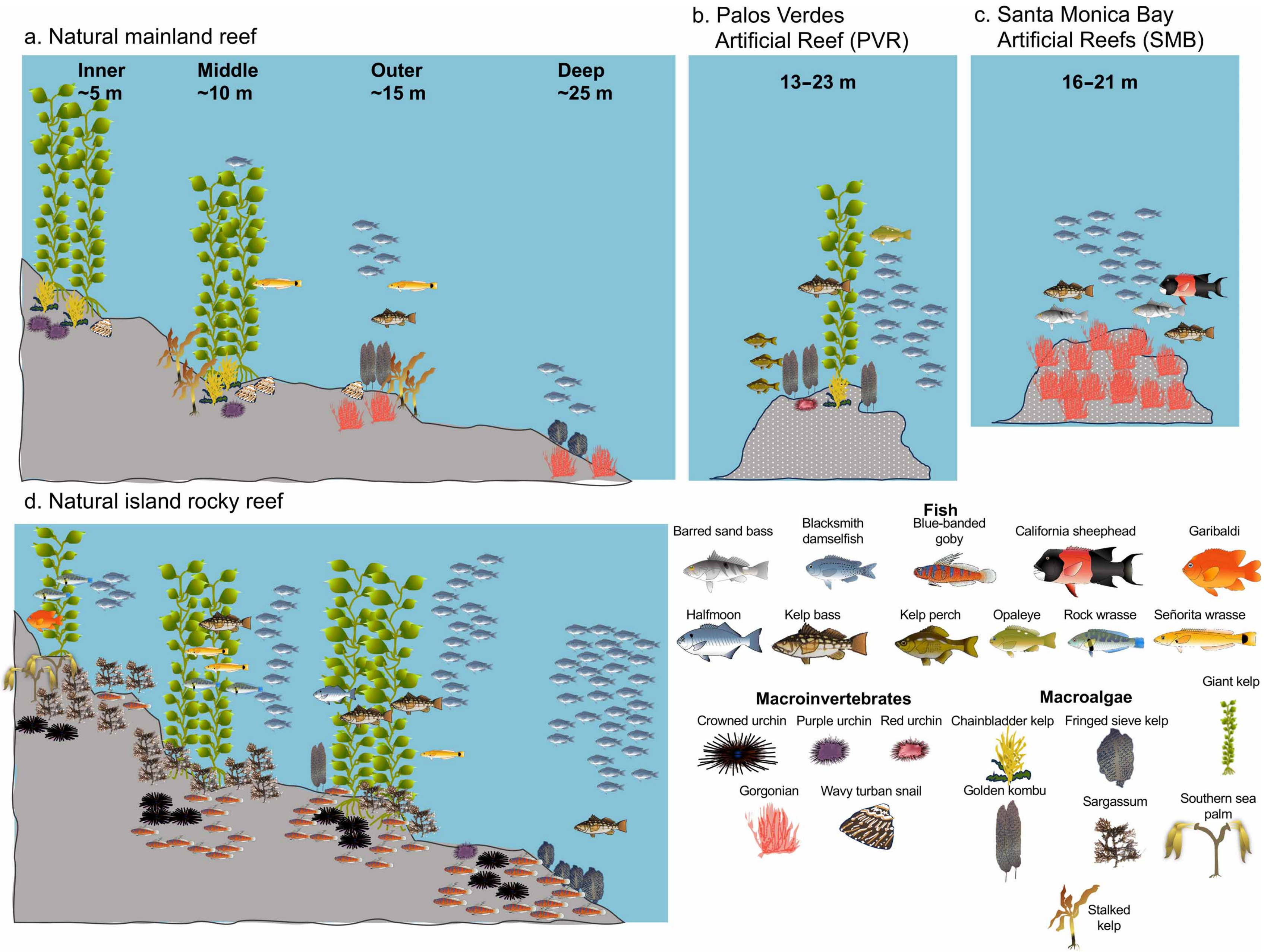

Fig. 2. Depth-based rocky reef community structure (based on count densities) in (a) natural mainland, (b,c) artificial mainland, and (d) natural island reefs. Frequencies of taxa displayed are based on average density observed at a given depth zone, reef type, and reef location. For fish, taxa at densities greater than 0.5 ind. 100 m^{-2} are included. For macroalgae and macroinvertebrates, taxa at densities greater than 0.2 ind. 100 m^{-2} are included. For exact density values of the most common species, see Figs. 4–6. Fish illustration credit: Larry Allen

grouper *Mycteroperca xenarcha* and giant sea bass) (Fig. S3b). In comparison, on 66 natural reef sites across the SCB, we recorded 69 fish, 103 macroinvertebrates, and 20 macroalgae taxa (Figs. 1 & 2a,d).

3.1. Species abundance, diversity, and community composition on artificial reefs

Fish density (both count and biomass-based) was higher on artificial reefs than on outer and deep natural mainland reefs (Figs. 3 & 4; Figs. S4 & S5a,d). However, artificial reefs supported similar numbers of fish species as mainland reefs at similar depths (Fig. 3; Fig. S5e). Count-based Simpson's diversity index at artificial reefs was similar to that observed at natural mainland reefs at similar depths, and the biomass-based Simpson's diversity index was consistent across all reefs surveyed (Fig. 3; Fig. S5h,k).

Macroalgae density at PVR was similar to densities found on natural reefs, while densities on SMB were significantly lower (near nonexistent) (Fig. 3; Fig. S5b). Average richness of macroalgae was lower on artificial reefs in comparison to natural reefs in similar settings, but richness at PVR was higher than at SMB (Fig. 3; Figs. S4 & S5f). Simpson's diversity index for macroalgae at PVR was similar to that observed at outer and deep mainland reefs, and higher than the diversity at SMB (although not significantly so) (Fig. 3; Figs. S4 & S5i). At PVR, golden kombu *Laminaria farlowii* and giant kelp dominated the community (Figs. 2 & 5).

Artificial reefs hosted a subset of the diversity of macroinvertebrate species on natural reefs. However, SMB reefs had far higher macroinvertebrate abundance than all other sites surveyed (Figs. 3 & 6; Fig. S5c). Crowned urchin *Centrostephanus coronatus* and wavy turban snails *Megastraea undosa* were less abundant, while the stalked tunicate *Styela montereyensis* was more common on artificial reefs than on natural reefs (Fig. 6). Due to a high density of golden gorgonians *Muricea californica*, macroinvertebrate densities at the SMB complexes were higher than at PVR, where the community was instead dominated by red urchin *Mesocentrotus franciscanus* (Fig. 6). The average number of taxa present on artificial reefs was significantly lower than on natural mainland reefs at similar depths (Fig. 3; Fig. S5g). Simpson's diversity index of macroinvertebrate communities on PVR was similar to that found on natural outer mainland reefs, but lower than that observed on natural deep mainland reefs (Fig. 3; Fig. S5j). Simpson's diversity index of macroinvertebrate communities on SMB artificial reefs was significantly lower than that found in natural reefs at similar depths (Fig. 3; Fig. S5j). Simpson's diversity index was higher for PVR than SMB artificial reefs, but not significantly so (Fig. 3; Fig. S3j).

Overall, artificial reefs supported significantly different community structure from natural reefs in similar settings (outer and deep zones of mainland reefs), although reef type only explained 9% of the variance, indicating substantial overlap ($F_{1,105} = 10.2$, $p < 0.001$; Fig. 7c). Variance differed between natural and artificial reefs, (PERMDISP, $F_{1,105} = 9.5$, $p = 0.003$; Fig. 7c), suggesting that differences in both composition and dispersion drove the disparity between the 2 reef types. Older-generation artificial reefs located in SMB supported distinct rocky reef communities from natural mainland reefs (outside of 95% confidence interval for mainland reefs), while the more recently constructed reefs of PVR supported communities more similar to natural mainland reefs (inside of the 95% confidence interval; Fig. 7c).

3.2. Species abundance and diversity across depth on island and mainland natural reefs

Patterns in fish abundance and diversity across depths varied between island and mainland sites (Fig. 3; Figs. S4 & S5). While overall fish density and biomass were higher at island sites (Fig. S4, Mann-Whitney *U*-tests, abundance: $W = 1619$, $p < 0.0001$, biomass: $W = 2628$, $p < 0.0001$), more fish taxa were represented on average at mainland sites ($W = 5907$, $p < 0.0001$), and average Simpson's diversity index was higher at mainland sites when weighted by count ($W = 6130$, $p < 0.0001$). At a finer scale, we found that island sites had significantly higher mean densities of fish than mainland sites in the middle, outer, and deep depth zones (Fig. 3; Fig. S5a). At island sites, average ± SD fish density and variability in fish density ranged from 35 ± 42 ind. 100 m^{-2} at inner depth zones to 108 ± 131 at deep depth zones. Mean fish density did not vary significantly across depth zones at mainland sites, nor did fish biomass density vary significantly across depth zones for either island or mainland sites. There was no difference in the mean number of fish taxa observed across depth zones at island sites. However, deep zones at mainland sites had significantly more fish taxa than inner and middle zones (Fig. 3; Fig. S5e). On average, significantly more fish taxa were represented at mainland sites than island sites (16.3 ± 4.4 vs. 13.7 ± 2.5). For both island and mainland sites, the count-based Simpson's

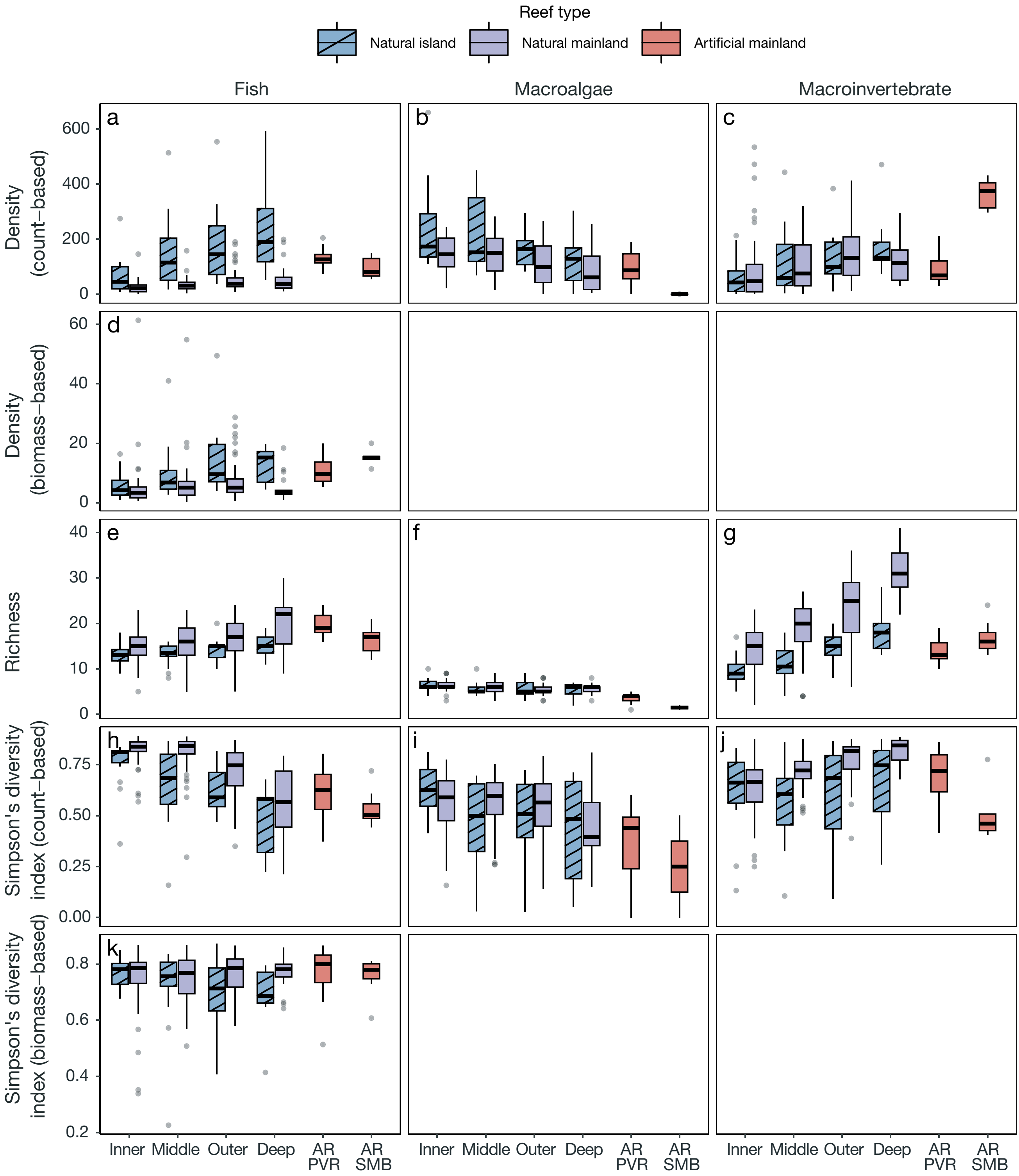

Fig. 3. Metrics of density, richness, and diversity for (a,d,e,h,k) fish, (b,f,i) macroalgae, and (c,g,j) macroinvertebrates across inner (n = 65, target depth = 5 m), middle (n = 64, target depth = 10 m), outer (n = 56, target depth = 15 m), and deep (n = 26, target depth = 25 m) zones, and artificial reefs (ARs) (PVR: Palos Verdes Restoration Reef: n = 18; SMB: Santa Monica Bay: n = 7) for both island (blue) and mainland (natural = purple, artificial = red) sites. Artificial reefs range from ~15 to 25 m depth. From top to bottom, metrics are density (count per 100 m^2), density (kg per 100 m^2), species richness, Simpson's diversity index (based on relative counts), and Simpson's diversity index (based on relative biomass). Points represent the averaged annual metric across all transects for a given site and zone. Count data were available for all taxa (#), biomass data (kg) were available for fish only (d,k). Median displayed as horizontal bar, interquartile range (IQR) as box, first and third quartile (Q1&Q3) ± 1.5 × IQR as whiskers, and outliers as points. See Fig. S5 for Dunn's post hoc test by group

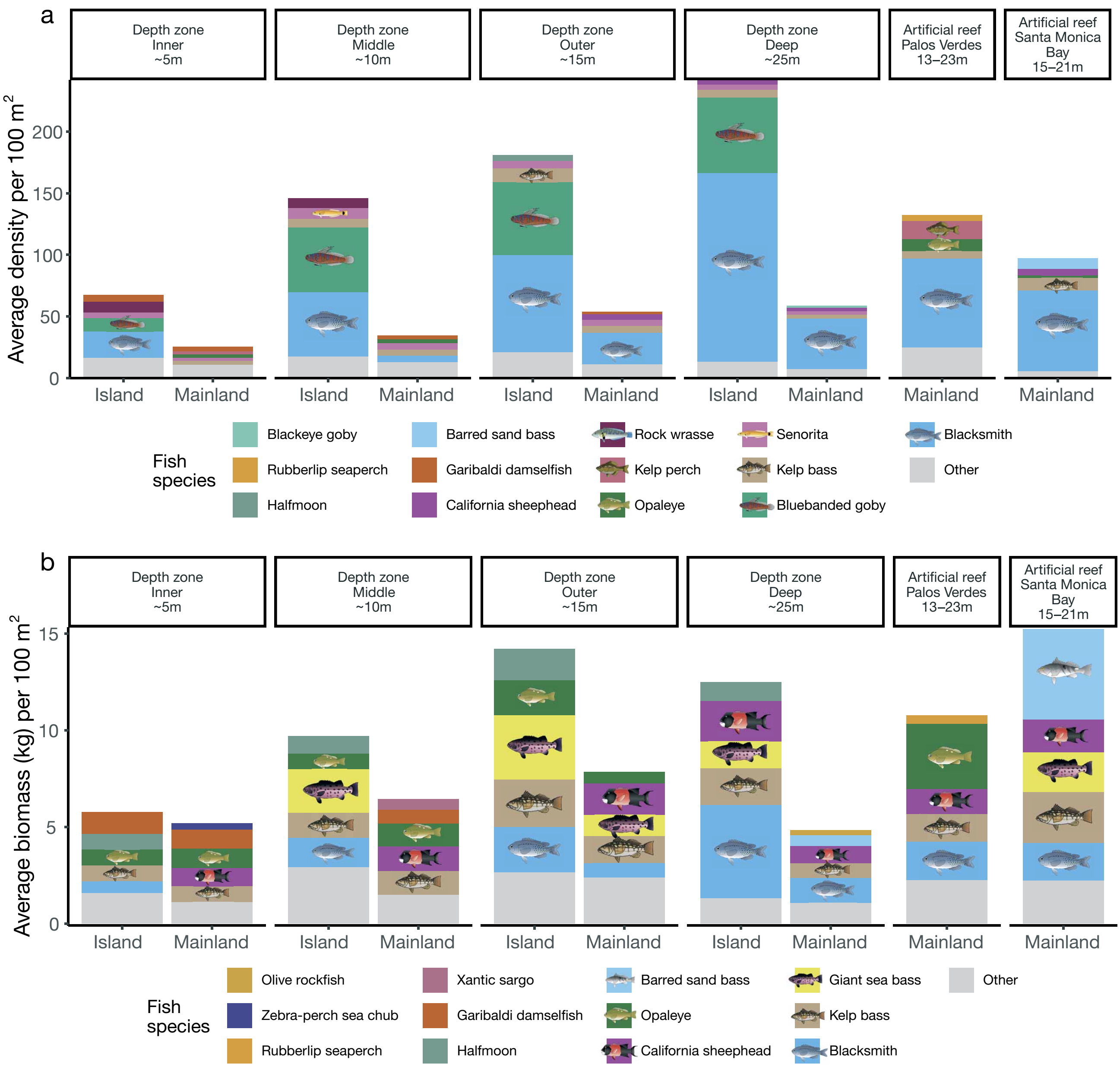

Fig. 4. Overall fish (a) density and (b) biomass, highlighting 5 species with the highest abundance for all depth zones and artificial reefs across island and mainland sites. For natural island sites, n = inner: 16, middle: 16, outer: 15, deep: 7. For natural mainland sites, n = 49, 48, 41, 19. For artificial reefs, Palos Verdes Restoration Reef (PVR) n = 18, Santa Monica Bay (SMB) n = 7. Species sorted in bars from least abundant (top) to most abundant (bottom) overall. Abundance of all other species summed into grey bars. Species icons of most abundant species were included when space permitted

diversity index was higher at shallower sites (Fig. 3; Fig. S5h). However, this pattern was not maintained for biomass-based Simpson's diversity index (Fig. 3; Fig. S5k). On mainland reefs, fish abundance was higher at sites within MPAs (abundance: $W = 3860$, $p < 0.0001$; biomass: $W = 4231$, $p < 0.0001$), and this difference was most pronounced in outer and deep zones (Fig. S6). However, there was no difference in richness or Simpson's diversity index (richness: $W = 2763$, $p = 0.57$, Simpson's diversity index for abundance: $W = 2520$, $p = 0.72$, Simpson's diversity index for biomass: $W = 2472$, $p = 0.58$). On island reefs, there were no differences in density, biomass, or richness between sites inside and outside the MPA (abundance: $W = 418$, $p = 0.36$; biomass: $W = 401$, $p = 0.54$; richness: 364, $p = 1$; Simpson's diversity index for abundance: $W = 360$, $p = 0.95$, Simpson's diversity index for biomass: $W = 338$, $p = 0.66$).

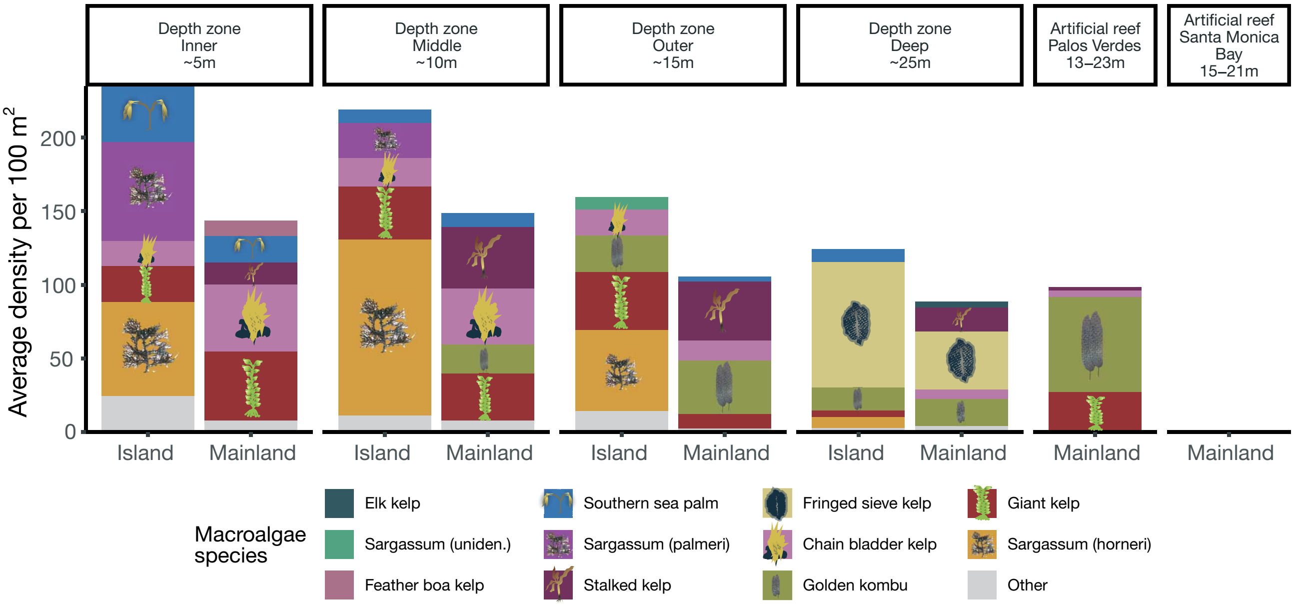

Fig. 5. Overall macroalgae density. Details as in Fig. 4

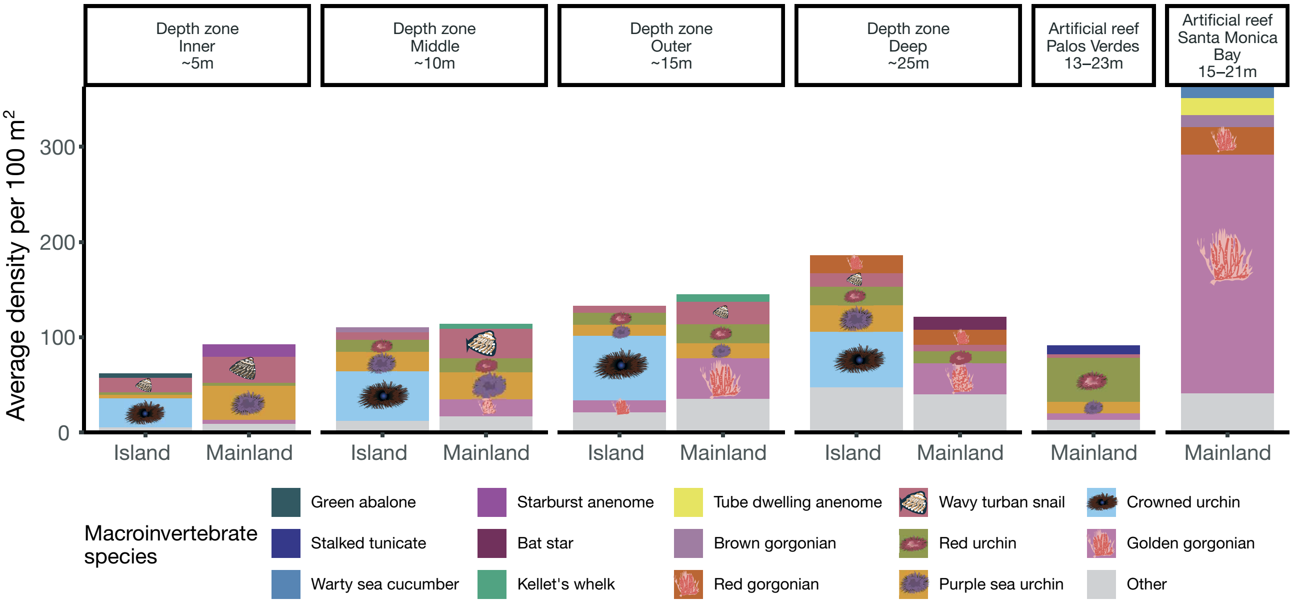

Fig. 6. Overall macroinvertebrate density. Details as in Fig. 4

Macroalgae abundance and richness declined with depth, but most comparisons in abundance and diversity metrics between depth zones for both island and mainland reefs were not significant. However, we observed significantly higher macroalgae richness on inner versus outer mainland reefs (Fig. 3; Fig. S5f). While Simpson's diversity index varied more across deeper sites than shallower sites, there were no significant differences in the average Simpson's diversity index across depth zones for sites at any location (Fig. 3; Fig. S5f). Overall, while mean macroalgae density was higher at island sites (Fig. S4, Mann-Whitney *U*-tests, $W = 2920$, $p < 0.001$), we found no difference in richness ($W = 4402.5$, $p = 0.67$) or in Simpson's diversity index between island and mainland sites ($W = 4326$, $p = 0.82$). There were no clear differences between macroalgae density and diversity across depth inside and outside MPAs (Fig. S6).

Overall, there was no difference in macroinvertebrate density between island and mainland sites (Fig. S4, Mann-Whitney *U*-tests, $W = 4310$, $p = 0.86$), but both richness ($W = 6648$, $p < 0.0001$), and average

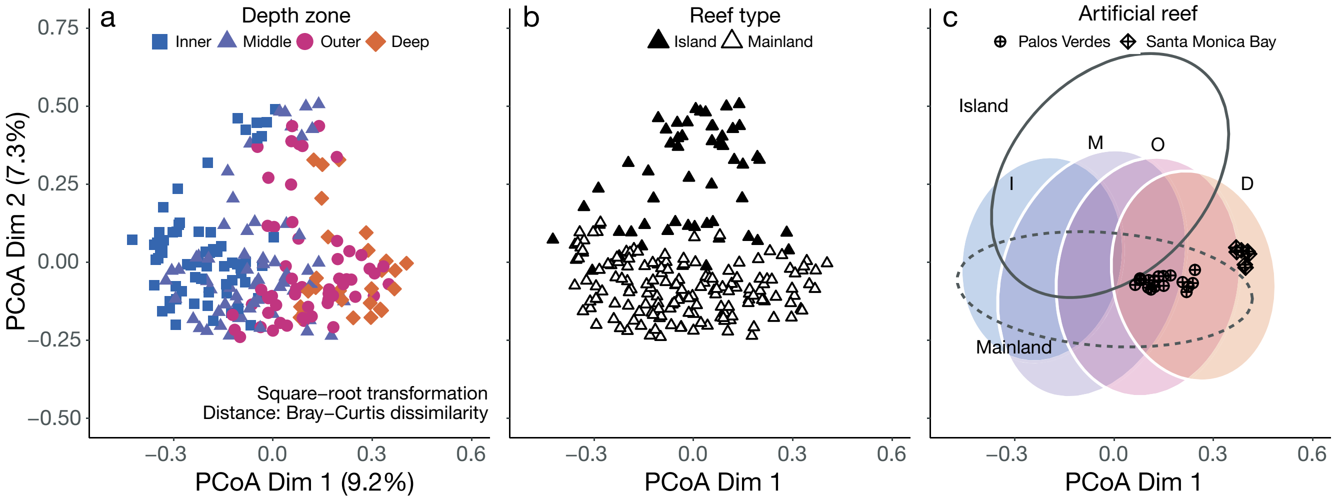

Fig. 7. Principal coordinates analysis (PCoA) plot illustrating the distribution of site rocky reef community assemblages (i.e. pooled fish, macroinvertebrate, and macroalgae). (a,b) Points represent individual natural reef sites, colored by depth zone (a) or reef type (b). (c) Location of Palos Verdes (PVR) and Santa Monica Bay (SMB) mainland artificial reef sites in comparison to the 95% confidence interval for all natural sites from each depth zone (colored ellipses, I: inner; M: middle; O: outer; D: deep) and reef type (outlined ellipses)

Simpson's diversity index were higher at mainland sites ($W = 5560$, $p < 0.001$). While deeper sites tended to have more macroinvertebrates, most comparisons in abundance between depth zones for both island and mainland reefs were not significant. However, we did observe significantly more macroinvertebrates on outer natural mainland reefs compared to inner reefs (Fig. 3; Fig. S5c). On mainland reefs, macroinvertebrate richness was significantly higher in deep zones in comparison to inner and middle zones (Fig. 3; Fig. S5g). Simpson's diversity index for macroinvertebrates at outer and deep mainland sites was higher than at inner mainland sites, but did not differ across depth zones at island sites (Fig. 3; Fig. S5j). There were no clear differences between macroinvertebrate density and diversity across depth inside and outside MPAs (Fig. S6).

3.3. Community composition across depths on natural reefs

Community composition of natural rocky reefs in SCB (i.e. pooled fish, macroinvertebrate, and macroalgae) differed significantly by depth zone (PERMANOVA, $F_{3,207} = 16$, $R^2 = 0.19$, $p < 0.001$; Fig. 7a), and location (mainland vs. island; $F_{1,209} = 34$, $R^2 = 0.14$, $p < 0.001$; Fig. 7b). Additionally, the relationship between depth zone and community composition varied between island and mainland habitats (depth zone × location interaction: $F_{3,203} = 2.3$, $R^2 = 0.02$, $p < 0.001$). By repeating PERMANOVA for each pairwise combination, we found significant differences between all depth zones ($p < 0.001$; Fig. 7a). Differences between depth zones and reef locations were explained by differences in community composition, not by differences in dispersion (PERMDISP ANOVA; depth zones: $F_{3,207} = 0.45$, $p = 0.72$; reef location: $F_{1,209} = 0.50$, $p = 0.48$). Reefs within MPAs exhibited significantly different community composition than reefs outside MPAs, and this difference was not explained by differences in dispersion. However, MPA status only explained 3% of the variation observed (PERMANOVA, $F_{1,209} = 6.4$, $p < 0.001$; PERMDISP ANOVA, $F_{1,209} = 0.76$, $p = 0.38$; Fig. S7a). The significant structure we identified across depths and reef locations was maintained when multivariate analyses were repeated for taxa-specific communities. Additionally, the amount of variance explained by depth zone, location, and their interaction was consistent across taxa (fish: depth zone = 18%, location = 11%, interaction = 2%; macroalgae: 17, 14, 2.9%; macroinvertebrates: 16, 14, 2.2%) (Fig. S8).

Abundance-based fish density increased with depth, primarily due to increases in blacksmith for mainland sites and both blacksmith and the cryptic bottom-dwelling bluebanded goby *Lythrypnus dalli* for island sites (Fig. 4a). However, when accounting for biomass, there were no clear dominant species for either mainland or island reefs (Fig. 4b). Rather, sargo *Anisotremus davidsonii*, blacksmith, opaleye, Garibaldi *Hypsypops rubicundus*, barred sand bass, and giant sea bass all exhibited high relative biomass in at least 1 depth zone. Kelp bass was common across all depth zones. California sheephead was common across depth zones on mainland sites while blacksmith and halfmoon *Medialuna californiensis* were both common across depth on island sites.

Giant kelp, the foundational species in southern California rocky reef ecosystems, was common across all but deep mainland reef sites (Fig. 5). Devil weed *Sargassum horneri* (a nonnative member of the genus) was absent from mainland sites, but dominated the macroalgae community in the inner, middle, and outer zones of island sites. Fringed sieve kelp *Agarum fimbriatum* was abundant at deep island and mainland sites. Stalked kelp *Pterygophora californica* was abundant across depth zones at mainland sites, but was rare at island sites. Chain bladder kelp *Stephanocystis osmundacea* was abundant across all depth zones in mainland habitats and across inner to outer zones on island sites (Fig. 5).

As mean macroinvertebrate density, richness, and diversity increased with depth, the dominant species shifted (Fig. 6). On the mainland, purple sea urchins *Strongylocentrotus purpuratus* and wavy turban snails dominated the community at inner sites. Purple and red urchins were both common between the middle and deep zones. Gorgonians began to appear frequently (brown: *Muricea fruticosa* and golden: *M. californica*) in the outer zone, and these colonial cnidarians were highly abundant in deep zones. For island sites, inner zones were dominated by crowned urchin and wavy turban snails. Crowned urchins remained dominant across depth zones at the islands, with red and purple urchins, snails, and red gorgonians *Leptogorgia chilensis* increasing in relative abundance with depth.

4. DISCUSSION

Here, we show that artificial reefs in the SCB can support subtidal communities that resemble those on nearby natural rocky reefs at similar depths. Yet, even within a 30 km radius, community composition on artificial reefs can differ dramatically — particularly for macroinvertebrates and macroalgae — highlighting the importance of local context in marine infrastructure planning and implementation. Spatial variation in natural reef community composition provides critical insights for designing effective artificial reefs in nearshore ecosystems. In subtidal environments, strong environmental gradients occur over small spatial scales (Twist et al. 2020). This characteristic is true of California's subtidal rocky reef ecosystems and is reflected in the differences we observed in species richness, diversity, and community composition across a relatively narrow depth gradient. At the site level, these patterns vary by taxa group, with macroalgae often exhibiting opposite trends than fish and invertebrates. Additionally, our findings support previous research suggesting that zonation arising within island reefs is distinct from that observed on mainland reefs (Benedetti-Cecchi et al. 2003).

In this study, artificial reefs mostly built from quarry rock and natural reefs at comparable depths supported similar rocky reef communities. For fishes, there were higher densities with similar diversity on the artificial versus natural reefs. The planktivorous blacksmith dominated fish communities across all reefs. However, we observed stark and important differences in overall community diversity and composition between artificial reefs built in the 1960s–1980s in SMB and those built off the Palos Verdes Peninsula in 2020 (PVR) (Williams et al. 2022). The former are located on soft bottom habitat far from large natural reefs — reflective of artificial reefs built in California and globally during the second half of the 20th century (Lewis & McKee 1989). They were intentionally placed in nonoptimal locations (soft bottom habitat) to avoid negatively impacting natural reefs. These earlier generation reefs were designed as fishing reefs, optimizing attraction to enhance the sport fishing industry (Carlisle et al. 1963), and in the case of SMB, were located in an area with limited light availability and relatively warm water (Schroeter et al. 2015). These reefs have supported high biomass of barred sand bass unseen on any other reefs in the SMB, potentially a result of this species' preference for deeper ecotonal habitats that are abundant on the SMB artificial reefs (Anderson et al. 1989), and proximity to spawning aggregations (Erisman et al. 2011). While SMB artificial reefs supported higher fish densities and biomass than natural mainland reefs, they were associated with more divergent communities of macroalgae and macroinvertebrates than natural mainland reefs. In contrast to natural reefs, these reefs did not support macroalgae and were dominated by a single macroinvertebrate taxon — gorgonians — possibly due to competitive release from algae.

Unlike the SMB artificial reefs, PVR (Williams et al. 2022) hosted species at densities similar to natural reefs. The recently constructed reef was built adjacent to natural rocky reef habitat to enhance dispersal opportunities and within a cold nutrient-rich zone near the shelf break to promote the growth of giant kelp. As opposed to SMB, PVR was built to restore lost habitat and increase fish and invertebrate production. While macroalgae were nearly absent on the

SMB artificial reefs, we observed that PVR supported similar densities to natural mainland reefs at the same depth stemming from successful giant kelp and golden kombu establishment. We observed lower macroalgae diversity on PVR than on natural reefs; however, the reef has only been in existence since 2020, limiting the duration of time (<3 yr) that macroalgal species have had to become established. However, despite its early successional stage, we observed higher macroalgae density and diversity on PVR than on the SMB artificial reefs. In contrast, macroinvertebrate density was over 2 times higher on SMB artificial reefs than on natural reefs at the same depth, fully driven by high densities of gorgonians (octocorals of the order Malacalcyonacea) — most notably, the golden gorgonian. While gorgonians were also common on natural reefs at northern sampling sites in the general area of the SMB artificial reefs, previous research supports that gorgonians excel at colonizing human-made structures (Zeevi Ben-Yosef & Benayahu 1999). Macroinvertebrate densities on PVR were more reflective of densities found on natural reefs, although we observed a higher relative proportion of red urchins. This finding upholds previous work noting that artificial reefs could be used as a tool to maintain catch and access in California's lucrative red urchin fishery (California Department of Fish and Wildlife 2019). Overall, we found that smaller reefs built to boost recreational fishing opportunities located on soft bottom habitat far from large natural reefs supported distinctive communities from larger artificial reefs built with the intention of restoring complex rocky reef communities of the SCB. However, we note that PVR is a reef in early successional phases. Observations made within the first 3 yr post construction may not be representative of its long-term trajectory (Kraufvelin et al. 2023).

The artificial reefs surveyed for this study were all located near the mainland and at moderate subtidal depths. However, patterns in natural reef habitats across SCB more broadly can help us anticipate the characteristics of rocky reef communities that will establish on novel human-made structures across the region. For both fish and macroinvertebrates, density and richness were higher in deeper reef habitats (~15–25 m). Deeper reef zones have a larger water column, and therefore provide more 3-dimensional habitat for fish to exploit. Niche opportunities also increase for fish with depth as the midwater zone expands (Larson & DeMartini 1984). Depth preferences of rocky reef macroinvertebrates are highly variable (Kato & Schroeter 1985, Claisse et al. 2013, Hovel et al. 2015), but the observed increase in density with depth was largely driven by an increase in gorgonian density.

In contrast, macroalgae densities, which are highly limited by light accessibility, were highest at the shallowest sites, matching previous observations across the northeast Pacific (Aleem 1973, Konar et al. 2009). Regionally, reefs with a high abundance of canopy-forming macroalgae tend to support more diverse fish communities overall. However, within those reefs, fish density is often greatest at the edges of the kelp canopy and in areas where kelp density is relatively low (Willis & Anderson 2003). High-density planktivorous fishes such as blacksmith benefit from the increased availability of planktonic food resources near the kelp forest edge where water flow and mixing can concentrate prey (Foster & Schiel 1985). Similarly, gorgonians, which orient themselves perpendicular to dominant current flows to maximize plankton capture (Grigg 1977), thrive in deeper habitats where lower kelp densities allow for favorable water flow conditions. In contrast with fish and macroinvertebrates, macroalgae richness was relatively consistent across depth.

On deeper reefs, fish and macroalgae communities were typically dominated by 1 or 2 species, resulting in low evenness. In contrast, macroinvertebrate communities exhibited greater evenness in their composition at depth when compared to shallow zones. The evenness of macroinvertebrate taxa we observed on natural reefs stands in contrast to observations in high-latitude rocky reefs in the Pacific where patterns in zonation can be driven by a single species (Konar et al. 2009), and also in contrast to our observations at the SMB artificial reefs that were dominated by gorgonians. In the case of fish, we were able to compare abundance-based versus biomass-based metrics. Low evenness in fish diversity in the outer and deep depth zones was primarily driven by blacksmith, a high-density small-bodied species, and therefore this trend was not reflected in the biomass-based metrics (Bray 1980).

Differences in community composition with depth were discernible in multivariate analysis, but not completely distinct. As predicted, adjacent depth zones exhibited more similar community composition than distant zones. There was no overlap between the shallowest and deepest zones, suggesting that we may have found more distinct zonation if we had looked over a larger depth range (Parsons et al. 2016). Depth zones of island reefs shared more common community composition than mainland sites, which can be attributed to higher habitat heterogeneity across depths at mainland sites. Because of the shallow slope associated with mainland reefs, depth zones can be 100s of meters apart. At the same time, mainland reefs also tend to be less cohesive and frequently intersect with soft bottom habitat. In contrast, depth zones of steep island sites are in closer proximity to each other, and only past the deep depth zone (and therefore past our maximum sampling depth) does the habitat transition to soft bottom (Pondella et al. 2015). Sampling methods that can safely capture this ecotone (e.g. remotely operated vehicles) may reveal more extreme compositional differences; however, *in situ* biodiversity surveys are a more effective tool for monitoring diversity in comparison to other methods (Jessop et al. 2022). Similar to previous studies, we found that community zonation varied with the level of human activity (Richardson et al. 2023); however, MPA status explained a very low proportion of the variation observed.

Variability in fish density across depth was largely driven by the abundance of the blacksmith, an abundant planktivorous reef-associated species. Blacksmith increased in density with depth on both island and mainland sites, reaching nearly 500 ind. 100 m^{-2} at deep sites around Santa Catalina Island and nearly 200 ind. 100 m^{-2} at deep sites around the Palos Verdes Peninsula off the mainland. We expect that the high densities observed at depth are related to the species' preference for incurrent reef boundaries with high flow and plankton abundance (Hobson & Chess 1976, Bray 1980, Bray et al. 1986). Blacksmith tend to feed outside the kelp canopy where there is greater current flow and corresponding flux of zooplankton (Bray 1980). This area typically coincides with the outer and deep depth zones when giant kelp is present. Similar to the role they play on nutrient-deprived tropical reefs (Roopin et al. 2011), planktivorous fish play a critical role on temperate rocky reefs by producing urea (Bray et al. 1986, Shrestha et al. 2025). Weak upwelling in the SCB in the late summer and fall leads to low nitrate concentrations, during which time blacksmith help maintain nitrogen available for kelp to absorb (Lees et al. 2024). Artificial reefs designed to support both kelp and fish densities can trigger a positive feedback loop where increased biogenic habitat provides refuge for fish, supporting a larger blacksmith population that subsequently releases more ammonia back into the habitat for kelp to absorb (Layman & Allgeier 2020, Shrestha et al. 2025). In addition to providing readily accessible nitrogen to rocky reef ecosystems, blacksmith also serve as a prey source for larger-bodied fish such as kelp bass and therefore act as a critical vector for energy transfer between the pelagic zone and rocky reef ecosystems (Johnson et al. 1994, Puckeridge et al. 2021).

On average, macroalgae density was higher on island than mainland reefs, and this dichotomy was especially pronounced at shallow depths with higher light availability. The high abundance of kelp we observed at island reefs may be linked to water quality, which is typically better around islands due to limited runoff and pollution (Conversi & McGowan 1994). Island reefs also hosted especially dense populations of the brown macroalgae genus *Sargassum*. Similar to previous characterizations of the species' natural history in the SCB, we observed highest densities at intermediate subtidal depths where individuals take advantage of moderate wave action and light attenuation (Marks et al. 2018). While the native *S. palmeri* outnumbered the invasive devil weed *S. horneri* in the most shallow zones, devil weed outnumbered the native *Sargassum* in the deeper zones. Devil weed dominated the macroalgae community at intermediate depths on island reefs, while fringed sieve kelp *Neoagarum fimbriatum* dominated at the deepest depths surveyed.

Native to western Japan and South Korea, devil weed was first identified in the SCB in 2003 and is now established along the SCB and into Baja California (Mexico) (Marks et al. 2015). The species struggles to establish in stable and established communities, and is therefore in low abundance in well established kelp forests (likely due to competition with giant kelp) and in urchin barrens (likely due to predation by urchins) (Zhang et al. 2017, Caselle et al. 2018, Sullaway & Edwards 2020). However, the nonnative species forms large mats within rocky reefs in a transitional state (e.g. MPAs designated in the early 2000s) where seemingly neither giant kelp nor urchins are at high enough abundance to exclude devil weed. Across all depth zones, the invasive *Sargassum* was at least an order of magnitude more common on islands than on the mainland, consistent with its preference for the warmer waters present around the more southern Channel Islands included in this study (Marks et al. 2015). While artificial reefs can act as a haven for nonnative aquatic species and therefore facilitate range expansions, we did not observe devil weed on artificial reefs in the SCB (Sheehy & Vik 2010). Despite its role in widespread landscape change in southern California rocky reef ecosystems, devil weed appears to be a disturbance opportunist rather than a driver of community transformation and has relatively limited impacts on higher trophic levels (Ginther & Steele 2020).

In the SCB, the differences in patterns of diversity and species composition across depths are a function of island biogeography, habitat heterogeneity, local oceanography, and proximity to human activity. Richness of all taxa was higher on the mainland. This observation was consistent across depth zones, although most pronounced in deep zones for fish and macroinvertebrates. We hypothesize that reduced dispersal opportunities to and among island sites, coupled with a heterogenous mainland shoreline, drove this island/mainland dichotomy common to the island biogeography literature (MacArthur & Wilson 1967, Sandin et al. 2008). There were over 20 taxa that we only observed on mainland reefs, including multiple species of rockfish, soft bottom species such as the thornback ray *Platyrhinoidis triseriata* and black croaker *Cheilotrema saturnum*, and estuarine species such as the bay pipefish *Syngnathus leptorhynchus*. Proximity to diverse habitats present on the mainland coast likely permit more niche differentiation and therefore higher richness (Ebeling & Larson 1980, Pondella & Allen 2000). We also observed greater macroinvertebrate and macroalgae richness on the mainland. However, the difference in richness was least pronounced for macroalgae, which require hard substrates to anchor to the seafloor and therefore cannot exploit the soft bottom habitats abundant in the shallow subtidal of the mainland (Duarte et al. 2022).

On rocky reefs, population dynamics, resource availability, and feeding behavior vary diurnally and seasonally (McIlwain et al. 2011, Cyronak et al. 2020). Mobile species can adjust their depth over the course of a day, and many taxa exhibit changes in abundance and position over the course of a year. Therefore, the patterns we describe in species abundance, diversity, and community composition across depth are most representative of daytime conditions in the summer and fall. However, because species richness and abundance on reefs are often higher during the day (Azzurro et al. 2007), these surveys capture a substantial portion of reef diversity. As noted earlier, there are currently no artificial reefs in the shallow subtidal zone or around offshore islands in the study region. Based on the depth-related patterns observed in this study, we expect that communities on new artificial structures placed in these areas would differ from those in the deeper subtidal habitats where artificial reefs are currently located in southern California.

5. CONCLUSIONS

The footprint of marine infrastructure is expanding in southern California due to an increased reliance on marine resources and renewed interest in artificial reef development as a tool for restoration (Institute for Applied Economics 2020, California Department of Fish and Wildlife 2024). Globally, most artificial reefs are constructed at depths similar to those surveyed in this study, making our findings broadly applicable for setting baseline expectations in artificial reef community analyses (Ramm et al. 2021). Proximity to natural reef habitat, complexity, design criteria, and environmental conditions impact species abundance and diversity on artificial reefs (Ambrose & Swarbrick 1989, Granneman & Steele 2015, Tsiamis et al. 2020). Our findings reveal depth-driven shifts in abundance and diversity across Southern California rocky reefs, although the magnitude and nature of these shifts vary by taxon.

In the context of ongoing environmental change, documenting baseline ecological patterns is increasingly critical for assessing the resilience of dynamic and at-risk ecosystems. An understanding of depth associations for a diverse array of rocky reef species can improve detection of depth shifts associated with temperature, oxygen availability, and direct human impacts, which have already been observed across taxa (Meyer-Gutbrod et al. 2021, Richardson et al. 2023). The persistence of giant kelp forests in the SCB remains uncertain, as persistent runoff and rising ocean temperatures pose significant challenges (Carr & Reed 2016, Berberian et al. 2024). These findings highlight the importance of aligning artificial reef design with ecological objectives to ensure that novel structures support biodiversity and resilience in a rapidly changing marine environment.

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