Rhodolith structural loss decreases abundance, diversity, and stability of benthic communities at Santa Catalina Island, CA

Scott S. Gabara[1,2,3,*], Scott L. Hamilton[1], Matthew S. Edwards[2], Diana L. Steller[1]

[1]Moss Landing Marine Laboratories, 8272 Moss Landing Rd., Moss Landing, CA 95039, USA
[2]Department of Biology & Coastal Marine Institute Laboratory, San Diego State University, San Diego, CA 92182, USA
[3]Coastal and Marine Sciences Institute, Davis, CA 95616, USA

ABSTRACT: Species that increase habitat structural complexity often have a disproportionate influence on their ecosystems. Rhodoliths are bed-forming unattached coralline algae which increase benthic structural complexity and enhance biodiversity in coastal soft-bottomed ecosystems worldwide. Consequently, their degradation due to anthropogenic disturbance, such as crushing from boat mooring chains, may lead to reduced biodiversity and ecosystem functioning. To examine how anthropogenic disturbance impacts rhodolith community dynamics, we used a comprehensive sampling and analytical approach to compare macroalgal, invertebrate (infauna and epifauna), and fish assemblages between rhodolith beds and adjacent mooring-disturbed crushed rhodolith sand. Sampling was conducted during 2 sampling times across 3 sites at Catalina Island, CA, USA. Our results demonstrate that the more heterogeneous structure provided in less disturbed rhodolith beds supported greater community richness and abundances than crushed rhodolith sands. Specifically, disturbance-related rhodolith structural loss was associated with significantly reduced richness of invertebrates and abundance of macroalgae, invertebrates, and fish. In particular, deposit-feeding infaunal tanaids were far more abundant in rhodolith beds and drove much of the difference in invertebrate abundance between habitats. Further, spatiotemporal variation in the infaunal invertebrate assemblages was 54 % lower in the rhodolith beds than crushed rhodolith sand, suggesting that rhodolith beds support more stable communities. Our results suggest that structured rhodolith bed habitats support more abundant, diverse, and stable benthic communities than do disturbed rhodolith sand habitats. Better management of rhodolith ecosystems and the factors that disturb them could help maintain coastal biodiversity and stability.

KEY WORDS: Community structure · Habitat complexity · Maerl · Rhodolith · Disturbance · Foundation species · Coralline algae

INTRODUCTION

High biodiversity is often associated with increased habitat structural complexity in both terrestrial (e.g. Simpson 1964) and marine (e.g. Ormond et al. 1997, Kamenos et al. 2004b,c) ecosystems. This occurs, at least in part, as complex habitats alter environmental parameters (Bruno & Bertness 2001, Levin et al. 2010) and stabilize predator–prey relationships (Kamenos

et al. 2004c). Species that increase habitat complexity often play important roles in how their ecosystems function. For example, as the primary habitat-forming structure in some ecosystems, foundation species can transform 2-dimensional homogeneous landscapes into more complex 3-dimensional ones that provide a greater array of microhabitats (Simpson 1964, Dayton 1972, Bruno & Bertness 2001). By modulating resource availability through their structure, autogenic ecosys-

tem engineers can also serve a food provision role for communities (Jones et al. 1994). Therefore, evaluating the relationships between foundation species and their associated communities can help us understand how their losses might impact larger patterns of biodiversity across a range of habitats.

In marine systems, kelps (Graham 2004, Schiel & Foster 2015), salt marsh plants and sea grasses (Orth et al. 1984, Bertness & Hacker 1994, Bertness et al. 1999, Beck et al. 2001), mangroves (Nagelkerken & Faunce 2008, Nagelkerken et al. 2008, 2010), corals (Luckhurst & Luckhurst 1978, Alvarez-Filip et al. 2009) and rhodoliths (Kamenos et al. 2004b,c, Graham et al. 2016) have all been identified as important ecosystem engineers in their respective environments. Species within these groups provide benefits to their communities by creating structurally-complex habitats that reduce environmental and predation stress, enhance retention of propagules and particulates, increase the supply of resources, and potentially serve as food (Bruno & Bertness 2001, Graham 2004). For example, in the tropics and subtropics, mangrove prop-roots and pneumatophores create complex hard structures in otherwise soft sediment environments that support greater assemblages of marine plants, algae, invertebrates, and fishes (reviewed in Nagelkerken et al. 2008). Likewise, the interstitial spaces between the branches of geniculate (Kelaher et al. 2001), and non-geniculate (De Grave & Whitaker 1999) coralline algae in temperate, subtropical, and tropical systems similarly provide habitat and refuge for a variety of macroalgae and invertebrates.

In coastal California, USA, kelp forests support highly diverse assemblages of macroalgae, invertebrates, and fishes, and their storm-induced losses can result in shifts to low-diversity barren grounds that are dominated by one or a few species of crustose coralline algae (Ebeling et al. 1985). This, in turn, can lead to reduced abundances of primary consumers that shift their diets to less productive phytoplankton phytodetritus (Graham 2004). Consequently, changes in the distribution and abundance of such foundation species can have far-ranging impacts on local communities, energy fluxes, decomposition rates, carbon sequestration, and the magnitude of nutrient subsides exported to adjacent systems (reviewed in Ellison et al. 2005). The overall influence of foundation species on the ecosystems they support is generally related to their persistence, the strength with which species associate with them, and the potential for functional redundancy of their role (Witman 1985, Bertness & Hacker 1994, Shelton 2010).

Rhodoliths are free-living red coralline algae (Order Corallinales) that have a world-wide distribution (Foster 2001). When aggregated, they create beds that provide hard complex biogenic structure (i.e. interstitial branch spaces) over what would otherwise be a soft sedimentary benthos (Foster 2001, Steller et al. 2003, Foster et al. 2007). Consequently, coralline algal rhodoliths may be considered foundation species that enhance larval settlement and metamorphosis (Steller & Cáceres-Martínez 2009), provide refuge from predation (Kamenos et al. 2004b,c), aggregate food resources (Grall et al. 2006), retain waterborne and algal detritus (Grall et al. 2006), and reduce water flow which thereby increases larval retention (Steller et al. 2003). As a result, these beds generally support greater species abundance, richness, and diversity than nearby sedimentary habitats (Cabioch 1968, Bosence 1979, De Grave 1999, Steller et al. 2003). Less well understood is how disturbance-induced changes to rhodolith structural complexity within these beds impact their associated communities.

Descriptions of rhodolith bed community composition are increasing globally in areas including Alaska (e.g. Konar et al. 2006) and California (Tompkins & Steller 2016) in the USA, the Gulf of California, México (e.g. Steller et al. 2003, Foster et al. 2007, Riosmena-Rodríguez et al. 2010), Brazil (e.g. Villas-Boas 2014), the Central Mediterranean (e.g. Sciberras et al. 2009), the North Eastern Atlantic (e.g. Keegan 1974, Bosence 1979, Grall et al. 2006), and the South Eastern Atlantic (e.g. Amado-Filho et al. 2012, Figueiredo et al. 2012). Previous studies have described the biodiversity of dominant species and their abundances in rhodolith (also known as maerl) bed communities. However, most of these studies are limited in spatial and temporal scope, and descriptions of entire community assemblages are lacking. While some studies describe temporal changes in secondary algal cover (Piazzi et al. 2002, Steller et al. 2003, Amado-Filho et al. 2010, Pascelli et al. 2013), few assess temporal changes in overall community composition, especially for higher trophic level predators such as fishes (but see Foster et al. 2007, Neill et al. 2015, Sheehan et al. 2015a). For example, in a study describing rhodolith bed habitat for 7 beds at Santa Catalina Island, California (hereafter referred to as Catalina), macroalgal and macroinvertebrate communities were characterized in 2 beds, both experiencing 2 anthropogenic disturbance levels, revealing that mooring disturbance reduced floral and faunal richness and abundance (Tompkins & Steller 2016). However, it remains unclear if and how the disturbance impacts the entire

community, including the assemblages of macroalgae, infaunal invertebrates, epibenthic invertebrates, and fishes. This information gap is important given that chronic disturbances from boat mooring chains and spreader lines have reduced live rhodolith cover in these beds, diminishing habitat structural complexity (Tompkins 2011, Tompkins & Steller 2016).

The overarching objective of this study was to compare spatiotemporal patterns of community composition in rhodolith beds and adjacent crushed rhodolith sands at Catalina. To address this, we asked the following 3 questions: (1) does community composition differ between rhodolith-based habitats with varying disturbance levels, (2) do the communities vary over time and space, and (3) which taxa drive the differences in community composition among habitats, sampling times, and sites? This study is the first comprehensive quantitative description of the macroalgae, invertebrate, and fish communities in rhodolith beds in southern California. It provides baseline information on spatial and temporal patterns of this ecosystem and how rhodolith degradation may impact coastal biodiversity.

MATERIALS AND METHODS

Study site

Catalina is part of the Channel Islands archipelago off the Southern California coast. The island sits in a northwest–southeast orientation and is exposed to warm water from the Southern California Countercurrent. Diverse and productive kelp beds propagate over rocky reefs and dominate much of the nearshore subtidal habitats. Recently, the locations and cover of live and dead rhodolith thalli *Lithothamnion australe* Foslie were described for 7 rhodolith beds on the leeward side of the island (Tompkins & Steller 2016). These beds, located in protected bays, range in depth from 4 to 21 m and are heavily impacted by anthropogenic activities. In particular, physical disturbance from boat mooring chains have fragmented the beds into patchy aggregations of live rhodoliths among dead (non-pigmented) crushed rhodolith sands (Gabara 2014, Tompkins & Steller 2016).

Sampling design

To quantify differences in community composition between live rhodolith beds and crushed rhodolith sands at Catalina, the benthos within 3 rhodolith beds and 3 adjacent crushed rhodolith sand habitats were surveyed by divers during April and December 2013. The 3 rhodolith bed survey sites were randomly selected from the 7 beds described by Tompkins (2011). These sites, aligned from north to south, are Cherry Cove (6.4–8.2 m depth), Isthmus Cove (5.5–6.4 m), and Avalon Harbor (7.6–11.0 m; Fig. 1). Rhodolith bed sampling locations were defined as areas with >50% cover of live rhodoliths, while adja-
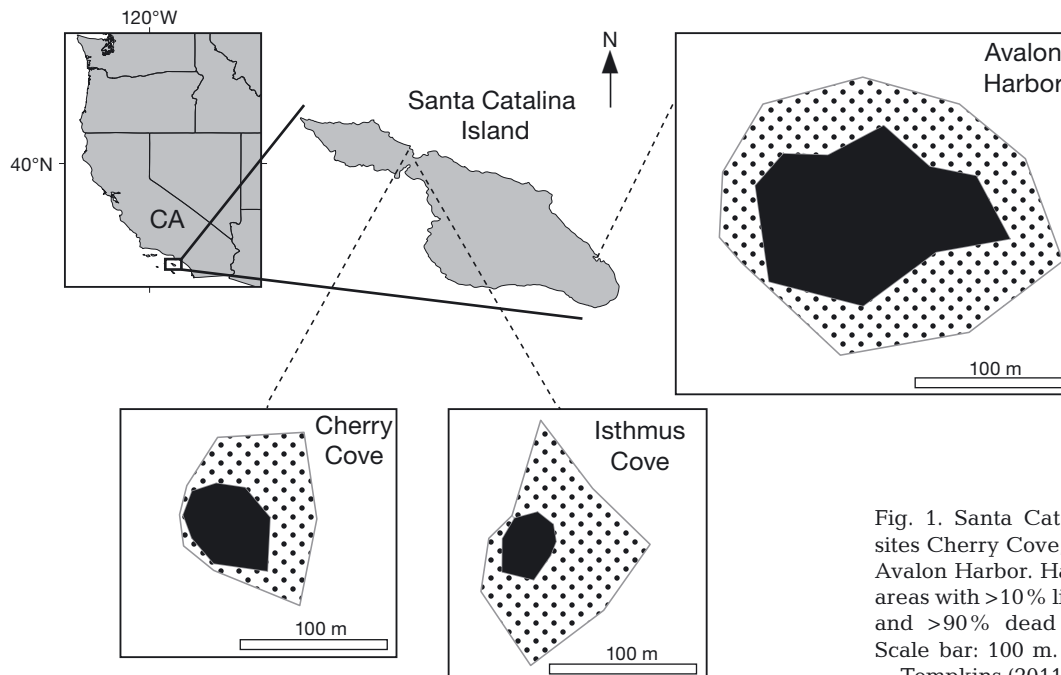

Fig. 1. Santa Catalina Island survey sites Cherry Cove, Isthmus Cove, and Avalon Harbor. Habitats depicted are areas with >10% live rhodolith (black) and >90% dead rhodolith (dotted). Scale bar: 100 m. Map adapted from Tompkins (2011) with permission

cent crushed rhodolith sands were defined as locations with >90% cover of calcium carbonate sediment (i.e. crushed rhodoliths) that were adjacent (~2−5 m) to mooring chains (Fig. 2).

Benthic surveys were conducted to quantify the primary substrate and the associated richness and abundance of macroalgae, infaunal invertebrates, epibenthic invertebrates, and fishes. The surveys were conducted along four 20 m transects in each rhodolith bed and adjacent crushed rhodolith sand habitat within each site, and during each sampling time. Primary substrates were recorded as live rhodolith, crushed rhodolith sand (carbonate), or silicate sand. Secondary substrates, if present, were recorded as either attached epiphytic macroalgae or attached macroinvertebrates. The associated community sampling included cover of macroalgae and visual counts of epibenthic invertebrates and fishes (body sizes >2.5 cm). Transect locations within each of the 2 habitat types were randomly allocated while minimizing differences in other environmental parameters such as depth, swell exposure, proximity to mooring chains, and distance to the nearest kelp bed. Transect length (20 m) was selected to ensure 4 replicate transects would fit within each habitat, with a minimum of 5 m between them. Percent cover of the primary and secondary substrates was estimated using uniform point contacts, with substrate type recorded every meter along each transect. The density of epibenthic invertebrates was recorded within a 2 m swath along each 20 m transect (sample area = 40 m^2). Fish density was estimated within a 20 × 2 × 2 m corridor along each transect (sample area = 80 m^3, with data reported per m^2 swath).

Infaunal invertebrate densities and sediment characteristics were estimated along each 20 m transect
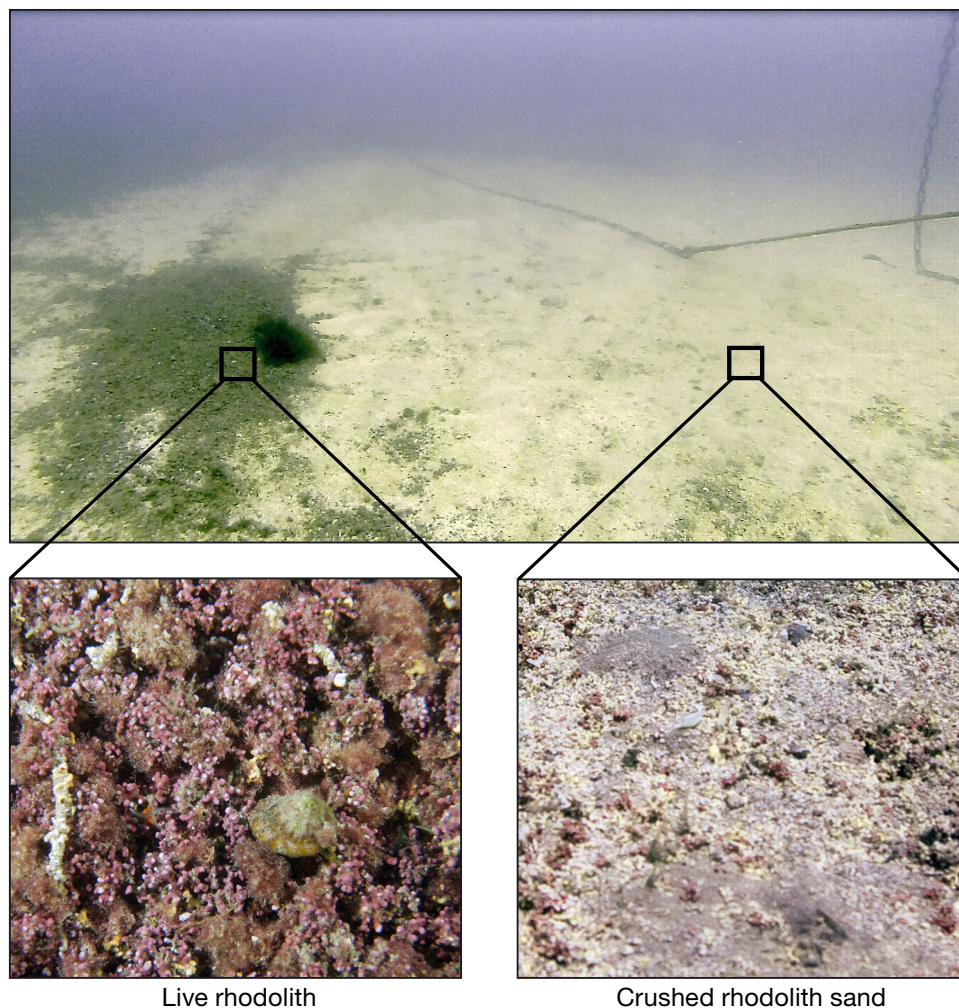

Fig. 2. Representative photo of surveyed habitat types. Live rhodolith shown on the left extending into the background and crushed rhodolith sand habitat shown on right with adjacent mooring chain and spreader line

Live rhodolith

Crushed rhodolith sand

using 6.5 cm diameter × 10 cm deep sediment cores (sample volume = 331.83 cm^3). Core size and depth were previously determined as being adequate for sampling both the living rhodolith layer (i.e. top 4–5 cm of the benthos) and the underlying sediments (Tompkins 2011). Invertebrates living within the interstitial spaces between the branches (cryptofauna) of living rhodoliths and invertebrates in the underlying sediments (infauna) are collectively referred to as infauna, as their vertical positions within the core sample were indistinguishable post-collection (Steller et al. 2003). Two cores were taken at random distances along each transect and the infaunal abundances within these 2 cores were averaged for community analyses, yielding 1 sample for each of the 4 transects (i.e. 4 replicates habitat^{-1}, for 3 sites, during 2 sampling times; n = 48). All core sample contents were transported to the University of Southern California Wrigley Institute of Environmental Studies (WIES) on Catalina, and stored in a −80°C freezer for preservation for identification. Frozen material was later thawed and rinsed over nested sieves (4.75, 2, and 0.5 mm). The retained organisms were identified to lowest taxonomic resolution possible using a Leica S6D dissecting microscope, and were used to estimate infaunal taxon richness. To compare sediment grain size between the 2 habitats, sediments retained on or passed through the nested sieves were divided into 4 size classes (>4.75, 4.75–2.0, 2.0–0.5, and <0.5 mm), dried at 60°C for 48 h, and weighed to the nearest 0.1 g.

Statistical analyses

Univariate statistical analyses (*t*-tests, ANOVA, regression) were conducted using R studio 0.99.903 (R Development Core Team 2016), and multivariate analyses (non-metric multi-dimensional scaling [nMDS], permutational multivariate analysis of variance [PERMANOVA], similarity percentage analysis [SIMPER]) were conducted using PRIMER-E v.6.0 (Clarke 1993, Clarke & Warwick 2001). All data were checked for univariate and/or multivariate normality by visual examination of residuals and/or bivariate draftsman plots, respectively. When necessary, data were log transformed to meet assumptions of homogeneity of variance.

To visualize differences in sediment size composition among habitats, sampling time, and sites, sediment size class dry weights (4.75, 4.75–2.0, 2.0–0.5, and <0.5 mm) from all cores taken within a habitat were square-root transformed to reduce the inflated influences of sediment classes with large proportions

and correct issues with multivariate normality (Clarke & Green 1988). Resemblance matrices based on Euclidean distance were then constructed and corresponding nMDS ordinations based on these similarities were created to visually represent similarities/differences in the sediment composition.

The effects of habitat, site, and sampling time on taxon richness were estimated for both total taxon richness (i.e. combined macroalgae, infaunal invertebrates, epibenthic invertebrates, and fishes) and for each of the functional groups separately. We performed 3-way mixed model ANOVAs to test for the effects of habitat (fixed factor), site (random factor), and sampling time (fixed factor) on total and functional group taxon richness. We explored the 3-way ANOVAs by conducting separate *a priori* 2-way ANOVAs during each sampling time to test for habitat and site effects on total and functional group taxon richness. We then followed these tests with *a priori* 2-sample *t*-tests to evaluate differences in functional group taxon richness between the 2 habitats at each site.

To visualize differences in macroalgal, infaunal invertebrate, epibenthic invertebrate, and fish assemblages among habitats, sampling times, and sites, estimates of individual taxon abundances were first square-root transformed as above. Separate resemblance matrices based on Bray-Curtis similarities were then created for each of the 4 functional groups, and corresponding nMDS ordinations based on these similarities were created to visually represent similarities/differences in the assemblages.

Vectors representing the influence of different sediment size classes or the primary taxa driving the ordinations were overlaid on the nMDS plots (Clarke & Warwick 2001). Following this, quantitative differences in the sediment size classes (based on Euclidean distance) or community assemblages (based on the Bray-Curtis similarities) among habitats, sampling times, and sites were evaluated for each functional group separately using 3-way PERMANOVAs (Clarke & Warwick 2001). For each test, habitat was blocked within site and considered as a fixed factor, sampling time was considered a fixed factor, and site was considered a random factor. To test for differences in community assemblages between habitats and among sites within a sampling time, separate 2-way PERMANOVAs were performed for each sampling time. Pair-wise comparisons were then used to determine if assemblages differed between habitats at a site within a sampling time for each functional group. Prior to testing, homogeneity of multivariate dispersions were checked using a PERMDISP test

(Anderson et al. 2008). All inferences were based on 9999 permutations (Anderson & ter Braak 2003), or when the number of possible permutable units was unreasonable (which occurred for the factors habitat and sampling time for the community analyses), a Monte Carlo test was performed (Anderson & Robinson 2003, Sturaro et al. 2014). SIMPER analyses were then used to assess the relative contribution of each taxon to the observed differences in the assemblages among habitats, sampling times, and sites (Clarke & Warwick 2001). Lastly, the relationships between tanaid density, which was the most abundant infaunal taxon in the rhodolith beds, and the dry weight of sediments in each of the 4 size classes were evaluated using separate linear regressions on a subset of cores (due to sediment data loss from 6 of 48 cores taken within the rhodolith bed, n = 42).

RESULTS

Sediments

The mean (±SE) benthic percent cover of live rhodolith within the rhodolith beds was 59.6 ± 9.7% and 50.8 ± 3.5% in April and December 2013, respectively. In contrast, adjacent crushed rhodolith sand habitat lacked large live rhodoliths and was dominated by carbonate (i.e. crushed rhodolith) and silicate sediment, which together averaged 90.2 ± 5.4% cover in April 2013 and 97.5 ± 1.5% in December 2013. The substrate in the rhodolith beds was composed of significantly different sediments than crushed rhodolith (pseudo-$F_{1,77}$ = 15.246, p = 0.016; Fig. 3A, Table S1 in the Supplement at www.int-res.com/articles/suppl/m595p071_supp.pdf). Rhodolith sediment was larger and more variably sized than the crushed rhodolith sediments, where ~60 to 90% was composed of the smallest grain size class considered (<0.5 mm), though this habitat relationship changed with sampling time and site (Fig. 3B,C, Table S1). Specifically, relative to the rhodolith beds, the crushed rhodolith sediment generally had less sediment in the >4.75, 4.75−2, and 2−0.05 mm size classes, and much more of the <0.05 mm size class (Fig. 3A).

Taxon richness

Three-way mixed model ANOVAs revealed that total taxon richness and taxon richness for the infaunal and epibenthic invertebrate functional groups
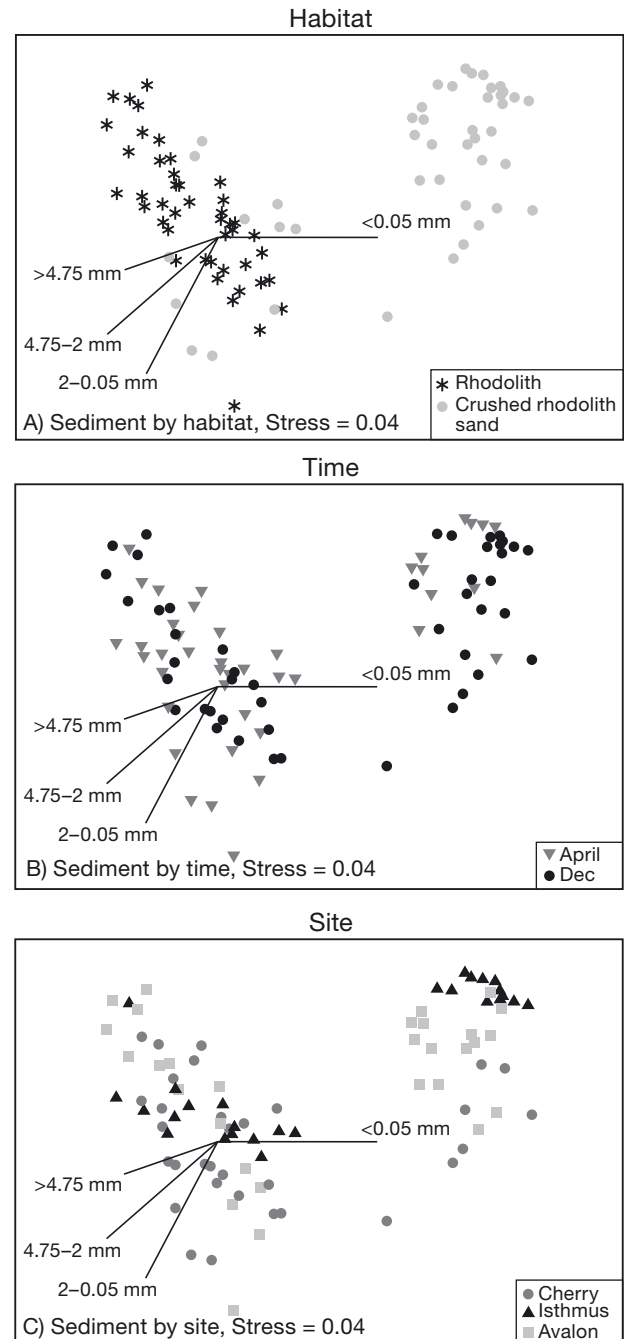

Fig. 3. Non-metric multidimensional scaling (nMDS) plots depicting the sediment composition by (A) habitat, (B) time, and (C) site, based on square-root transformed Euclidean distance similarity matrices of dry weight composition from 4 sediment size classes using a subset of cores (due to sediment data loss from 8 of 96 total cores, n = 88). Sediment size classes were >4.75, 4.75−2, 2−0.05, and <0.05 mm

were significantly greater in the rhodolith beds than in the crushed rhodolith sand habitat (see Table S2 in the Supplement). Rhodolith habitat did not support more total taxa than the crushed rhodolith habitat

during the April 2013 sampling time (22.1 ± 3.9 vs. 14.3 ± 1.8 taxa, ANOVA: $F_{1,18}$ = 13.894, p = 0.065), but did support more total taxa during the December 2013 sampling time (19.8 ± 1.5 vs. 10.6 ± 3.4 taxa, ANOVA: $F_{1,36}$ = 64.987, p = 0.015; Table S3 in the Supplement). Rhodolith beds consistently supported greater infaunal invertebrate taxon richness than the crushed rhodolith sand habitat (ANOVA: $F_{1,36}$ = 860.200, p = 0.001; Table S2C), and this was consistent across sampling times and sites (Table S2C). In contrast to infaunal invertebrate taxon richness, the taxon richness for the total and macroalgae, epibenthic invertebrate, and fish functional groups, did vary with sampling time and site (Tables S2 & S3). During each sampling time, the effect of habitat was examined at each site separately, and t-tests revealed rhodolith beds consistently supported greater total taxon richness (see Fig. S1); this was mainly driven by the infaunal and epibenthic invertebrate functional groups (Fig. 4).

Fig. 4. Mean (±SE) functional group taxon richness for each site (n = 4 transects) by habitat and sampling time. Significant richness differences from t-tests between rhodolith and crushed rhodolith sand are given above bars. Significance denoted as ***p < 0.001; **p < 0.01; *p < 0.05; and blank p > 0.05

Community composition

Differences in community assemblages between habitats and sampling times and among sites were observed for each of the 4 functional groups (macroalgae, infaunal invertebrates, epibenthic invertebrates, and fishes); however, the importance of factors varied by the functional group examined (Fig. 5, Table 1). For instance, when considered on their own, marginally non-significant differences in macroalgal assemblages were observed between the rhodolith beds and crushed rhodolith sands (PERMANOVA: pseudo-$F_{1,36}$ = 4.770, p = 0.055) and significant differences among the 3 study sites (pseudo-$F_{2,36}$ = 7.047, p = 0.0001; Tables 1A & 4A, Fig. 5A,C). However, the 3-way interaction of habitat, site, and sampling time was marginally non-significant (pseudo-$F_{2,36}$ = 2.100, p = 0.054; Table 1A). After separating sampling times, the habitat × site interaction was significant for April 2013, and habitat for December 2013, suggesting rhodolith and crushed rhodolith sand support different macroalgal assemblages only at one site (Cherry Cove) during April 2013 and potentially at all sites in December 2013 (Tables S4A & S5A in the Supplement).

When pooling sampling times, macroalgal bottom cover was approximately 3.1 times greater in the rhodolith beds than the crushed rhodolith sand habitats, and this was driven by only a few taxa (Table 2A). Specifically, brown algae in the Order Dictyotales (i.e. *Dictyopteris undulata* and *Dictyota binghamiae*) were 2.9 times more abundant, contributing 31.6% to dissimilarity between habitats, and fleshy red algae (e.g. *Polysiphonia* spp., *Chondracanthus canaliculatus*, and *Rhodymenia* spp.) were 7.4 times more abundant, contributing 29.0% to dissimilarity between habitats (Table 2A, Figs. 5A & 6A). Unidentified low-lying turf algae were 2 times more abundant in the rhodolith beds and contributed 10.5% to the dissimilarity between habitats. Geniculate coralline algae, composed mostly of epiphytic *Lithothrix* spp., were only observed in the rhodolith beds and contributed 9.8% to the dissimilarity between habitats (Table 2A, Figs. 5A & 6A). In contrast, other brown algae, which included *Zonaria farlowii*, drift *Macrocystis pyrifera*, and rare or unidentified species, exhibited little differences in abundance between habitats but were more variable in the crushed rhodolith sands, and contributed 14.1% to the observed dissimilarity between habitats (Table 2A, Figs. 5A & 6A).

Similar to macroalgal patterns, infaunal invertebrate assemblages were significantly different between the rhodolith beds and crushed rhodolith
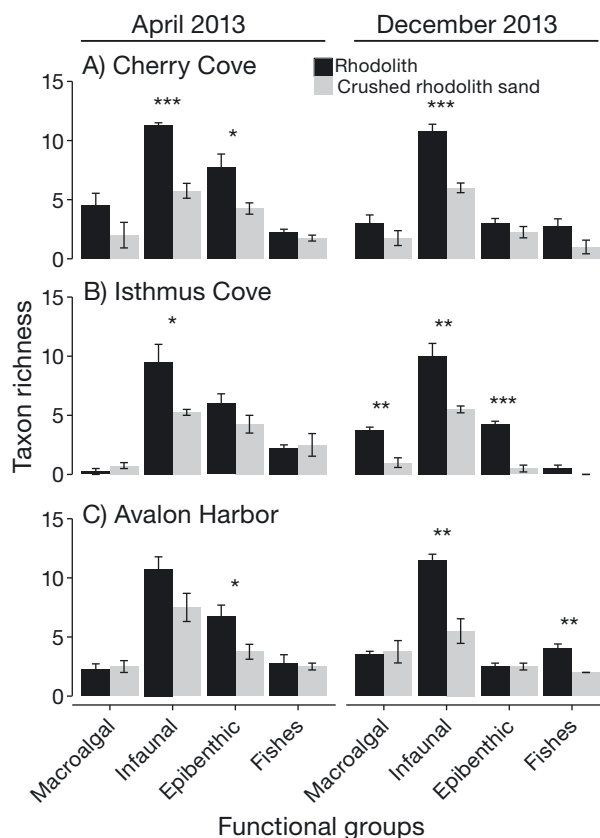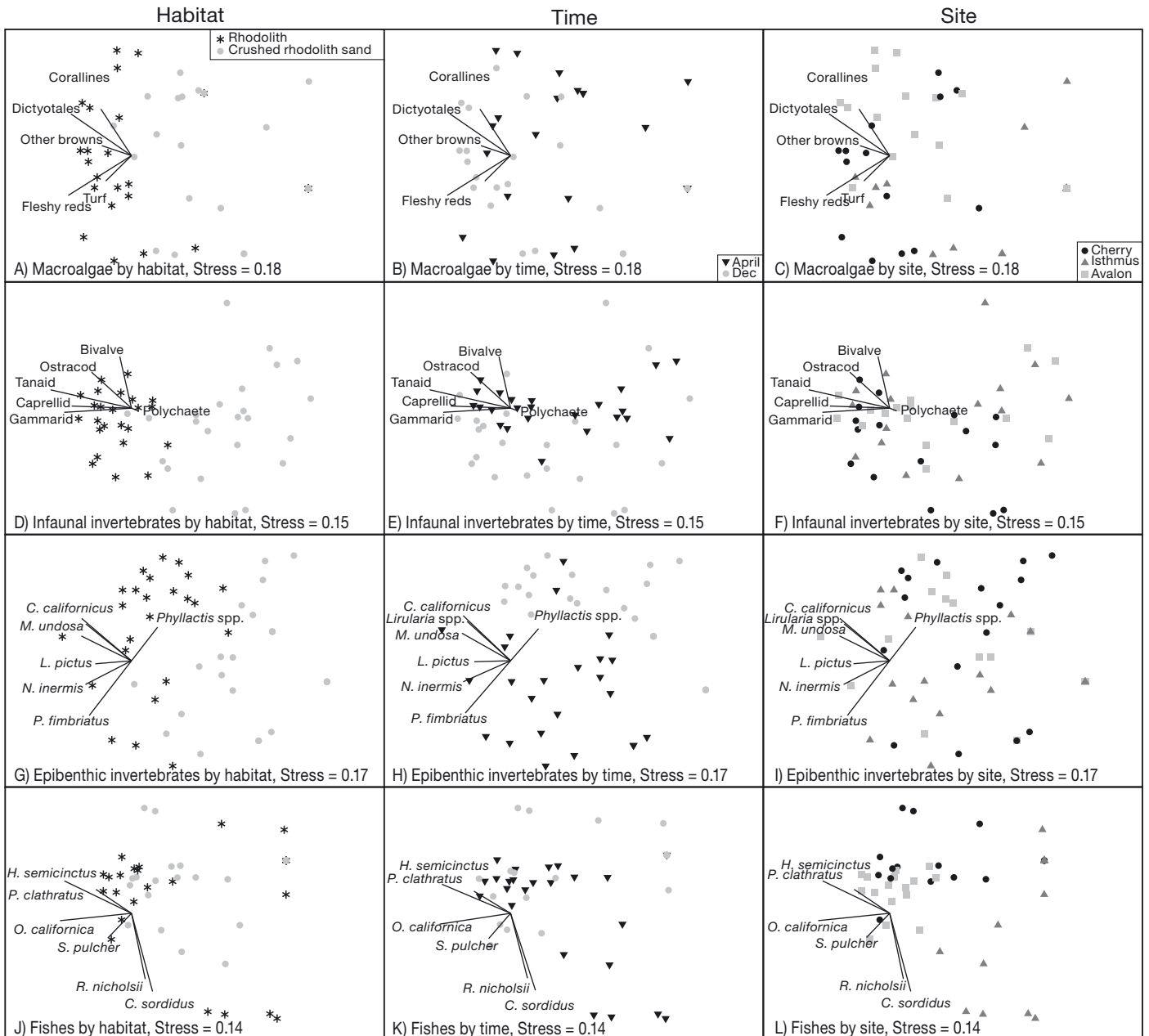
Fig. 5. Non-metric multidimensional scaling (nMDS) plots based on square-root transformed Bray-Curtis similarity matrices from transects (n = 4) of 4 functional groups relative to habitat, sampling time, and site columns. Functional groups are rows (A–C) macroalgae, (D–F) infaunal invertebrates, (G–I) epibenthic invertebrates, and (J–L) fishes. Distances between points represent relative dissimilarities in community assemblages. Habitat symbols are dark asterisk (rhodolith) and gray circle (crushed rhodolith sand). Sampling time symbols are dark inverted triangle (April 2013) and gray circle (December 2013). Site symbols are dark circle (Cherry Cove), dark inverted triangle (Isthmus Cove), and gray square (Avalon Harbor). Vectors are the magnitude and direction of the primary taxa driving the ordination. See Tables 2–4 for full species names

sands (PERMANOVA: pseudo-$F_{1,36}$ = 12.692, p = 0.003; Table 1B, Fig. 5D) and among the 3 study sites (pseudo-$F_{2,36}$ = 2.224, p = 0.015; Tables 1B & 4B, Fig. 5D). Infaunal assemblages did not, however, differ between the April 2013 and December 2013 sampling times (pseudo-$F_{1,36}$ = 2.536, p = 0.097; Table 1B).

However, the habitat × site interaction differed between sampling times (habitat × site × time, pseudo-$F_{2,36}$ = 1.947, p = 0.030; Table 1B, Fig. 5D–F). Variation in infaunal assemblages in April 2013 were driven by habitat differences (pseudo-$F_{1,18}$ = 6.996, p = 0.011; Table S4B, Fig. 5D–F). However, in December

Table 1. Separate 3-factor PERMANOVA results on the effect of habitat, site, and sampling time on assemblages of (A) macroalgae, (B) infaunal invertebrates, (C) epibenthic invertebrates, and (D) fishes. For each test, habitat and sampling time were considered fixed factors, and site was considered a random factor. All inferences were based on 9999 permutations except for the habitat and sampling time factors, which were evaluated using Monte Carlo tests due to a limited number of possible permutable units. Significant (p < 0.05) values are in **bold**

Source	df	SS	MS	Pseudo-F	p
(A) Macroalgae					
Habitat	1	11125	11125	4.770	0.055
Site	2	16974	8486.9	7.047	**0.0001**
Time	1	5480.1	5480.1	3.614	0.094
Time × habitat	1	6275.5	6275.5	2.482	0.209
Time × site	2	3032.7	1516.3	1.259	0.304
Habitat × site	2	4664.4	2332.2	1.937	0.076
Habitat × site × time	2	5057	2528.5	2.100	0.054
Residual	36	43354	1204.3		
Total	47	95962			
(B) Infaunal invertebrates					
Habitat	1	16328.00	16328.00	12.692	**0.003**
Site	2	2547.30	1273.70	2.224	**0.015**
Time	1	2302.90	2302.90	2.536	0.097
Time × habitat	1	1398.60	1398.60	1.254	0.363
Time × site	2	1816.40	908.18	1.586	0.109
Habitat × site	2	2572.90	1286.40	2.246	**0.012**
Habitat × site × time	2	2230.60	1115.30	1.947	**0.030**
Residual	36	20621.0	572.81		
Total	47	49817.0			
(C) Epibenthic invertebrates					
Habitat	1	19357	19357	9.494	**0.008**
Site	2	5256.1	2628.1	3.531	**0.001**
Time	1	16168	16168	7.243	**0.014**
Time × habitat	1	3554	3554	1.479	0.327
Time × site	2	4464.2	2232.1	2.999	**0.003**
Habitat × site	2	4077.6	2038.8	2.739	**0.007**
Habitat × site × time	2	4804.8	2402.4	3.228	**0.002**
Residual	36	26795	744.32		
Total	47	84476			
(D) Fishes					
Habitat	1	2779.2	2779.2	2.430	0.167
Site	2	28901	14450	21.016	**0.0001**
Time	1	9596	9596	2.060	0.202
Time × habitat	1	522.87	522.87	0.339	0.757
Time × site	2	9317.2	4658.6	6.775	**0.0001**
Habitat × site	2	2287.1	1143.5	1.663	0.131
Habitat × site × time	2	3083.9	1542	2.243	**0.042**
Residual	36	24753	687.59		
Total	47	81240			

2013, habitat, site, and the habitat × site interaction were all significant, suggesting more spatial variation in the habitat effect on assemblages (Table S4B). Pair-wise comparisons revealed infaunal invertebrate assemblages differed between rhodolith and crushed rhodolith sand and were significant, or mar-

ginally non-significant, for all sites during both sampling times (Table S5B). Overall, infaunal invertebrates were 3.5 times more abundant in the rhodolith beds than the crushed rhodolith sands, and as with macroalgae, this was driven by a few taxonomic groups (Table 2B). Tanaids, by far the most abundant infauna observed, were 5.2 times more abundant in the rhodolith beds and explained 26.4% of the observed dissimilarity between habitats, and gammarid amphipods were 3.3 times more abundant, contributing 12.5% to the dissimilarity between habitats (Table 2B, Figs. 5D & 6B). Caprellid amphipods, ostracods, isopods, and ophiuroids, which were all more abundant within the rhodolith beds (Fig. 6B), each contributed <10% to the observed dissimilarity between habitats (Table 2B).

Epibenthic invertebrate assemblages varied significantly among the 2 habitats (PERMANOVA: habitat, pseudo-$F_{1,36}$ = 9.494, p = 0.008; Table 1C, Fig. 5G), the 2 sampling times (pseudo-$F_{1,36}$ = 7.243, p = 0.014; Table 1C, Fig. 5H), and the 3 study sites (pseudo-$F_{2,36}$ = 3.531, p = 0.001; Table 1C, Fig. 5I). For epibenthic invertebrates, similar to infaunal assemblages, the interaction of habitat × site differed between the 2 sampling times (habitat × site × time, pseudo-$F_{2,36}$ = 3.228, p = 0.002; Table 1C) and pair-wise comparisons revealed an effect of habitat at all sites during both sampling times except for Isthmus in April 2013 (Table S5C). Overall, the differences between habitats were primarily due to greater abundances of the gastropods *Megastraea undosa* (40 times more, contributing 23.9% to dissimilarity) and *Californiconus californicus* (2.2 times more, contributing 19.5% to dissimilarity) in rhodolith beds. The gastropod *Lirularia* spp. was only observed in the rhodolith beds and contributed 18.3% to dissimilarity in assemblages between habitats (Table 2C). The predatory nudibranch *Navanax inermis* and the white urchin *Lytechinus pictus* were also more abundant within rhodolith beds than crushed rhodolith sand, each contributing <10% to dissimilarity in assemblages between habitats (Table 2C). Abundances of epibenthic invertebrates decreased from April 2013 to December 2013 (Table 3C) and were less variable, especially in the rhodolith beds (0.60 ± 0.33 to 0.39 ± 0.03 ind. m^{-2} in rhodolith beds and 0.17 ± 0.06 to 0.04 ± 0.02 ind. m^{-2} in crushed rhodolith sand). Dissimilarity in epibenthic invertebrate assemblages between the 2

Table 2. Effect of habitat. Relative contribution of taxa within the functional groups (A) macroalgae, (B) infaunal invertebrates, (C) epibenthic invertebrates, and (D) fishes to the dissimilarity in assemblages by habitat. Similarity percentage (SIMPER) analysis listed for taxa contributing at least 5% to dissimilarity. Abundance values (mean ± SE) are averages of 24 transects for macroalgae, 48 cores for infaunal invertebrates, and 24 transects for epibenthic invertebrates and fishes, for each habitat within a site, across both sampling times. Average abundance of all taxa, including those contributing <5% to dissimilarity between habitats, is listed at the bottom for each functional group

Taxa (A) Macroalgae	Rhodolith Cover (%)	Sand Cover (%)	Contr. (%)
Dictyotales	15.2 ± 5.7	5.2 ± 2.2	31.58
Fleshy reds	12.9 ± 4.0	1.7 ± 0.4	29.02
Other browns	2.5 ± 1.5	2.7 ± 0.8	14.10
Turf	4.6 ± 2.8	2.3 ± 1.4	10.47
Geniculate corallines	4.4 ± 2.6	0	9.82
All taxa total	39.6 ± 9.34	12.92 ± 3.33	3.1× different
(B) Infaunal invertebrates	Density (ind. m^{-2})	Density (ind. m^{-2})	
Tanaids	12304 ± 2022	2355 ± 895	26.39
Gammarids	4744 ± 798	1425 ± 329	12.46
Caprellids	2323 ± 870	716 ± 195	8.92
Ostracods	1457 ± 464	170 ± 48	8.41
Isopods	628 ± 188	25 ± 8	7.15
Ophiuroids	719 ± 232	100 ± 52	6.99
All taxa total	25808 ± 2443	7372 ± 1279	3.5× different
(C) Epibenthic invertebrates	Density (ind. m^{-2})	Density (ind. m^{-2})	
Megastraea undosa	0.12 ± 0.05	0.003 ± 0.002	23.87
Californiconus californicus	0.11 ± 0.03	0.05 ± 0.02	19.53
Lirularia spp.	0.07 ± 0.3	0	18.31
Lytechinus pictus	0.03 ± 0.01	0.01 ± 0.01	9.41
Navanax inermis	0.03 ± 0.01	0.004 ± 0.003	8.30
All taxa total	0.49 ± 0.15	0.11 ± 0.04	4.5× different
(D) Fishes	Density (ind. m^{-2})	Density (ind. m^{-2})	
Oxyjulis californica	0.20 ± 0.08	0.07 ± 0.03	34.46
Paralabrax clathratus	0.07 ± 0.03	0.05 ± 0.02	22.56
Citharichthys sordidus	0.07 ± 0.07	0.01 ± 0.01	11.32
Semicossyphus pulcher	0.004 ± 0.002	0.005 ± 0.003	8.10
Rhinogobiops nicholsii	0.02 ± 0.02	0.001 ± 0.001	5.57
All taxa total	0.38 ± 0.10	0.15 ± 0.04	2.5× different

sampling times were driven primarily by the sand anemone *Pachycerianthus fimbriatus* and the urchin *L. pictus* which were more abundant in April 2013, and by *C. californicus*, which was more abundant during December 2013 (Table 3C).

Fish assemblages did not vary significantly between the 2 habitats (PERMANOVA: pseudo-$F_{1,36}$ = 2.430, p = 0.167; Table 1D, Fig. 5J) and the 2 sampling times (pseudo-$F_{1,36}$ = 2.060, p = 0.202; Fig. 5L), but did among the 3 sites (pseudo-$F_{2,36}$ = 21.016, p = 0.001; Table 1D, Fig. 5K). Furthermore, the habitat × site interaction did differ between sampling times (habitat × site × time interaction, pseudo-$F_{2,36}$ = 2.243, p = 0.042; Table 1D) with habitat and site driving variation in fish assemblages in April 2013 and only site having an effect on assemblages in December 2013 (Table S4D). Among-site variation was primarily driven by 2 taxa, the senorita wrasse *Oxyjulis californica* and the kelp bass *Paralabrax clathratus*, and differences in these 2 taxa contributed from 57.5 to 72.7% to the observed variation in assemblages among the sites (Table 4D). Although habitat was not significant, 57.1% of the variation in fish assemblages between the rhodolith beds and crushed rhodolith sands were also driven primarily by these 2 taxa, with 2.9 times greater abundance of *O. californica* and 1.4 times greater abundances of *P. clathratus* within the rhodolith beds (Table 2D, Fig. 6D).

Sediment size and tanaid associations

Infaunal tanaids were approximately 5 times more abundant in the rhodolith beds than in the crushed rhodolith sand habitat (Table 2B). This difference contributed more than 26% to the overall differences in community composition between the 2 habitats (Table 2B, Fig. 6B). Tanaid abundances within the rhodolith beds were not significantly associated with the amount of sediments in either of the 2 larger size categories (regressions: sediment size >4.75 mm, $F_{1,40}$ = 0.077, p = 0.783, r^2 = 0.023, Fig. 7A; sediment size 4.75–2 mm, $F_{1,40}$ = 3.846, p = 0.057, r^2 = 0.065; Fig. 7B), but instead they were positively associated with the amount of sediments in each of the 2 smaller size categories (regressions: sediment size 2–0.5 mm, $F_{1,40}$ = 6.53, p = 0.015, r^2 = 0.119, Fig. 7C; sediment size <0.05 mm, $F_{1,40}$ = 10.26, p = 0.0027, r^2 = 0.184; Fig. 7D) within rhodolith cores. Together, this suggests that habitat characteristics other than sediment size alone were important to supporting greater abundances of tanaids within the rhodolith beds.
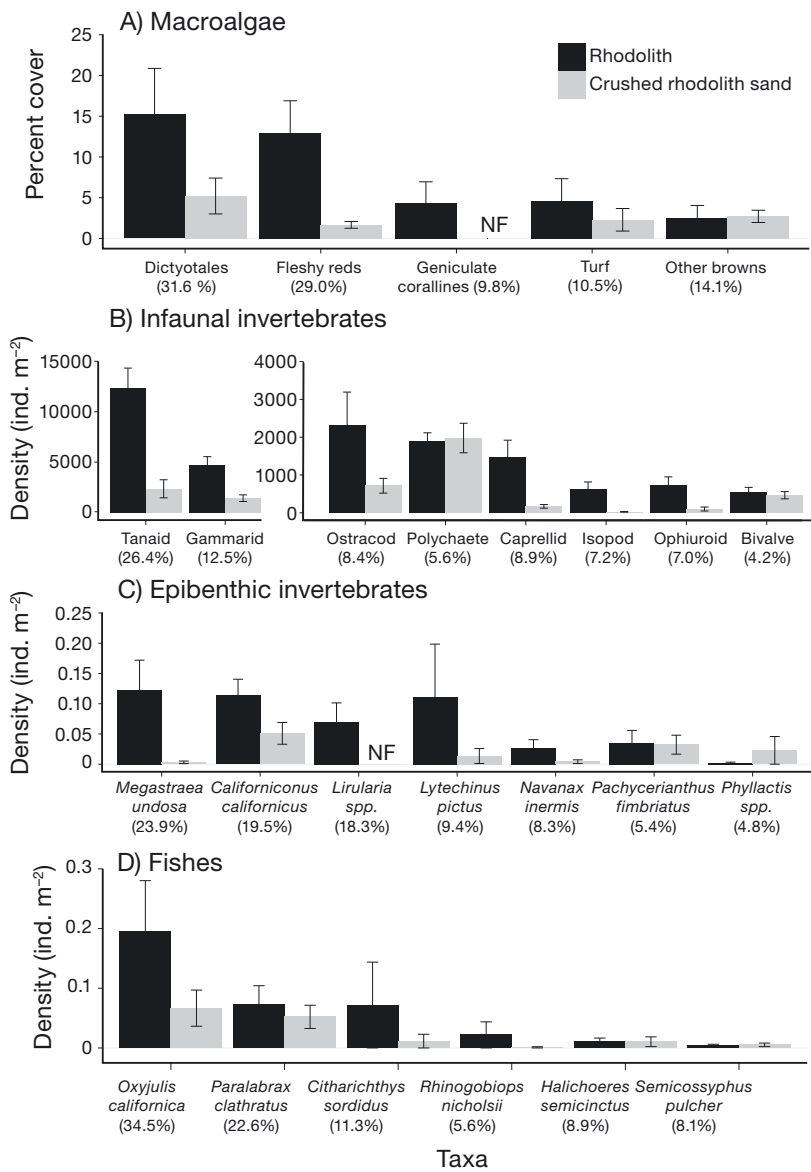
Fig. 6. Mean (±SE) abundance of dominant species from functional group taxa relative to habitat for (A) macroalgae, (B) infaunal invertebrates, (C) epibenthic invertebrates, and (D) fishes within rhodolith (black) and crushed rhodolith sand (gray) habitats, with percent contribution to dissimilarity from SIMPER under taxon names. Means and error bars for a habitat are from pooled transects, sites, and sampling times (n = 24); NF: not found

DISCUSSION

Loss of structural complexity

Features of the physical and biogenic habitat can greatly influence the abundance and diversity of associated taxa and thus ecosystem functioning (MacArthur & MacArthur 1961, Ellison et al. 2005, Loke & Todd 2016). In many coastal ecosystems, habitats are based on the structure of biogenic foun-

dation species, whose demography, ecology, and responses to environmental perturbations play important roles in ecosystem dynamics (Dayton 1972). Our study suggests that Catalina Island rhodoliths with greater structural complexity support a greater abundance and diversity of associated organisms from multiple functional groups than less structurally complex crushed rhodolith carbonate and silicate sands. Specifically, the impact of structural loss appeared to reduce the abundance of macroalgae, invertebrates, and fish within rhodolith habitat, with invertebrate abundance and diversity being most affected, similar to previous findings for macroalgae and epibenthic invertebrates (Tompkins 2011, Tompkins & Steller 2016). Infaunal tanaid densities were greatly reduced with the loss of rhodolith structural complexity, potentially because they use rhodoliths as habitat or food provision (Kamenos et al. 2004a,b,c, Grall et al. 2006). Interestingly, tanaid abundance increased with increasing proportion of fine sediments within rhodolith habitat. This suggests that more heterogeneous sediment distributions within rhodolith beds, which include fine sediments, may contribute to increased invertebrate abundance. These findings are similar to correlations of increasing invertebrate abundance and richness with greater mud presence in New Zealand rhodolith beds (Neill et al. 2015).

Our data suggest that structural loss of rhodoliths can lead to biodiversity and abundance declines, likely through reductions in important microhabitats that they create for associated organisms (Steller et al. 2003), providing refuge from predation (Rogers et al. 2014) and the retention of food resources such as detritus, benthic diatoms, biofilms, and prey invertebrates (Grall et al. 2006, Steller & Cáceres-Martínez 2009, Pereira-Filho et al. 2015). However, our data showed that community differences between habitats were primarily due to changes in organism abundance rather than taxon richness, with substantially more individuals observed within rhodolith beds than in the

Table 3. Effect of sampling time. Relative contribution of taxa within the functional groups (A) macroalgae, (B) infaunal invertebrates, (C) epibenthic invertebrates, and (D) fishes to the dissimilarity in assemblages by sampling time. See Table 2 legend for further information on sampling and table layout. Average abundance of all taxa, including those contributing <5% to dissimilarity, between sampling times is listed at the bottom of each functional group. See Table 2 legend for further information on sampling and table layout

Taxa (A) Macroalgae	April 2013 Cover (%)	December 2013 Cover (%)	Contr. (%)
Dictyotales	6.0 ± 2.4	6.1 ± 1.0	30.59
Fleshy reds	5.6 ± 3.9	5.2 ± 1.6	21.86
Turf	2.9 ± 2.9	2.6 ± 1.2	19.61
Other browns	3.5 ± 1.4	2.8 ± 0.6	15.65
Geniculate corallines	2.1 ± 2.1	2.1 ± 0.9	6.23
All taxa total	21.0 ± 8.0	31.5 ± 9.7	1.5× different
(B) Infaunal invertebrates	Density (ind. m^{-2})	Density (ind. m^{-2})	
Tanaids	7736 ± 2577	6923 ± 2843	19.40
Ostracods	559 ± 172	2480 ± 809	14.54
Gammarids	3064 ± 1094	3105 ± 805	13.07
Polychaetes	1865 ± 232	2000 ± 387	9.54
Caprellids	1155 ± 560	471 ± 151	8.07
Bivalvia	377 ± 94	625 ± 115	7.23
All taxa total	16295 ± 4531	16885 ± 4586	1.0× different
(C) Epibenthic invertebrates	Density (ind. m^{-2})	Density (ind. m^{-2})	
Pachycerianthus fimbriatus	0.07 ± 0.01	0	29.95
Californiconus californicus	0.01 ± 0.01	0.06 ± 0.03	19.96
Lytechinus pictus	0.04 ± 0.01	0.004 ± 0.004	10.49
Megastraea undosa	0.06 ± 0.05	0.06 ± 0.04	9.61
Lirularia spp.	0.09 ± 0.03	0.08 ± 0.02	6.71
All taxa total	0.35 ± 0.17	0.20 ± 0.08	1.8× different
(D) Fishes	Density (ind. m^{-2})	Density (ind. m^{-2})	
Oxyjulis californica	0.14 ± 0.06	0.12 ± 0.08	35.03
Paralabrax clathratus	0.08 ± 0.03	0.04 ± 0.02	27.14
Halichoeres semicinctus	0.001 ± 0.001	0.020 ± 0.008	14.85
Semicossyphus pulcher	0.003 ± 0.002	0.006 ± 0.003	7.31
Rhinogobiops nicholsii	0.023 ± 0.022	0.00 ± 0.00	5.72
All taxa total	0.33 ± 0.08	0.19 ± 0.07	1.7× different

crushed rhodolith sands. The similarity in taxon richness and abundance of some taxa between disturbed and less disturbed rhodolith habitats may be due to the proximity of the sampling areas and mobility of many organisms sampled. In particular, rhodolith bed disturbance was associated with reduced bottom cover of macroalgae, especially brown algae in the Order Dictyotales, fleshy red algae, and geniculate coralline algae, as well as reduced abundances of infaunal tanaids and epibenthic gastropod invertebrates, and reduced abundances of fishes, especially senorita *Oxyjulis californica*. Of all taxa reported in this study, only 2 taxa were exclusively in rhodolith beds: the gastropod *Lirularia* spp. and geniculate

coralline algae (mainly *Lithothrix* spp.) growing epiphytically on the rhodolith thalli. This study supports a growing body of evidence that homogenizing structurally complex habitats leads to a loss of biodiversity and reduced abundances of associated organisms (Airoldi et al. 2008).

Our findings strongly suggest that rhodolith community descriptions need to incorporate a temporal component to sampling regimes. The significant differences in community assemblages between habitats occurred at more sites during the December 2013 sampling time, suggesting that richness and abundance of macroalgae, infaunal invertebrates, and epibenthic invertebrates differed more between rhodolith habitat and crushed rhodolith sand during this time period. Greater taxon richness or density of macroalgae, invertebrates, or fish within rhodolith habitats during certain seasons may be due to greater larval supply, availability of attachment substrate or microhabitats, or post-settlement survivorship. Similar to other studies, community assemblages also varied by site, with Avalon Harbor supporting greater infaunal invertebrate, epibenthic invertebrate, and fish densities than Cherry Cove and Isthmus Cove when sampling times were combined (Sheehan et al. 2015b). Spatiotemporal variability in the magnitude of difference between rhodolith and crushed rhodolith community assemblages suggests future studies on disturbance impacts to rhodolith bed communities should consider the effects of site and sampling time.

Abundance

Rhodolith beds are capable of supporting high abundances of associated organisms, but their overall influence appears to vary across geographic locations (Steller et al. 2003, Konar et al. 2006, Foster et al. 2007, Sciberras et al. 2009). Results from this and

previous studies suggest that California rhodolith beds may support a lower diversity and abundance of associated organisms compared to other locations (Tompkins & Steller 2016). In studies from the eastern Pacific, the densities of invertebrates reported for a rhodolith bed in the Gulf of California, Mexico were 54 times greater (1 402 000 ind. m^{-2}; Steller et al. 2003), and within an Alaskan rhodolith bed were 438 times less (~60 ind. m^{-2}; Konar et al. 2006) than invertebrate densities estimated in Catalina Island rhodolith beds (25 808 ind. m^{-2}; this study). The reasons for this may include differences in rhodolith bed sizes, the density of rhodoliths, rhodolith morphological complexity, or differences in disturbance levels (Tompkins & Steller 2016).

The reduced size of Catalina rhodoliths relative to rhodoliths from other Eastern Pacific populations may be a major factor influencing the low biodiversity estimates in this study. Catalina Island rhodoliths *Lithothamnion australe* are much smaller (0.3–2.5 cm thallus diameter; Tompkins 2011) than sizes reported for *Lithophyllum margaritae* (2–8 cm, Steller & Foster 1995; 2.1–4.8 cm, Steller et al. 2003) and *Lithothamnion muelleri* (1.5–15 cm, Foster et al. 2007; 0.5–16 cm, McConnico et al. 2014) in the Gulf of California, or for *Phymatolithon calcareum* in Alaska (2.0–7.0 cm; Konar et al. 2006). Among-site differences have been attributed to variation in local physical factors (irradiance, temperature, hydrodynamic forces, nutrients) and biotic factors (fouling, bioturbation), as well as physical characters of the rhodolith species that makes the bed (reviewed in Foster 2001, Foster et al. 2013, Sheehan et al. 2015b). Other factors that may actively reduce rhodolith bed size, density and/or morphology globally include anthropogenic disturbance such as crushing from boat moorings and anchors (Steller et al. 2003, Tompkins & Steller 2016), dredging (De Grave & Whitaker 1999, Hall-Spencer & Moore 2000), fish farming (Hall-Spencer et al. 2006), and trawling (Bordehore et al. 2003). Of these, crushing from boat moorings likely plays a significant role at Catalina in reducing bed size and homogenizing the benthos by turning rhodolith beds into crushed rhodolith sand (Tompkins & Steller 2016). This can have dramatic impacts on the diversity and abundance of sand-associated taxa (Tompkins & Steller 2016) much in the way that dredging and trawling of soft-bottom habitats has been shown to reduce faunal diversity and cause shifts in community assemblages toward filter-feeding bivalves and polychaetes (De Grave & Whitaker 1999). These community shifts are likely long lasting, as rhodolith

beds have slow growth (Foster 2001) and therefore have shown little recovery on the scale of years post-dredging (Hall-Spencer & Moore 2000), further exacerbating the impact.

Temporal variation

Rhodolith beds are characterized by seasonal changes in the relative abundance of macroalgae and infaunal and epibenthic invertebrates, likely in response to environmental changes in water temperatures and nutrients, and environmentally driven recruitment pulses (Steller et al. 2003, Foster et al. 2007). A limitation of our temporal sampling selection of only 2 time sampling points was our inability to examine seasonal changes in assemblages (as our 2 time points were also within different seasons) and thus a lack of replication within those seasons. Research within rhodolith beds should estimate seasonal changes of flora and fauna by performing replicate sampling within seasons, providing the ability to compare within- versus among-season variation in rhodolith-associated community assemblages. Despite our limitations, temporal fluctuations of epibenthic invertebrates in Catalina rhodolith beds were consistent with other studies that detected large changes in invertebrate composition over time (Steller et al. 2003, Kamenos et al. 2004b, Foster et al. 2007). Specifically, differences in white urchins *Lytechinus pictus*, turban snails *Megastraea undosa*, sea cucumbers *Parastichopus parvimensis*, and seahares *Aplysia californica* were observed between sampling times within the Catalina rhodolith beds. Juveniles of both *L. pictus* and *M. undosa* were observed within rhodolith sediment core samples, suggesting these taxa may either preferentially settle there (e.g. on coralline algae) or have greater growth and survivorship relative to adjacent crushed rhodolith sands (Kamenos et al. 2004b,c, Steller & Cáceres-Martínez 2009). Interestingly, the differences in *L. pictus* densities between our sampling times appear similar to fluctuations in echinoderms reported for the Gulf of California, with greater densities observed in spring and seasonal declines to almost zero during fall (Foster et al. 2007). Similarly, more *L. pictus* were detected in both habitats during April 2013, possibly due to annual settlement and/or recruitment events. However, other explanations for the observed decreases of infaunal and epibenthic *L. pictus* densities between sampling times may also be due to seasonal changes in foraging of fish predators, increased cryptic sheltering behavior by urchins (Bernstein et al.

Table 4. Effect of site. Relative contribution of taxa within the functional groups (A) macroalgae, (B) infaunal invertebrates, (C) epibenthic invertebrates, and (D) fishes to the dissimilarity in assemblages for paired site comparisons Cherry–Isthmus, Cherry–Avalon, and Isthmus–Avalon. Similarity percentage (SIMPER) analysis listed for taxa contributing at least 5% to dissimilarity. Abundance values (mean ± SE) are averages of 16 transects for macroalgae, 32 cores for infaunal invertebrates, and 16 transects for epibenthic invertebrates and fishes, for each habitat within a site, across both sampling times. Average abundance of all taxa, including those contributing <5% to dissimilarity, and overall change in abundance between sites for a comparison are listed at the bottom of each functional group. Contr.: Contribution to dissimilarity

Taxa	Cherry	Isthmus	Contr. (%)	Taxa	Cherry
(A) Macroalgae					
	Cover (%)	Cover (%)			Cover (%)
Dictyotales	12.2 ± 6.1	3.1 ± 3.1	29.99	Dictyotales	12.2 ± 6.1
Fleshy reds	11.9 ± 5.9	5.3 ± 5.3	23.42	Fleshy reds	11.9 ± 5.9
Turf	5.6 ± 4.0	2.2 ± 2.2	21.16	Other browns	4.1 ± 2.1
Other browns	4.1 ± 2.1	0.6 ± 0.6	18.22	Turf	5.6 ± 4.0
Geniculate corallines	0.3 ± 0.3	0.0 ± 0.0	6.16	Geniculate corallines	0.3 ± 0.3
All taxa total	34.1 ± 11.6	11.3 ± 8.8	3.0× different	All taxa total	34.1 ± 11.6
(B) Infaunal invertebrates	Density (ind. m^{-2})	Density (ind. m^{-2})			Density (ind. m^{-2})
Tanaids	6866 ± 669	6951 ± 3858	18.65	Tanaids	6866 ± 669
Gammarids	3664 ± 1460	3118 ± 1424	14.88	Ostracods	942 ± 398
Ostracods	942 ± 398	1884 ± 1323	13.73	Gammarids	3664 ± 1460
Bivalvia	330 ± 202	509 ± 59	8.54	Caprellids	1055 ± 669
Caprellids	1055 ± 669	556 ± 191	8.41	Polychaetes	1658 ± 167
Polychaetes	1658 ± 167	1997 ± 211	7.28	Bivalvia	330 ± 202
All taxa total	16314 ± 5724	15862 ± 6857	1.0× different	All taxa total	16314 ± 5724
(C) Epibenthic invertebrates	Density (ind. m^{-2})	Density (ind. m^{-2})			Density (ind. m^{-2})
Californiconus californicus	0.10 ± 0.04	0.06 ± 0.03	22.97	*Californiconus californicus*	0.10 ± 0.04
Pachycerianthus fimbriatus	0.03 ± 0.02	0.04 ± 0.02	20.81	*Pachycerianthus fimbriatus*	0.03 ± 0.02
Phyllactis spp.	0.04 ± 0.03	0.00 ± 0.00	11.17	*Megastraea undosa*	0.02 ± 0.01
Lytechinus pictus	0.01 ± 0.01	0.04 ± 0.02	9.60	*Phyllactis* spp.	0.04 ± 0.03
Navanax inermis	0.006 ± 0.05	0.04 ± 0.02	8.50	*Lirularia* spp.	0.05 ± 0.05
Megastraea undosa	0.02 ± 0.01	0.03 ± 0.02	7.80	*Lytechinus pictus*	0.01 ± 0.01
All taxa total	0.20 ± 0.03	0.21 ± 0.06	1.1× different	All taxa total	0.20 ± 0.03
(D) Fishes	Density (ind. m^{-2})	Density (ind. m^{-2})			Density (ind. m^{-2})
Paralabrax clathratus	0.10 ± 0.04	0.01 ± 0.01	29.85	*Oxyjulis californica*	0.08 ± 0.03
Oxyjulis californica	0.08 ± 0.03	0.008 ± 0.005	27.69	*Paralabrax clathratus*	0.10 ± 0.04
Citharichthys sordidus	0.00 ± 0.00	0.13 ± 0.010	17.94	*Halichoeres semicinctus*	0.02 ± 0.01
Halichoeres semicinctus	0.02 ± 0.01	0.00 ± 0.00	8.41	*Semicossyphus pulcher*	0.00 ± 0.00
Rhinogobiops nicholsii	0.00 ± 0.00	0.04 ± 0.03	6.94		
All taxa total	0.20 ± 0.09	0.18 ± 0.15	1.1× different	All taxa total	0.20 ± 0.09

1981), emigration to adjacent habitats as described elsewhere for urchins (Schroeter et al. 1983), and/or fluctuations in resource availability due to temperature changes (Steller et al. 2003, Foster et al. 2007).

Benthic grazer densities, such as *M. undosa* and *L. pictus*, differed between sampling times and may have altered macroalgal assemblages and percent cover, but few studies have examined grazer effects on epiphytic algae within rhodolith beds (Scherner et al. 2011). Future work should investigate potential interactions and feedbacks of these invertebrate community members on rhodolith survival and growth (Bracken et al. 2007). More experimentation is needed within rhodolith habitats to better understand the community dynamics of these understudied systems and their role as foundation species.

CONCLUSIONS

As one of the first ecological studies conducted in Santa Catalina Island rhodolith beds, these data establish patterns of how the abundance and composition of associated communities vary with habitat,

Avalon	Contr. (%)	Taxa	Isthmus	Avalon	Contr. (%)
Cover (%)			Cover (%)	Cover (%)	
15.3 ± 6.6	29.50	Dictyotales	3.1 ± 3.1	15.3 ± 6.6	35.02
4.7 ± 3.0	22.18	Fleshy reds	5.3 ± 5.3	4.7 ± 3.0	17.67
3.1 ± 0.8	16.92	Other browns	0.6 ± 0.6	3.1 ± 0.8	15.65
2.5 ± 2.1	16.67	Turf	2.2 ± 2.2	2.5 ± 2.1	13.56
6.3 ± 3.6	10.58	Geniculate corallines	0.0 ± 0.0	6.3 ± 3.6	12.70
31.9 ± 11.0	1.1× different	All taxa total	11.3 ± 8.8	31.9 ± 11.0	2.8× different
Density (ind. m^{-2})			Density (ind. m^{-2})	Density (ind. m^{-2})	
8171 ± 3372	21.93	Tanaids	6951 ± 3858	8171 ± 3372	22.18
1733 ± 744	11.66	Gammarids	3118 ± 1424	2473 ± 467	14.05
2473 ± 467	11.45	Ostracods	1884 ± 1323	1733 ± 744	11.86
829 ± 659	9.02	Polychaetes	1997 ± 211	2143 ± 632	10.16
2143 ± 632	8.94	Caprellids	556 ± 191	829 ± 659	8.11
664 ± 197	8.30	Bivalvia	509 ± 59	664 ± 197	5.83
17595 ± 4864	1.1× different	All taxa total	15862 ± 6857	17595 ± 4864	1.1× different
Density (ind. m^{-2})			Density (ind. m^{-2})	Density (ind. m^{-2})	
0.09 ± 0.04	21.93	*Californiconus californicus*	0.06 ± 0.03	0.09 ± 0.04	29.50
0.04 ± 0.03	20.09	*Pachycerianthus fimbriatus*	0.04 ± 0.02	0.04 ± 0.03	21.02
0.14 ± 0.08	14.00	*Lytechinus pictus*	0.04 ± 0.02	0.14 ± 0.14	13.56
0.002 ± 0.002	12.55	*Navanax inermis*	0.04 ± 0.02	0.002 ± 0.002	10.77
0.02 ± 0.01	6.92	*Megastraea undosa*	0.03 ± 0.02	0.14 ± 0.08	10.56
0.14 ± 0.14	6.79	*Lirularia* spp.	0.03 ± 0.02	0.02 ± 0.01	5.75
0.40 ± 0.26	2.0× different	All taxa total	0.25 ± 0.08	0.42 ± 0.27	1.7× different
Density (ind. m^{-2})			Density (ind. m^{-2})	Density (ind. m^{-2})	
0.30 ± 0.09	45.74	*Oxyjulis californica*	0.008 ± 0.005	0.30 ± 0.09	44.90
0.006 ± 0.006	27.00	*Paralabrax clathratus*	0.01 ± 0.01	0.006 ± 0.006	21.49
0.009 ± 0.004	12.42	*Citharichthys sordidus*	0.13 ± 0.010	0.009 ± 0.004	12.42
0.003 ± 0.002	8.42	*Semicossyphus pulcher*	0.03 ± 0.02	0.003 ± 0.002	6.58
		Halichoeres semicinctus	0.00 ± 0.00	0.02 ± 0.01	5.29
0.41 ± 0.13	2.1× different	All taxa total	0.18 ± 0.15	0.41 ± 0.13	2.3× different

season, and by site. These data establish a baseline for future studies to compare temporal trends in Catalina rhodolith beds and with rhodolith beds worldwide. We observed patterns consistent with the structural reduction of rhodolith habitat associated with reduced abundance of all functional groups. This was most pronounced for infauna and epibenthic invertebrates; taxa utilizing rhodoliths as substrate for attachment, refuge from predation (Hall-Spencer 1998, Figueiredo et al. 2007), or as substrate for diatoms, biofilms, or for aggregating other food particles (Grall et al. 2006). Low recovery potential of

rhodolith bed communities is tied to slow growth rates of rhodoliths on the scale of mm yr^{-1} (Potin et al. 1990, Hall-Spencer & Moore 2000). With such low recovery potential, relatively small anthropogenic disturbances can have long-lasting effects on rhodolith population structure and their associated communities through reduced structural complexity (Steller & Cáceres-Martínez 2009).

Rhodolith beds are an excellent system to study the impact of structural complexity on smaller scales relative to more well-studied canopy-forming foundation species (Graham et al. 2007). More work is
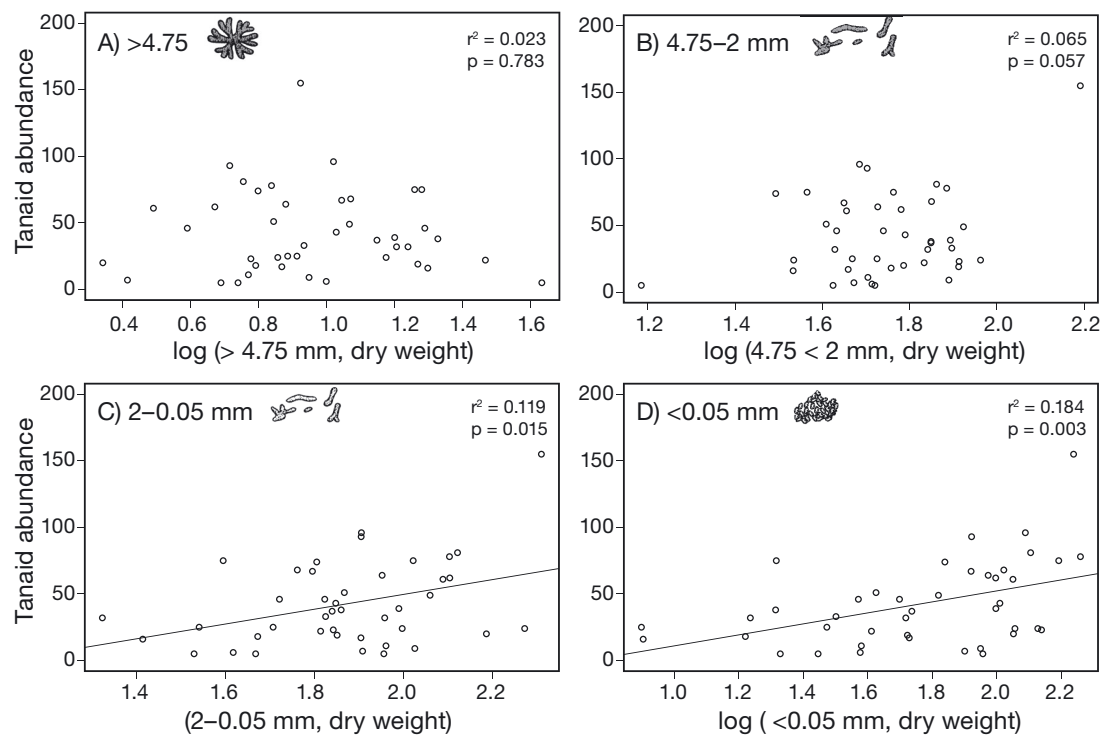
Fig. 7. Relationship between infaunal tanaid abundance relative to the log of dry weight of sediment size classes using a subset of cores (due to sediment data loss from 6 of 48 cores taken within rhodolith habitat, n = 42). Sediment was divided into (A) >4.75 mm, (B) 4.75–2 mm, (C) 2–0.05 mm, and (D) <0.05 mm

needed to determine the role of rhodoliths, relative to other foundation species, in provisioning energy and habitat in the Pacific and worldwide (Graham et al. 2016). Areas for future studies on rhodolith bed disturbance should consider impacts to trophic interactions (Kamenos et al. 2004c), food web trophic pathways (Grall et al. 2006), patterns of succession following disturbance (Hall-Spencer & Moore 2000), and the impacts of habitat fragmentation (as observed in seagrass landscapes; Hovel & Lipcius 2001) on community structure and function.

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