Sea anemone microhabitats enhance the diversity and biomass of mobile invertebrates on temperate rocky shores

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ABSTRACT: Sea anemones of the genus *Anthopleura* are abundant in rocky intertidal communities of the eastern Pacific, but their role as habitat and facilitators of biodiversity in this system has been overlooked. We provide evidence for a previously undescribed mechanism of facilitation associated with these cnidarians on temperate rocky shores. Sea anemones in the genus *Anthopleura* slowly release stored water at low tide, which helps them maintain ideal temperature conditions via evaporative cooling. This behavior results in leakage of water to surrounding intertidal habitats, producing unique microhabitats in the upper intertidal zone. We hypothesized that mobile invertebrate communities would use this habitat during low tides to ameliorate abiotic stress. In an *in situ* experiment spanning 3 sites along the coast of California, USA, it was found that maximum temperatures and relative desiccation rates were lower in sea anemone-associated microhabitats as compared to adjacent rock habitats. Observational surveys revealed higher richness and biomass of mobile invertebrates in sea anemone microhabitats, and these differences were supported by manipulative experiments that included both adding and removing sea anemones. Our results support a novel community-wide facilitation driven by an adaptation of intertidal sea anemones. The effects of sea anemone microhabitat on upper shore biodiversity were associated with site and sea anemone species and may suggest a facilitative role of a temperate cnidarian–algal mutualism in mitigating stress and enhancing biodiversity.

KEY WORDS: Biodiversity · Facilitation · Microhabitat · Rocky intertidal · Sea anemone

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1. INTRODUCTION

Positive interactions, including mutualism and facilitation, are an integral aspect of many ecosystems (Bertness & Callaway 1994, Stachowicz 2001). Examples include scleractinian corals and their dinoflagellate symbionts that provide structure for some of the most biodiverse ecosystems on earth (Bergsma 2012, Roth 2014) and ribbed mussels and cordgrass in salt marshes that provide a hard substrate for a diverse set of other species (Bertness 1984, Altieri et al. 2007, Angelini et al. 2015). The habitat that these species provide can increase the realized niches of associated species in stressful environments through facilitation (Crotty & Bertness 2015). Rocky intertidal habitats are harsh environments for marine organisms, and the upper distributional limits of species are typically set by abiotic stressors such as temperature and desiccation (Connell 1972). Some well-established groups that provide refuge to other spe-

cies in the rocky intertidal zone include mussels (Witman 1985, Seed 1996), rockweeds (Schmidt et al. 2011, Elsberry & Bracken 2021), and surfgrass (Crouch 1991, Moulton & Hacker 2011). These groups increase biodiversity largely by providing habitat — and ameliorating stress — for mobile invertebrates. Here, we propose that another well-known group of temperate rocky intertidal organisms, sea anemones, may also provide favorable microhabitats during low tides.

Sea anemones in the genus *Anthopleura* are prominent members of rocky intertidal zone communities in the northeastern Pacific Ocean, with members of the genus extending from Baja California, Mexico, to Alaska, USA (Hand 1955). Three species in this genus — *A. elegantissima*, *A. sola*, and *A. xanthogrammica* — maintain mutualistic symbioses with algae (Secord & Augustine 2000). Their tidal range extends from the subtidal zone to the upper intertidal zone, where they are usually found in habitats exposed to high levels of solar irradiance (S. A. Bedgood unpubl. data). Their densities are highest in the mid- and upper intertidal zones (S. A. Bedgood unpubl. data). All 3 species host algal symbionts that can provide 13 to 70% of their dietary carbon (Fitt 1982, Levine & Muller-Parker 2012). Sea anemones are not completely sessile (Bedgood et al. 2020), and anemones with algal symbionts move towards light to maximize the photosynthesis of algae, choosing high-light habitats (Pearse 1974, Secord & Muller-Parker 2005). However, the light intensities required to maximize algal photosynthesis also result in high temperatures during daytime low tides that can result in a breakdown of the anemone–algal mutualism (dysbiosis; Muller-Parker et al. 2007). At low tide, sea anemones leak water from their gastrovascular cavity (Shick & Dykens 1984; Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m715p057_supp.pdf), reducing their temperature by evaporative cooling (Bingham et al. 2011), and it has been hypothesized that this behavior reduces the risk of dysbiosis or loss of algae. Bingham et al. (2011) found that *A. elegantissima* lost up to 91% of its wet weight via release and evaporation of water over 9 h in a wind tunnel, maintaining body temperatures as much as 6°C below ambient temperatures. This behavior has the potential to produce a unique microhabitat by ameliorating extreme temperatures and reducing local desiccation stress in the vicinity of sea anemones during low tides, especially in the upper intertidal zone, where sea anemones are one of the only biotic habitat providers (S. A. Bedgood pers. obs.).

Sea anemones in the genus *Anthopleura* employ 2 major life history strategies: solitary and clonal aggregating (Pearse & Francis 2000). The solitary strategy, here represented by *A. sola*, is aggressive towards other anemones and is therefore found alone. The clonal aggregating species, *A. elegantissima*, reproduces asexually, creating large clonal mats in the intertidal zone (Francis 1979). *A. sola* anemones are on average larger (3–4 cm diameter) than *A. elegantissima* (1–2 cm diameter) and have a larger biomass per area (Bedgood 2021), but *A. elegantissima* colonies have more interstitial spaces, both on the edges of colonies and between individuals within a colony.

The present study investigates whether *A. elegantissima* and *A. sola* sea anemones provide favorable microhabitats at low tide to a diverse group of mobile invertebrates along the California coastline. To accomplish this, we compared sea anemone habitat (areas surrounding sea anemones) to adjacent rock habitat (Fig. 1A). We hypothesized that sea anemones would ameliorate temperature and desiccation stress, enhancing mobile invertebrate diversity and abundance, and predicted that (1) maximum temperatures and rates of desiccation during low tides would be lower in sea anemone microhabitat, (2) mobile invertebrate richness and biomass would be higher in sea anemone microhabitat, and (3) manipulating sea anemone microhabitat (removal or addition) would change the richness and/or biomass of mobile invertebrates.

2. MATERIALS AND METHODS

2.1. Sites and habitat

We chose 3 rocky intertidal sites along the California coast with unique mobile invertebrate community assemblages, including (from north to south) Kenneth S. Norris Rancho Marino Reserve (hereafter RMR; 35.5392° N, 121.0152° W), Coal Oil Point Reserve (hereafter COP; 34.4072° N, 119.8785° W), and Corona del Mar State Beach (hereafter CDM; 33.5882° N, 117.8677° W). In the upper intertidal zone at these 3 sites, sea anemones and occasionally rockweed algae are the only conspicuous biotic habitat providers. Only *Anthopleura elegantissima* can be found in the exposed upper intertidal zone at CDM, but our other 2 sites included both *A. elegantissima* and *A. sola*. We established paired survey plots with sea anemone habitat and adjacent rock habitat (CDM n = 19, COP n = 36, RMR n = 43). The
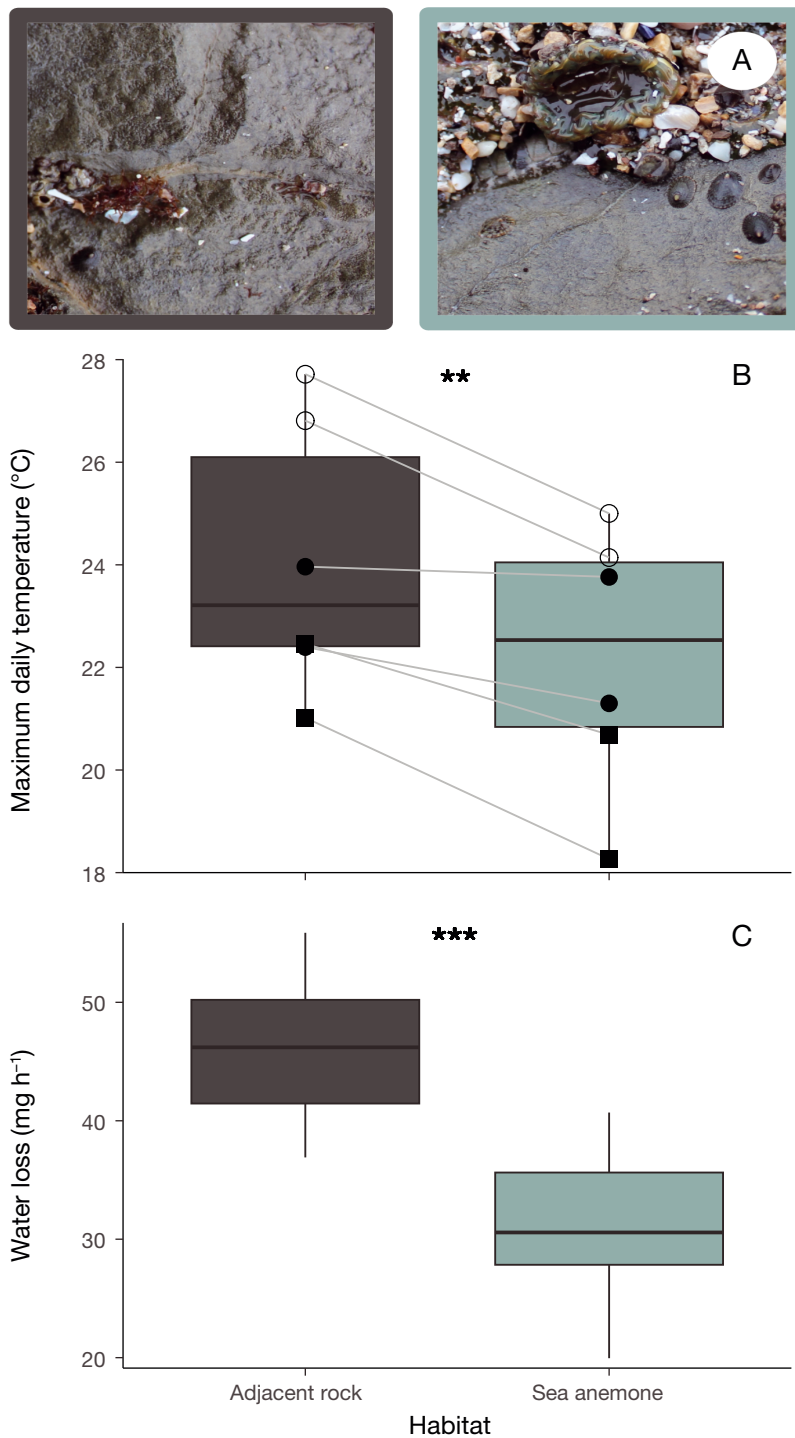
Fig. 1. Abiotic factors measured in sea anemone (light gray) and adjacent rock habitats (dark gray). (A) Example of paired habitat plots from Corona del Mar State Beach (CDM). (B) Maximum daily temperatures in each habitat. Points represent the mean temperature (n = 10) for each logger, with gray lines connecting paired loggers. Open circle: *Anthopleura elegantissima* habitat at CDM; filled circle: *A. elegantissima* habitat at Rancho Marino Reserve (RMR); filled square: *A. sola* habitat at RMR. (C) Relative desiccation (water loss) rates in each habitat type at RMR. These data are from different plots than temperature. Data were paired, but individual data points and connecting lines are not shown for simplicity (n = 18 pairs). **p < 0.01, ***p < 0.001

number of sea anemones in *A. sola* plots was always 1 because they are solitary, but *A. elegantissima* plots ranged in colony size between 5 and 18 individuals.

Sea anemone habitat was defined as the area immediately surrounding an anemone (*A. sola*) or anemone colony (*A. elegantissima*), from contact with the anemone(s) to 5 cm away from the anemone(s), creating a band along the perimeter (see Fig. S2). This band was chosen based on previous research by S.A.B. on the spatial patterning of mobile invertebrates around *A. elegantissima*. Most mobile invertebrates that associate with sea anemones are found in contact with the anemone column (Fig. S3). We established paired adjacent rock habitats at the same tide height between 10 and 30 cm from anemone habitat, measured from plot edge to plot edge. These survey areas were chosen to closely match the substrate immediately surrounding the paired anemone habitat, including orientation, crevices, and surface texture, but without the effect of water leakage from or contact with the nearby anemones. We took images of each sea anemone plot (scale included) and used ImageJ (Schneider et al. 2012) to measure the plot area. Adjacent rock plots were surveyed with a fixed circular quadrat (81 cm^2).

We used effective tidal elevations associated with the distributions of characteristic intertidal organisms (Benson 2002, Harley & Helmuth 2003) to identify a similar location for our sea anemone microhabitat plots in the mid- to upper intertidal zones at all 3 locations. This region varied in tide height among sites: between +0.55 and +1.02 m above mean lower low water (MLLW) at CDM (n = 19 pairs), between +0.37 and +1.02 m above MLLW at COP (n = 36 pairs), and between +0.31 and +1.28 m above MLLW at RMR (n = 43 pairs). We measured the elevation (above MLLW) of each plot pair because mobile invertebrate

communities are strongly influenced by elevation, even over a small range.

2.2. Abiotic measurements

We deployed 20 temperature loggers (CDM n = 2 pairs, COP n = 4 pairs, RMR n = 4 pairs) in anemone habitat and adjacent rock habitat across all 3 sites from July to August 2019, but data from COP were excluded because sand covered the loggers shortly after they were deployed. It was not clear which invertebrates would use these habitats at the time of deployment, so no modification was made to the loggers (i.e. mimicry of invertebrates for temperature logging; Fitzhenry et al. 2004, Lima & Wethey 2009). We filtered data to include the 10 lowest tides that fell within daylight hours (09:00–17:00 h) and took the highest temperature from each interval at RMR and CDM. To measure relative desiccation rates, we soaked 40 chipboard (a type of cardboard; RMR n = 20 pairs) discs that were 1.5 mm thick and 2 cm in diameter in saltwater before placing them in paired habitat plots for 2 h (during a daytime low tide) at RMR during August 2019. After collecting, we calculated the difference in weight of the discs between the start and end of exposure.

2.3. Community surveys

We counted mobile invertebrates, which included a broad range of animals including gastropods, crustaceans, and annelids, in paired established plots (see Section 2.1 for plot design) 2 times at our 3 sites (June 2019). We recorded and calculated 3 community metrics: richness, biomass, and proportional abundance between habitats. Mobile invertebrate species that are parasites of sea anemones (pycnogonids and wentletrap snails) were not included in our richness and biomass data because their presence in sea anemone habitat was likely driven by a trophic interaction not solely by amelioration of abiotic stressors, but they were included in our proportional abundance data. Our measure of proportional abundance was the proportion of individuals of a species found in either habitat type within paired plots during our observational surveys, where −1 indicates that all individuals were found in the adjacent rock plot and 1 indicates that all were found in the sea anemone plot.

To accurately calculate biomass without disturbing communities in our plots, we collected a representative sample (n = 8–13) of the 14 most common species

found in our survey plots at CDM and RMR, which made up 95% of the total species surveyed. Any uncommon species (7 total) were not included in the biomass calculation and were found exclusively in sea anemone habitat. To determine an average biomass for each species, we determined ash-free dry mass (AFDM) by drying individuals in a 60°C oven to constant mass (≥48 h), weighing them, and then combusting them in a muffle furnace at 450°C for 4 h. AFDM was the difference between the dried and combusted masses, standardized by plot area.

To confirm that the effects of sea anemones on mobile invertebrate communities were causal, we manipulated anemone presence experimentally. Using the same plots as the observational surveys and randomly assigning treatment pairs, we created 4 treatments: anemone control, rock control, anemone removal, and anemone addition. The control treatments were paired and unmanipulated. We created the anemone removal treatment by slowly lifting the anemone's pedal disc off the substrate with a metal Scoopula™ (Thermo Fisher Scientific), being careful not to disturb nearby mobile invertebrates. To create the anemone addition treatment, the unattached anemone was moved to the paired adjacent rock habitat, where it was held against the substrate with nylon mesh secured to the rock with 4 anchored screws (Fig. S4). After approximately 48 h, when the anemone had reattached in the new location, we removed the mesh. These manipulated and control plots were left for 1 mo before surveying the mobile invertebrate communities as described previously.

2.4. Statistical analyses

All analyses were conducted in R version 4.0.5 (R Core Team 2021). A compiled list of sample sizes for each group included in the analyses described here can be found in Table S1 in the Supplement. Analyses included general and generalized linear mixed models when plots were measured multiple times or general and generalized linear models when there was no need for a random effect (p. 4 in Bates et al. 2015, Wickham et al. 2019). When an interaction between main effects was predicted (i.e. habitat × site), we compared models with and without the interaction using Bayesian's information criterion. All models were checked for fit with quantile–quantile plots of residuals to confirm assumptions of distributions (e.g. normal, Poisson). We used the function car::Anova (Fox & Weisberg 2019) for ANOVAs using F-tests whenever possible and chi-square likelihood

ratio tests in combination with generalized linear mixed models. Post hoc analyses were completed with the package emmeans using Tukey's adjustment (Lenth 2021). We used p < 0.05 as alpha for all analyses.

We filtered the logger temperature data before analysis by excluding data outside of the peak daytime hours 09:00 to 17:00 h, when solar radiation would affect temperatures the most, and then removed all remaining data except maximum temperatures for each habitat during the 10 lowest low tides during the data collection period. We treated multiple measurements from a single logger as repeated measures. We used habitat type, sea anemone species, and site as main effects and logger identification as a random effect. We analyzed the desiccation data in a similar way but did not include site or a random effect because measurements were taken at 1 site (RMR) and were not repeated.

We included 2 congeneric sea anemone species in our study, but the experimental design was not fully factorial for community data: *A. sola* was included at only 2 sites, while *A. elegantissima* was included at all 3. Additionally, differences in tide height and structure of the microhabitat made comparisons between the associated communities of our 2 anemone species inappropriate. For these reasons, we analyzed them separately, using the same approach for both.

We used a permutational multivariate analysis of variance (PERMANOVA) using the function vegan::adonis2 (Oksanen et al. 2022) to compare differences in associated mobile invertebrate communities during the second observational survey between habitat types and among sites, with tide height as a covariate. We standardized invertebrate counts with plot areas. Because some of our plots contained all zeros (double-zero problem), we used the zero-adjusted Bray-Curtis method by adding a column with the smallest non-zero value across all plots in the matrix (Clarke et al. 2006). We visualized the data with non-metric multidimensional scaling (NMDS) plots.

The community richness data were analyzed with generalized linear mixed models with the Poisson distribution (count data), while the biomass data were analyzed with a Gamma distribution with a log link (right-skewed data). We created models with habitat type (sea anemones or adjacent rock) and site as main effects and with tide height as a covariate. During the observational period, invertebrates were counted at 2 time points (surveys), and plots were paired. We included plot pair nested within survey as a random effect. This controlled for variation among surveys and plot pairs because these were assumed to be uncorrelated with main factors. All post hoc analyses were generated with emmeans.

The experimental data were analyzed as described above, except plots were not paired and invertebrates were only counted once (1 survey). Unlike during the observational portion, comparisons were made between a manipulated plot and a respective control (e.g. anemone addition compared to adjacent rock). Anemones were removed from an anemone plot and placed in the paired adjacent rock plot to avoid shock to the anemone (abiotic changes due to spatial differences). Plots were therefore treated as independent for these analyses, and no random effects were included.

We analyzed proportional abundance data in 11 of the most common mobile invertebrate genera or species separately with 2-sided *t*-tests, using the proportion of individuals in each habitat (bounded −1 to 1) as a response variable and a null hypothesis of no difference between habitats (0). This allowed us to visualize differences among species densities with large variations in total counts. We also analyzed raw counts between habitats using paired *t*-tests and noted if >60% of weighted observations per invertebrate species were found with 1 sea anemone species (Table 1).

3. RESULTS

3.1. Abiotic differences

Maximum temperatures during daytime low tides were substantially lower in sea anemone habitat as compared to adjacent rock habitat ($F_{1,8}$ = 7.38, p = 0.026; Fig. 1B). CDM experienced higher temperatures than RMR ($F_{1,8}$ = 13.21, p = 0.007). There was a relationship between sea anemone species and maximum temperatures ($F_{1,8}$ = 7.14, p = 0.028), likely because *Anthopleura elegantissima* habitat was higher than *A. sola* habitat in the intertidal zone ($F_{1,94}$ = 52.98, p < 0.001), but this could also result from differences in habitat types (e.g. orientation) between sea anemone species. Relative desiccation rates were lower in sea anemone habitat than in adjacent rock habitat ($F_{1,33}$ = 61.00, p < 0.001; Fig. 1C) regardless of sea anemone species ($F_{1,33}$ = 0.98, p = 0.330).

3.2. Community differences

Adjacent rock plots had fixed areas (81 cm^2), but sea anemone plots varied in size because the peri-

Table 1. Eleven most common mobile invertebrate species found in plots during the observational period. Sample size represents paired plots (adjacent rock and sea anemone plot are 1 replicate) where at least 1 individual was present. If >60% of weighted counts were made within 1 group (4 groups: *Anthopleura elegantissima*, *A. elegantissima* adjacent rock, *A. sola*, and *A. sola* adjacent rock), we note they were 'frequently found with' a specific group. N/A: no 1 group contained >60% of weighted counts. Counts were weighted by the number of plots within each group

Species	Common group	Paired plots (n)	Plot count (mean ± SE) Rock	Anemone	Paired t	t-test of of count p	Frequently found with
Lottia austrodigitalis	Limpet	28	1.86 ± 0.34	0.61 ± 0.19	2.93	0.007	N/A
Lottia scabra	Limpet	57	1.42 ± 0.15	0.77 ± 0.13	3.23	0.002	N/A
Littorina spp.	Herbivorous snail	125	7.63 ± 1.01	5.63 ± 0.54	2.03	0.044	N/A
Lottia limatula	Limpet	24	0.33 ± 0.10	0.83 ± 0.13	−2.3	0.031	N/A
Lottia strigatella	Limpet	132	1.95 ± 0.27	4.94 ± 0.64	−5.45	<0.001	*A. elegantissima*
Nuttallina californica	Chiton	17	0.24 ± 0.11	0.82 ± 0.13	−2.58	0.020	*A. elegantissima*
Tegula funebralis	Herbivorous snail	73	1.10 ± 0.21	8.30 ± 1.21	−6.26	<0.001	*A. sola*
Lepidozona spp.	Chiton	49	0.04 ± 0.03	1.18 ± 0.06	−16	<0.001	*A. elegantissima*
Epitonium tinctum	Predatory snail	66	0.02 ± 0.02	3.73 ± 0.40	−9.21	<0.001	*A. sola*
Mopalia muscosa	Chiton	23	0	1.74 ± 0.32	−5.51	<0.001	*A. sola* exclusively
Acanthinucella punctulata	Predatory snail	11	0	1.27 ± 0.19	−6.53	<0.001	*A. sola*

meter length changed based on anemone size (*A. sola*) or colony size (*A. elegantissima*). *A. elegantissima* sea anemone plots were slightly larger in area (83.7 ± 2.00 cm², mean ± SE) than paired adjacent rock plots (81 cm²), but this difference was not significant ($F_{1,96}$ = 1.87, p = 0.175). *A. sola* sea anemone plots were slightly smaller in area (73.7 ± 1.48 cm²) than paired adjacent rock plots (81 cm²; $F_{1,79}$ = 24.06, p < 0.001).

The PERMANOVA test showed that both habitat (*A. elegantissima* $F_{1,95}$ = 3.93, p = 0.002; *A. sola* $F_{1,78}$ = 10.43, p = 0.001) and site (*A. elegantissima* $F_{1,95}$ =

13.99, p = 0.001; *A. sola* $F_{1,78}$ = 43.21, p = 0.001) explained differences among community compositions for both sea anemone species. These differences are visualized by NMDS plots in Fig. 2 (2-dimensional visualization; *A. elegantissima* stress = 0.24, *A. sola* stress = 0.17). Tide height had an effect on *A. elegantissima* communities ($F_{1,95}$ = 5.67, p = 0.001) but not on *A. sola* communities ($F_{1,78}$ = 0.94, p = 0.43).

Biomass was standardized by area, but richness was not because richness does not scale linearly with area. If differences in richness were affected by the
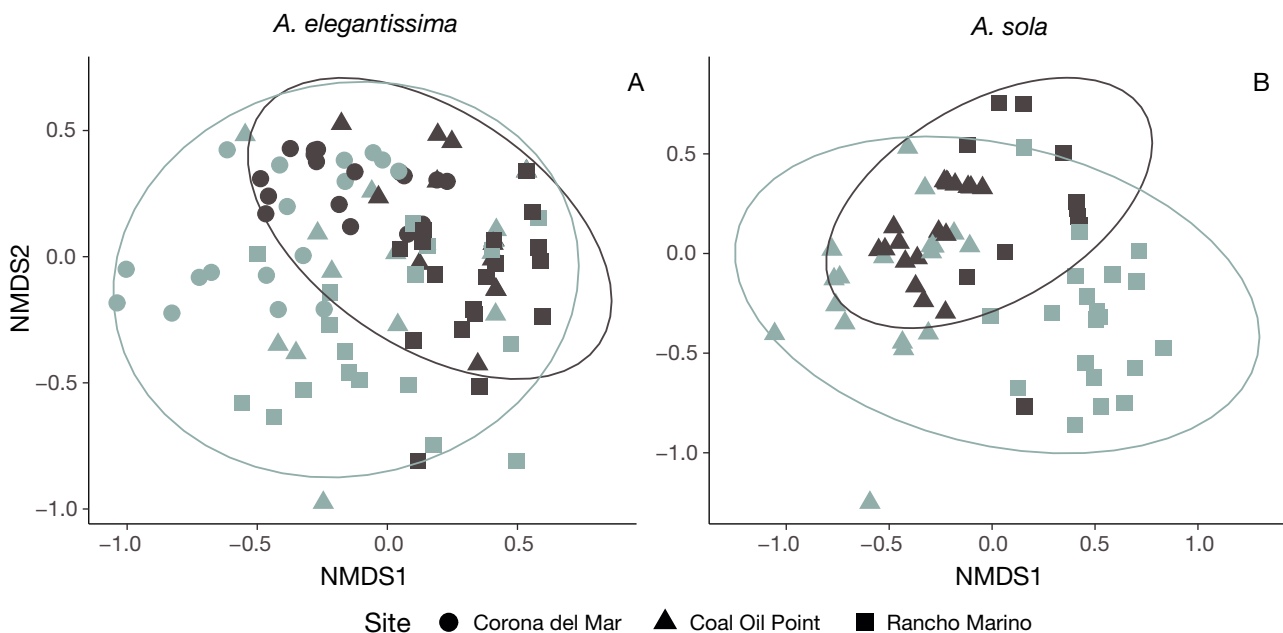

Fig. 2. Non-metric multidimensional scaling (NMDS) plots with Bray-Curtis dissimilarity of mobile invertebrate communities during the second observational survey separated by habitat type (light gray: sea anemone; dark gray: adjacent rock) and sites. (A) *Anthopleura elegantissima* sea anemone and adjacent rock habitats; stress = 0.24. (B) *A. sola* sea anemone and adjacent rock habitats; stress = 0.17. Ellipses represent 95% CI of a multivariate *t*-distribution of habitat type

small differences between *A. sola* and adjacent rock plots, it would favor higher richness in adjacent rock plots. Richness of mobile invertebrates was higher in sea anemone habitat than in adjacent rock habitat (Fig. 3A,B). Richness was affected by habitat in both

sea anemone species (*A. elegantissima* χ^2 =17.66, p < 0.001; *A. sola* χ^2 = 30.02, p < 0.001), and there was no effect of site on richness (*A. elegantissima* χ^2 = 1.50, p = 0.47; *A. sola* χ^2 = 1.96, p = 0.162). Similar to PERMANOVA results, tide height affected richness
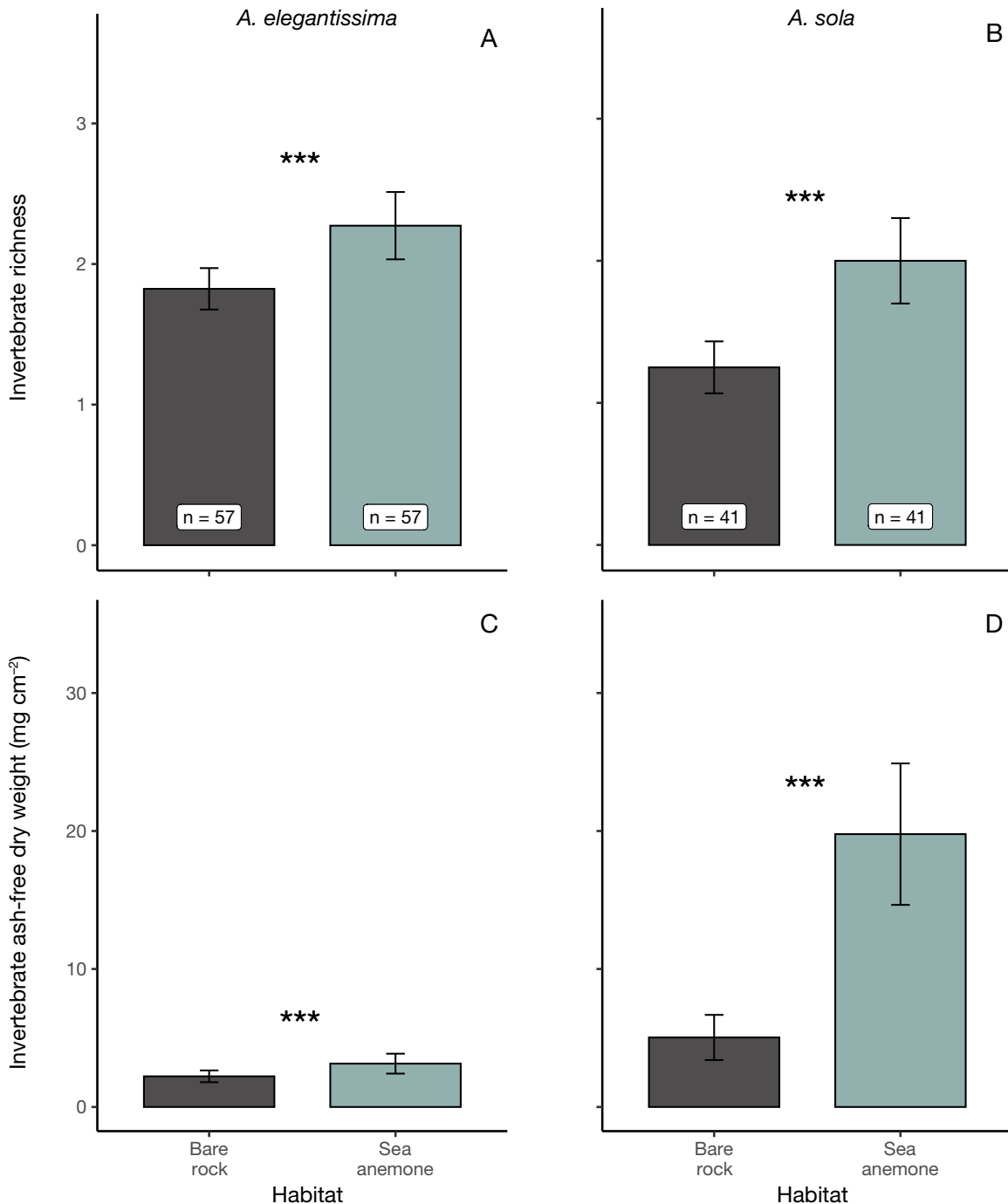
Fig. 3. Mobile invertebrate richness and biomass between habitats (rock: dark gray; sea anemone: light gray) during the observational period. (A,B) Invertebrate richness and (C,D) mobile invertebrate ash-free dry weight in (A,C) *Anthopleura elegantissima* and adjacent rock plots and (B,D) *A. sola* and adjacent rock plots. Sample sizes are listed at the bottom of bars in (A) and (B) and are the same between richness and biomass for respective bars. ***p < 0.001. Values are mean ± SE

only in the *A. elegantissima* analysis (χ^2 = 12.13, p < 0.001), increasing richness with tide height within the tidal range of this study (Fig. S5), but no effect of tide height was found in the *A. sola* analysis (χ^2 = 3.16, p = 0.076).

AFDM (biomass) of mobile invertebrates was generally higher in sea anemone plots than in adjacent rock habitat for both sea anemone species, but the magnitude of the difference between habitats was large between sea anemone species (Fig. 3). Biomass was affected by habitat (*A. elegantissima* χ^2 = 23.79, p < 0.001; *A. sola* χ^2 = 66.32, p < 0.001) but not by tide height (*A. elegantissima* χ^2 = 0.36, p = 0.551; *A. sola* χ^2 = 1.79, p = 0.181). There was an effect of site for *A. sola* (χ^2 = 59.87, p < 0.001); RMR had a higher overall biomass than COP for the *A. sola* analysis. There was also an interaction between habitat and site for *A. elegantissima* only (χ^2 = 13.16, p = 0.001), and a post hoc analysis showed that there was no difference in biomass between habitat types at one site, COP (z = 0.27, p = 0.786). The biomass of invertebrates between sea anemone species was starkly different. *A. elegantissima* plots had 3.14 ± 0.72 (mean ± SE) mg cm^{-2} AFDM as compared to 2.22 ± 0.43 mg cm^{-2} in the adjacent rock, a 41% larger mass. However, *A. sola* plots had 19.77 ± 5.13 mg cm^{-2} as compared to 5.04 ± 1.64 mg cm^{-2} in the adjacent rock, a 292% larger mass (Fig. 3C). This is because invertebrate species associated with *A. sola* tended to have a larger biomass than those associated with *A. elegantissima* (see Table 1). For example, *A. sola* plots at RMR frequently had 2 large herbivorous mollusk species with high biomass, *Mopalia muscosa* and *Tegula funebralis*.

One month after experimental manipulations, sea anemone addition plots tended to have higher richness and biomass than adjacent rock control plots, while anemone removal plots tended to have lower richness and biomass than sea anemone control plots (Fig. 4). However, effects of manipulation were sea anemone species specific. This could have been partly due to the low success of sea anemone addition treatments (Table S1). The addition of *A. sola* anemones increased richness and biomass in plots (richness $F_{1,10}$ = 16.82, p < 0.001; biomass $F_{1,10}$ = 5.70, p = 0.038), but the addition of *A. elegantissima* anemones (colony of ≥5) had no significant effect on either (richness $F_{1,28}$ = 0.04, p = 0.842; biomass $F_{1,28}$ = 0.13, p = 0.725). The removal of *A. sola* anemones decreased biomass but not richness (biomass $F_{1,32}$ = 11.10, p = 0.002; richness $F_{1,32}$ = 1.96, p = 0.171) because the abundance of large mobile invertebrate species decreased but were not absent from removal plots (S. A. Bedgood pers. obs., see Section 3.3). The opposite was true for the removal of *A. elegantissima* anemones, where richness decreased but biomass was unaffected (richness $F_{1,46}$ = 4.62, p = 0.037; biomass $F_{1,46}$ = 1.25, p = 0.270). There were fewer species present after the removal of *A. elegantissima* anemones, but other species (e.g. *Littorina*) took their place (S. A. Bedgood pers. obs.).

3.3. Mobile invertebrate density between habitats

Of the 11 most common species found in our plots, 7 were found in higher proportional density in sea anemone habitat, 2 were in higher proportional density in adjacent rock habitat, and 2 had no difference between habitats (Fig. 5, Table S2). Two species, the chiton *M. muscosa* and the predatory snail *Acanthinucella punctulata*, were exclusively found in sea anemone habitat during our surveys. *M. muscosa* was the most selective species, only being found tucked under the column of *A. sola* anemones during surveys (Table 1, 1.74 ± 0.32 ind. per anemone where present). The species found in the greatest number of plot pairs was *Lottia strigatella* (132 paired plots), and the most abundant species per plot was *T. funebralis* (8.30 ± 1.21 ind. in sea anemone plots). Both species were higher abundance in sea anemone habitat (*L. strigatella* t = −5.45, p < 0.001; *T. funebralis* t = −6.26, p < 0.001).

4. DISCUSSION

Our results support our hypothesis that sea anemones ameliorate temperature and desiccation stress, enhancing mobile invertebrate diversity and abundance and highlighting a novel community-wide role for *Anthopleura* sea anemones on temperate rocky shores. We found that sea anemone adjacent habitats had lower maximum temperatures and relative desiccation rates compared to the adjacent rock habitat and that these more benign intertidal habitats were favored by mobile invertebrates. We suggest that this results in higher richness and biomass of the mobile invertebrate communities in sea anemone habitat as compared to adjacent rock habitat, and our experimental manipulations suggest that the relationship is causal. However, future work should attempt to separate out the structural component of *Anthopleura* microhabitat from the unique water release behavior. This could be accomplished through sea anemone mimics deployed in adjacent habitat.
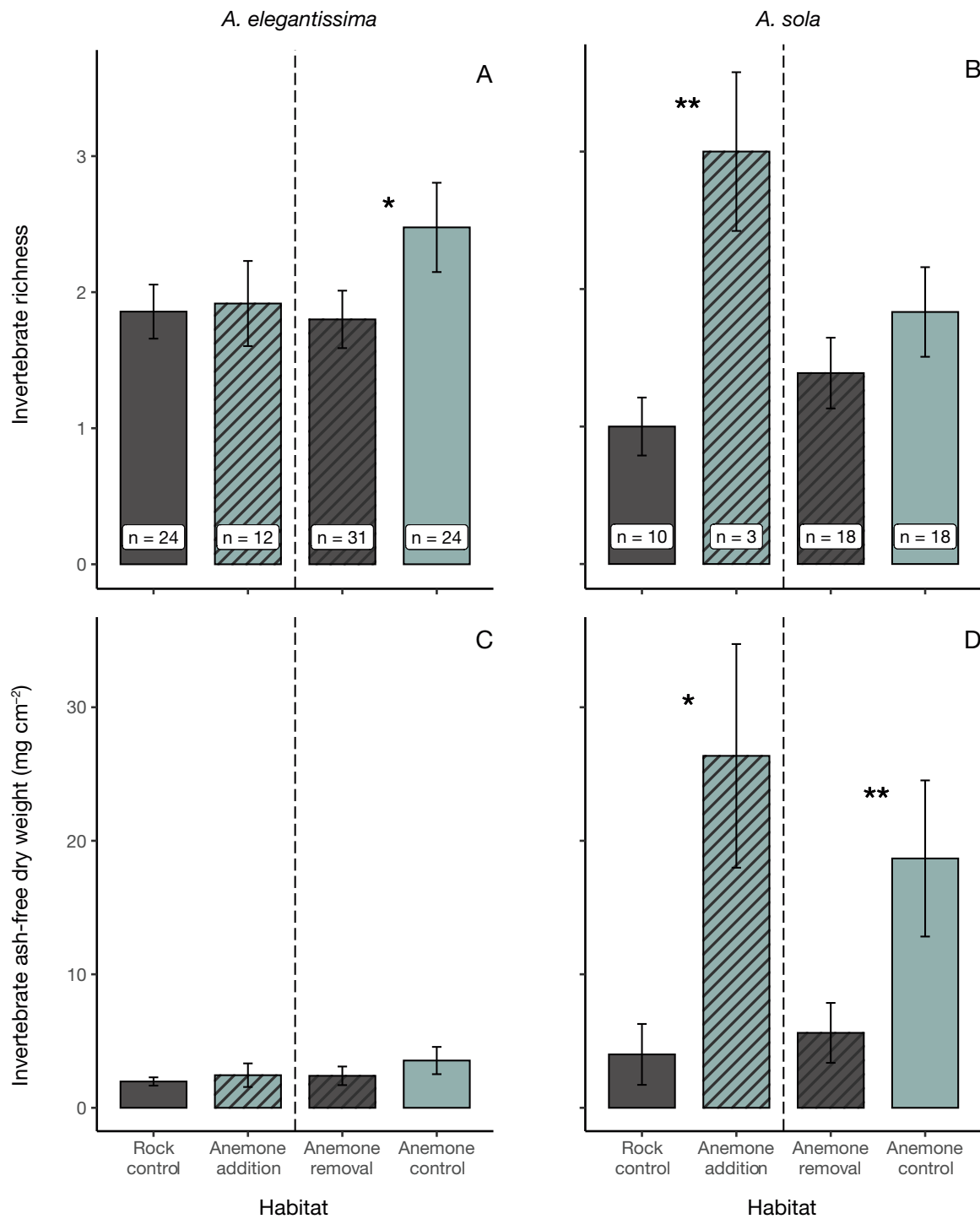
Fig. 4. Mobile invertebrate richness and biomass between habitats 1 mo after experimental treatments began. Vertical dashed lines separate paired comparisons; hatched bars represent manipulated plots while open bars represent controls. (A,B) Invertebrate richness and (C,D) mobile invertebrate ash-free dry weight in (A,C) *Anthopleura elegantissima* treatments with paired controls and (B,D) *A. sola* treatments with paired controls. Sample sizes are listed at the bottom of bars in (A) and (B) and are the same between richness and biomass for respective bars. *p < 0.05, **p < 0.01. Values are mean ± SE

Most mobile invertebrate species were found more frequently in sea anemone habitat than in adjacent rock habitat. *Epitonium tinctum*, a parasite of *An-*

thopleura sea anemones (Smith 1977), was almost always found in sea anemone habitat and likely used the anemones both as food and as a refuge during
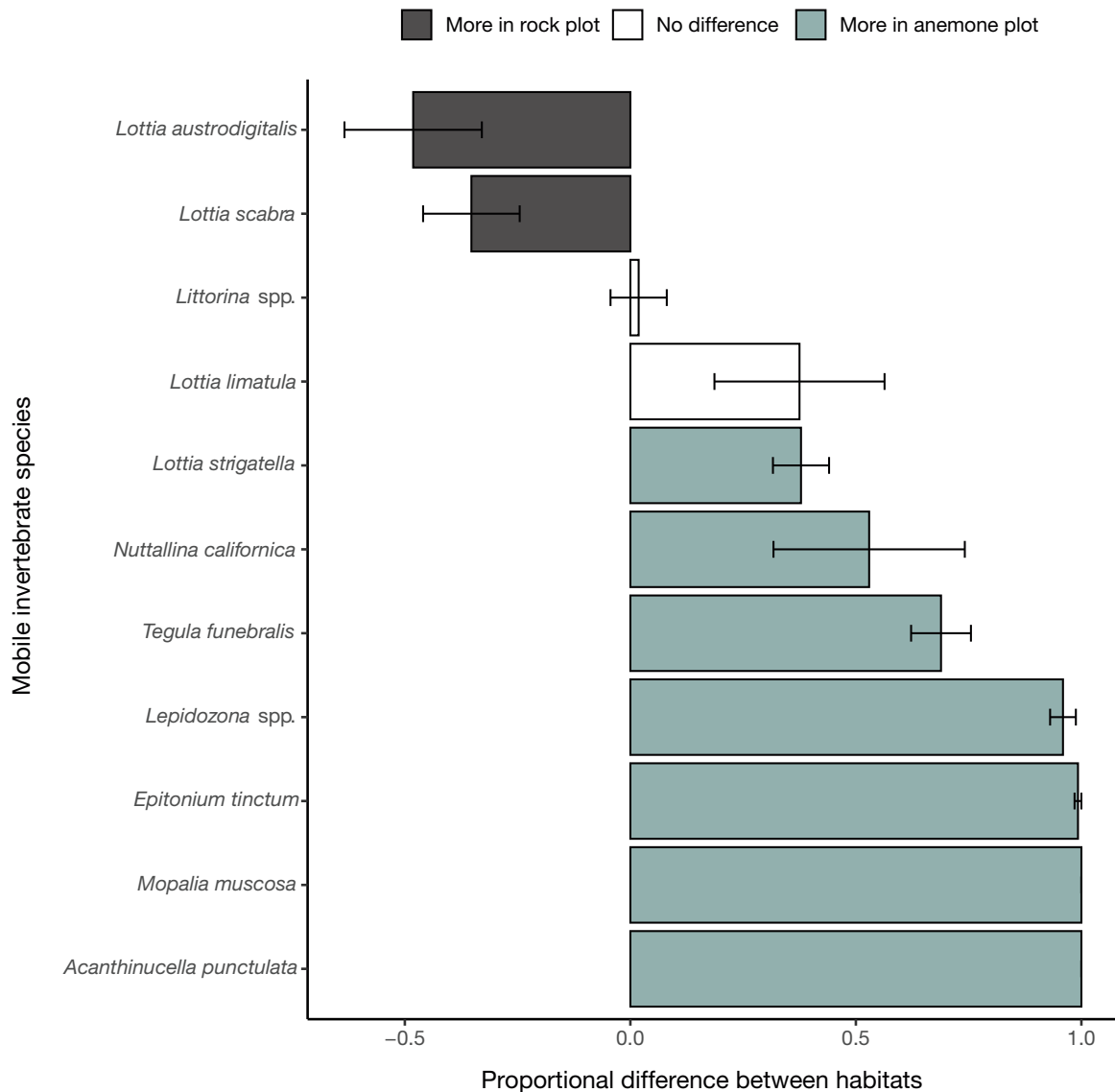
Fig. 5. Proportional density of individuals in each habitat of the most common mobile invertebrate species or genera found in our plots. Value of 1 indicates that all individuals were found in sea anemone habitat, 0 indicates an equal number found in each habitat, and −1 indicates that all individuals were found in adjacent rock habitat. Bar color illustrates a bias (or lack of) for either habitat type. Categories containing multiple species are indicated (spp.). Values are mean ± SE

low tides. All other species that preferred sea anemone habitat during low tide likely use this habitat as a temporary refuge, moving away from the sea anemone during high tides to forage since their food sources are found in adjacent habitat not next to anemones. The 2 species that preferred adjacent rock habitat, *Lottia austrodigitalis* and *L. scrabra*, are well adapted to survive in the upper intertidal zone, extending above our survey plots; they move to established areas during low tides that are not associated with sea anemone habitat (Frank 1965, Haven 1973).

The effect of site on richness and biomass was expected because each site had a unique community of mobile invertebrates, but the effect of sea anemone species on biomass was unexpected. Sea anemone size plays an important role in determining which invertebrates can take refuge in the microhabitat. *A. elegantissima* reproduces asexually, creating large but low-profile clonal mats, whereas *A. sola* reproduces only sexually and grows more vertically (Pearse & Francis 2000). Larger invertebrate species like the chiton *Mopalia muscosa* and the turban snail *Tegula funebralis* may only be able to take refuge next to

A. sola, where they would benefit from increased contact with the sea anemone. Our experimental results suggest that the habitat provided by *A. sola* may attract a wider range of larger mobile invertebrates.

The importance of the similar cnidarian–algal mutualism between tropical corals (Cnidaria: Scleractinia) and symbiotic algae has been well established, as the mutualism is essential for providing habitat and enhancing biodiversity in tropical low-nutrient ecosystems (Hatcher 1990, Urbina-Barreto et al. 2021). However, the broader effects of the mutualism between sea anemones (Cnidaria: Actinaria) and symbiotic algae have not been similarly studied in high-nutrient temperate systems. This may be because coral reefs depend on the coral–algal mutualism to provide resources in an otherwise nutrient-poor environment, whereas anemone–algal mutualisms on nutrient-rich temperate rocky shores, where primary producers are diverse and abundant (Muller-Parker & Davy 2001), are less obviously important. The sea anemone microhabitat described here could be a direct result of adaptation (water leaking at low tide) to maintain a stable symbiosis with symbiotic algae, keeping maximum temperatures within the thermal limits of the algae (Bingham et al. 2011). Future research should investigate whether the mutualism between these sea anemones and their algae directly results in the creation of this microhabitat. Here, we show that sea anemones that maintain a symbiosis with algae on temperate shores help to mitigate physical stress, allowing the persistence of a variety of taxa during stressful low tide conditions. We demonstrate the community-wide importance of temperate cnidarians, highlighting the role of these sea anemones in ameliorating stress and structuring communities.

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