Stargrazing: Trophic ecology of sea stars in the Galápagos rocky subtidal zone

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Research Article

Keywords: Sea stars, trophic ecology, herbivores, Galápagos, Asteroidea, urchin predators, marine reserves

Posted Date: June 7th, 2021

DOI: <https://doi.org/10.21203/rs.3.rs-192353/v1>

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Abstract

Sea stars (class Asteroidea) can play powerful and wide-ranging roles as consumers of algae and prey items in benthic ecosystems worldwide. In the Galápagos rocky subtidal zone, sea stars are abundant and diverse but their distribution, feeding habits and ecological impacts have received little attention. We compared diets and distributions across the six most abundant sea star species to examine functional roles of this important group. Bi-annual censuses carried out between 2006–2014 at two depths (6–8m, 12–15m) at 12 sites in Galápagos identified two abundance “hotspots” and revealed higher densities at locations with more heterogeneous benthic topographies. Field surveys revealed a high incidence of feeding (35–68% of individuals across species) and distinct diets were evident for each species in terms of food items and dietary breadth, suggesting niche partitioning. Most species can be classified as facultative herbivores, with diets dominated by crustose and turf algae supplemented by a small proportion of sessile invertebrates. The two most abundant species (*Pentaceraster cumingi* and *Nidorellia armata*) had the narrowest diets. Field prey selectivity experiments identified *P. cumingi* as a size-selective predator of the pencil urchin *Eucidaris galapagensis*. In field caging experiments, *N. armata* reduced biomass of unbleached crustose coralline algae and macroalgae by 72% and 52%, respectively. In the context of emerging threats such as disease, ocean acidification and climate change, a deeper understanding of distinct functional roles can inform ecological models and management plans.

1. Introduction

Sea stars (class Asteroidea) have played a pioneering role in experimental marine ecology as some of the first organisms to be manipulated in field experiments (Paine 1966; Menge 1982; McClintock 1994; Sanford 1999). They are widespread and versatile consumers that are represented in various trophic groups including predators, herbivores and detritivores (Menge 1982, Guillou 1996, Mah & Blake 2012, Martinez et al. 2017). As sea stars typically feed opportunistically and their diet varies depending on local availability of prey, they are usually considered generalists (Mauzey et al. 1968; Sloan 1980; Tokeshi et al. 1989). Sea stars also have versatile digestive systems, which can process multiple types and sizes of prey including many macroalgae (Martinez et al. 2017) and nearly all animal phyla (Jangoux 1982; Menge 1982). Sea star feeding can take place intraorally or extraorally, with extraoral feeding – where the stomach is everted over food items – being most common (Jangoux and Lawrence 1982). Many species have developed unique behavioral feeding techniques, such as digging and chipping off shells, which allow them to exploit prey types inaccessible to other species and may facilitate prey specialization and niche partitioning (Mauzey et al. 1968).

Sea star feeding habits can wield great influence in shaping the ecosystems around them, with impacts on community structure and aspects of ecosystem functioning recorded from polar to tropical latitudes (Dayton et al. 1974; Menge 1982; Scheibling 1982; McClintock 1994; De’ath and Moran 1998). Some species such as *Pisaster ochraceus* and *Heliaster helianthus* have been identified as keystone predators (Paine 1966; Menge and Freidenburg 2001; Gaymer and Himmelman 2008) because of their direct and indirect effects on the diversity and abundance of other species. In addition, predatory sea stars can drive

trophic cascades (Schultz et al. 2016) and alter the composition of subtidal benthic communities by preying on ecologically important herbivores such as sea urchins, and foundation species such as corals (Birkeland 1989) and mussels (Witman et al. 2003). Although diets and ecological roles are known to vary widely, research has often either focused on a single species (Dayton et al. 1977; Scheibling 1982; Wulff 1995; Schultz et al. 2016) or included groupings of “Asteroids” or “Echinoderms” in estimates of ecosystem functioning (Okey et al. 2004), rather than exploring trophic variation or interactions across species (Gaymer and Himmelman 2008; McClintock et al. 2008; Martinez et al. 2017).

Moreover, the bulk of studies on sea stars have taken place in the intertidal zone, where experiments can be more feasible to conduct and diversity tends to be lower than in the subtidal (Menge 1982). However, sea stars are also important components of subtidal communities (Mauzey et al. 1968; Dayton et al. 1974; Scheibling 1982; McClintock 1985; Wulff 1995; Martinez et al. 2017).

Trophic roles of sea stars in subtidal habitats may be broader (Menge 1982) or even completely different at the species level than in intertidal ecosystems (Gaymer and Himmelman 2008). The large area encompassed by subtidal ecosystems and the global ubiquity of sea stars necessitates a better understanding of sea star diversity and ecological function in subtidal habitats. This is particularly important given the multiple anthropogenic threats currently facing sea stars. For example, the outbreak of sea star wasting disease in North America during 2013 affected over 20 species and caused severe declines in sea star populations throughout the region (Menge et al. 2016; Montecino-Latorre et al. 2016). This mass mortality triggered changes in ecological dynamics, providing further evidence for the role of predatory sea stars in trophic cascades (Schultz et al. 2016). The effects of ocean acidification on sea stars’ calcified body structures and behavior are also of concern, with exposure to acidification in lab experiments leading to a reduction in feeding and growth rates (Appelhans et al. 2014). Sea stars are also under threat from collection for the aquarium and souvenir trades (Micael et al. 2009). Collectively, these impacts underscore the need for quantitative baseline data and manipulative experiments to elucidate the ecological roles of sea stars (Martinez et al. 2017), especially in priority conservation regions such as the Galápagos Marine Reserve.

In the Galápagos Islands, sea stars are a diverse and abundant group, but their ecological role has received little attention in comparison to other species such as sea urchins and sea cucumbers, perhaps due to a lack of value tied to human consumption (Gómez Alfaro 2010; Low 2012; Sonnenholzner et al. 2013). There are 44 species of sea stars reported from the Galápagos, 17 of which can be found in shallow depths (up to 20 m) and two of which are endemic (Maluf 1991). Overall, the number of Asteroid species and endemism increases with depth (Maluf 1991), but the role of other environmental variables in driving sea star distributions in the region is unknown. Information regarding the trophic ecology and ecological impacts of sea stars in the region is also sparse, despite their relatively high abundance and contribution to total biomass (Gómez Alfaro 2010; Sonnenholzner et al. 2013). For example, Okey et al. (2004) estimated the biomass of sea stars in Galápagos as 10.49 tonnes/km², higher than other important consumers such as lobsters (3.00–4.00), groupers (7.14) and sharks (0.75).

Previous efforts to include asteroids in a food web energy flow model of the Galápagos subtidal rocky reefs assumed that all sea star species were functionally equivalent with respect to diet, rates of production and consumption, life history, and habitat associations, combining them into a single functional group “Asteroids” (Okey et al. 2004). Similarly, all sea star species were lumped as Asteroids in a large-scale assessment of the effects of marine protected areas on benthic community structure and functioning in the Tropical Eastern Pacific (Edgar et al. 2011). Sea stars and sea urchins were also pooled into a single group in order to predict biomass changes resulting from the 1997–1998 El Niño (Wolff et al. 2012). Subsequent research suggests that pooling sea stars across species and with other echinoderm classes is not valid. For example, manipulative experiments with sea urchins in the Galápagos have revealed striking variation among species in terms of feeding rates, prey selectivity, grazing impact and susceptibility to predation (Irving and Witman 2009; Brandt et al. 2012; Witman et al. 2017).

A greater understanding of sea star functional roles and feeding behavior in the Galápagos could illuminate interactions impacting subtidal community structure and ecosystem functioning and inform future studies of the effects of functional diversity. We sought to fill this information gap by investigating the distribution and ecological roles of six common sea star species in shallow subtidal rocky reefs of the Galápagos Islands and by conducting feeding experiments with the two most abundant species, *Pentaceraster cumingi* and *Nidorellia armata*. To our knowledge, these represent the first manipulative feeding experiments involving sea stars conducted in the Galápagos subtidal ecosystem.

Four overarching questions were addressed in the present study, namely: 1) How does the abundance of sea stars vary among species, sites, habitats and depths in the Galápagos rocky subtidal zone? 2) What do sea stars consume and how do their diets vary among species, in terms of prey items and diet breadth? 3) Is predation by the common sea star *P. cumingi* on *Eucidaris galapagensis* pencil urchins size-selective? and similarly, 4) Does feeding by the common sea star *N. armata* affect the biomass of invertebrates, crustose coralline algae and benthic macroalgae?

2. Materials And Methods

2.1. Study area & sampling methods

We conducted abundance and feeding surveys of sea stars at 12 subtidal sites in the central Galápagos archipelago between June 2011 and January 2014 (Figs. 1 & 2; Supplementary Table 1). These sites span approximately 6,000 km² of the Galápagos Marine Reserve, which was designated in 1998 (Jones 2013). Marine communities at each site were monitored bi-annually along “shallow” (6–8 m) and “deep” (12–15 m) permanent transects where researchers have recorded temperature, abundance of mobile invertebrates, and epifaunal invertebrate community structure since 1999 (Witman et al. 2010; Beltram et al. 2019). The substrate at these sites largely consists of vertical rock walls and sloping rock ledges that often include “terraces” of horizontal rock substrate. Sandy habitats and patches of rock rubble occur at the base of ledges at some sites. Environmental conditions at the sites vary considerably in terms of the

strength of upwelling, topography, and the diversity and abundance of sessile filter feeders and consumers such as sea urchins, whelks and fish (Witman et al. 2010; Lamb et al. 2018, 2020).

Divers counted and recorded all sea stars along 30.0 m x 2.0 m transects, conducting one transect per site and depth during each sampling period. All statistical analyses were conducted on data at the transect level, and transects from different time periods were considered replicate surveys for each site and depth. Sites were categorized into one of three habitat categories: “wall” – a nearly vertical wall with no sediment-covered flat surfaces, “terrace” – alternating vertical and horizontal substrates with sediment accumulation, and “mixed” substrate of boulders, small walls, rubble, and sand (for examples see Fig. 3).

Feeding surveys were conducted at 12 sites from June 2011 to July 2012. Three 10.0 m x 2.0 m transects were conducted per site to assess sea star size and feeding. We collected diet data for the six most common species of sea stars (Fig. 1): *Asteropsis carinifera* (Lamarck 1816), *Mithrodia bradleyi* (Verrill 1867), *Nidorellia armata* (Gray 1840), *Pharia pyramidata* (Gray 1840), *Phataria unifascialis* (Gray 1840), and *Pentaceraster cumingi* (Gray 1840). Roving surveys were also conducted, comprising a search of the bottom area of several hundred square meters around the study site, with all sea stars encountered by divers recorded and checked for feeding. Sea stars were assumed to be feeding if the cardiac stomach was everted, and the prey encountered in the folds of the stomach or on the substratum directly beneath it was recorded. All species assessed are characterized in the literature as extraoral feeders, meaning that feeding behavior should be detectable through these methods (Jangoux and Lawrence 1982). Food categories encompassed pencil urchins (*Eucidaris galapagensis*), sessile invertebrates, sediment, macroalgae, diatoms, fleshy crustose algae (including *Hildenbrandia* sp. and *Codium* sp.) and crustose coralline algae (CCA) such as *Lithophyllum* sp. Sea star sizes were determined by measuring radial length (R) along the ambulacral groove, from the mouth to the tip of the longest arm. From June 2013 to January 2014, feeding surveys were restricted to *N. armata* at nine sites. These transects had a length of 30.0 m and a width of 1.5 m, and were used to evaluate size (R), feeding rates (by percent feeding) and prey items. We also surveyed feeding behavior of *P. cumingi* at one site (Islote Gardner) in January 2018 using the same method.

In order to cover a larger area of non-wall habitats and assess abundance patterns at a larger scale than the 60.0 m² transects, we also counted sea stars in two replicate 150.0 m² permanently marked plots using video surveys at five sites (BAL, CHA, GF, LC, and RB; Fig. 2 & Supplementary Fig. 1) in 2014 and 2015, with one plot video recorded each year at another site (RC). The plots were located on gently sloping rock substrate between 7 to 12 m depth, which was different than the primarily vertical rock walls where the sea star counts in the 60.0 m² transects were conducted. Using a GoPro5 camera, a diver video recorded the rectangular (30 x 5 m) plots in a pattern of alternating, overlapping lines on the sea floor while swimming above them. One plot was located within 20 m of the transect locations on the rock walls, while the other was at least 50 m away. For consistency, the same person (J. Witman) video recorded the same 150.0 m² plots each year and analysed the videos by counting sea stars to derive abundance data.

2.2. Design of experiments

To address prospective ecological impacts of the two most abundant sea stars, a prey selection experiment and a manipulative feeding experiment were carried out at the northeast corner of Baltra Island (BAL site, Fig. 2). The prey selection experiment with *P. cumingi* was conducted in January 2012, and the feeding experiment with *N. armata* between July and November 2013.

2.2.1. *P. cumingi* prey selection experiment

We hypothesized that *P. cumingi* is a size-dependent predator of *E. galapagensis* pencil urchins, given differences in survival across size classes and observations of predation documented in Dee et al. (2012) which were challenged by Martinez et al. (2017). Accordingly, we carried out a prey selection experiment (Fig. 4b) in January 2012, setting up cages at approximately 15m depth in a mixed habitat of sand and rubble at the base of rock slopes where *P. cumingi* is naturally abundant. Temperatures at the Baltra site, where this experiment occurred, averaged 24.6°C over the study period (Supplementary Table 2). Since *E. galapagensis* in the central Galápagos generally exhibits a bimodal size distribution with small (2.0–3.0 cm test diameter) and large (5.0–6.0 cm test diameter) modes (Dee et al. 2012), we used urchins in these two size classes to test for size-selective predation by *P. cumingi*.

The selectivity experiments were conducted in circular open bottom cages with a diameter of 1.10 m and area of 0.95 m², constructed of plastic-coated steel Aquamesh (Fig. 4b). The 3.5 cm mesh size was small enough to contain *P. cumingi* and *E. galapagensis* individuals, and exclude other urchin predators such as triggerfish (f. Balistidae) and Mexican hogfish (*Bodianus diplotaenia*) (Witman et al. 2017). A total of seven cages were deployed at 15m depth for four days. Each cage was stocked with one *P. cumingi* individual (R = 15.0–16.5 cm), five small *E. galapagensis* (2.0–3.0 cm test diameter), and five large *E. galapagensis* (5.0–6.0 cm diameter), to simulate natural densities of both species (Brandt et al. 2012; Witman et al. 2017; Lamb et al. 2020). Each sea urchin was tethered to a small, naturally occurring cobble to prevent escapes using a non-invasive tethering technique (Dee et al. 2012; Witman et al. 2017) to minimize procedural effects.

The cages were inspected by scuba divers at 20, 24 and 90 hours after the start of the experiment. At each time interval, feeding activity of the caged *P. cumingi* was noted and each of the ten urchins was classified as alive, consumed or escaped. Urchins were considered consumed by *P. cumingi* if predation was directly observed or if hollowed out urchin tests – characteristic of predation by *P. cumingi* (Fig. 4a) – were found in the cages during periodic inspections. Urchins were classified as escaped if they were missing from tethers with no evidence of predation. Escaped urchins were excluded from the analysis. Urchin test remains were counted and classified to one of the two size-class categories (small or large).

The design of the *P. cumingi* prey selection experiments was similar to that of many others (e.g. Murdoch 1969; Chesson 1983; Klecka and Boukal 2012) where predators were contained with different types of

prey. There were no control treatments lacking prey and electivity indices were calculated (Lechowicz 1982) to determine non-random prey choices.

2.2.2. *N. armata* feeding experiment

During surveys, *N. armata* was commonly observed at several of the study sites near bleached patches of CCA of the same size and shape as the adjacent sea star (Fig. 4d). Consequently, we hypothesized that these patches were generated by *N. armata* feeding. To test the hypothesis that *N. armata* causes bleaching of CCA through its feeding, as well as to assess overall impacts on the benthic community, a *N. armata* feeding experiment was conducted at the Baltra site from September to November 2013 (Fig. 4c & d). The average temperature during the *N. armata* experiment was 21.2°C (Supplementary Table 2). The experimental units consisted of circular plastic-coated steel mesh cages (Aquamesh, 3.5 cm openings) atop circular concrete bases (0.31m² area). Thirteen cages were set up at approximately 10 m depth at the Baltra site, with six replicate *N. armata* inclusion treatments and seven replicate controls (lacking *N. armata*). The mean size of *N. armata* used in the treatments was $R = 7.7 \pm 0.9$ cm. Each cage contained two square Plexiglas recruitment plates with coralline algae on them. Recruitment plates were strapped onto the concrete bases (Fig. 4c & d) using a harness of twine to hold them in place, and cages were bolted onto the concrete bases. All plates were labeled and photographed with a scale bar at the start and end of the experiment.

At the conclusion of the experiment, the plates were bagged, frozen, and subsequently processed for biomass by scraping organisms off the plates and separating them into categories of bleached CCA, healthy (non-bleached) CCA, sessile invertebrates and palatable macroalgae, such as *Ulva* spp., *Polysiphonia* spp., and *Ceramium* spp. (Lamb et al. 2020). Each sample was sun-dried over three days and then dry biomass weighed to a precision of ± 0.001 g.

2.3. Data analysis

We analyzed the abundance and distribution of each sea star species across the 12 study sites using 2-way analysis of variance (ANOVA), with site and depth as fixed, fully crossed factors. We did not include sampling period as a factor in this analysis due to uneven sampling effort for each site and time period. These tests were followed by Tukey's honest significant difference tests for significant factors and interactions. All data were $\log_{10}(x + 1)$ transformed prior to analysis to fit model assumptions. We also performed ANOVA tests on the video recorded sea star abundance data from 150 m² horizontal plots with site as the sole, fixed factor followed by Tukey's honest significant difference tests (Supplementary Fig. 1, Supplementary Table 4).

In order to determine differences in diet between sea star species, we first calculated the proportion of diet made up by each food/prey item by tallying the number of feeding observations for each sea star species by food category for each site. Thus "site" was considered as a replicate within each species for this analysis. Data were arc-sine square-root transformed prior to analysis, and species ordination values were created using the Bray-Curtis dissimilarity index. We then performed a multivariate dispersion

analysis on the feeding data to assess the breadth of diet for each species using the `betadisper()` function in the `vegan()` package in R (Oksanen et al. 2019). We also examined the multivariate composition of sea star diets using non-metric Multi-Dimensional Scaling (nMDS) to identify species-level variation in diets. The model converged after 20 iterations, with an acceptable stress value of 0.143. Differences in the multivariate structure of sea star diets between sites were revealed by Permutational Analysis of Variance (PERMANOVA). Similarity percentage analysis (SIMPER) was performed to examine the primary food groups contributing to variation between sea star species.

In the *P. cumingi* prey selectivity experiment one cage was excluded from the analysis due to an escaped *P. cumingi* between 24 and 90 hours into the experiment, leaving six replicates. Vanderploeg and Scavia's (1979) selectivity coefficient was used to test for differences in the selection of small vs large *E. galapagensis* pencil urchins using the equation in Lechowicz (1982). The selectivity coefficient W_i

$$W_i = r_i / p_i$$

$$\sum r_i / p_i$$

where

where r_i = proportion of food type i in the predators diet

p_i = proportion of food type i in environment

This index is constrained between 0 and 1.0 with values exceeding $1/n$ indicating preference while values below $1/n$ indicate avoidance and n = the number of prey types (Lechowicz 1982). In this experiment $n = 2$ prey types (small, large urchins) so W_i values >0.5 indicate preference while W_i values <0.5 indicate avoidance. Selectivity coefficients were calculated for each of the three time intervals that the results were recorded; 0 to 20 hours, 20 to 24 hours and 24 to 90 hours (Table 4).

We analyzed the results of the *N. armata* feeding experiment using the Mann Whitney U / Wilcoxon Ranked Sum non-parametric test, as data were not normally distributed. We compared biomass at the end of the experiment between control and *N. armata* inclusion cages for each of the prey groups (live CCA, bleached CCA, macroalgae, sessile invertebrates).

3. Results

3.1. Distribution & abundance of sea stars

Nine species of sea stars were recorded at 12 sites in the Galápagos between 2006 and 2014 in biannual monitoring surveys (Table 1). Six of these were abundant enough for subsequent feeding observations and experiments (Fig. 2). The two most abundant and widespread sea star species were *N. armata* and *P.*

cumingi, with a mean density across sites of 1.04 (2.38 SD) and 0.92 (3.46 SD) individuals per 100m², respectively (Table 1).

Table 1

Abundance of sea stars (per 100m²) across all 12 study sites in the Galápagos Islands, listed in order of decreasing mean density. Data represent the mean density of each sea star species in all transect surveys conducted bi-annually from January 2006 to February 2014 in n = 324 transects. Abundance patterns of the six most abundant species were analyzed statistically (Table 2).

Species	N	Mean Abundance (100m ²)	St Dev	St Err
<i>Nidorellia armata</i>	216	1.044	2.379	0.128
<i>Pentaceraster cumingi</i>	191	0.923	3.459	0.186
<i>Mithrodia bradleyi</i>	55	0.266	0.795	0.043
<i>Phataria unifascialis</i>	49	0.237	0.763	0.041
<i>Pharia pyramidata</i>	18	0.087	0.432	0.023
<i>Asteropsis carinifera</i>	16	0.077	0.414	0.022
<i>Coronaster marchenus</i>	11	0.053	0.481	0.026
<i>Linckia columbiae</i>	2	0.010	0.127	0.007
<i>Paulia horrida</i>	1	0.005	0.090	0.005

All of the six most abundant sea star species displayed significant spatial variation in abundance among sites (Table 2, and Supplementary Table 3). *N. armata* was globally the most abundant species on average, and reached a peak density of 5.39 (1.48 SD) individuals per 100m² at the RC site at 6m depth (Fig. 2). *P. cumingi* reached the highest density of any species at any site/depth, surpassing 8.4 individuals per 100m² at RB (15m depth). RC and RB represented abundance hotspots for sea stars, with the highest densities of all sea star species across depths (7.76 and 7.95 individuals per 100m², respectively). ANOVA and post hoc tests revealed that most species were more abundant at sites with terraces, such as RB and RC, than at sites with predominantly vertical wall habitats, such as CHE and DM (Fig. 3, Table 2, Supplementary Table 3). *M. bradleyi* and *A. carinifera* were abundant at the GF and CHA sites, which also have step-like terraces. *P. pyramidata* was most common at LC, while *P. unifascialis* was most abundant at BAL; both sites consist of basalt bedrock and boulders adjacent to sand. The only wall site with abundant sea stars was GAR, which is a section of vertical wall ~ 60m wide, framed on either side by small boulder fields and a sandy bottom at 40m depth. *P. cumingi* abundance was significantly higher at 15 than 6 m depth (0.78 and 0.33 individuals per 100m², respectively; adjusted $p = 0.02$, specifically at RB (5.1 and 2.3 individuals per 100m², respectively; adjusted $p = 0.03$) but depth was not a significant predictor of sea star abundance for any other species (Table 2, Fig. 2). There were not enough replicates to test for site or depth differences for *Coronaster marchenus*, *Linckia columbiae* or *Paulia horrida*.

Table 2
ANOVA models for each sea star species testing for differences by depth, site and their interaction (site:depth). See Supplementary Table 3 for pairwise comparisons from Tukey post-hoc tests.

Species	Factor	Df	Sum Sq	Mean Sq	F value	Pr(> F)
<i>Pentaceraster cumingi</i>	site	11	7.610	0.692	22.078	< 0.001
	depth	1	0.165	0.165	5.276	0.022
	site:depth	11	0.558	0.051	1.620	0.092
	Residuals	321	10.058	0.031		
<i>Nidorellia armata</i>	site	11	4.552	0.414	10.081	< 0.001
	depth	1	0.114	0.114	2.767	0.097
	site:depth	11	1.327	0.121	2.938	0.001
	Residuals	321	13.177	0.041		
<i>Mithrodia bradleyi</i>	site	11	0.740	0.067	5.416	< 0.001
	depth	1	0.017	0.017	1.336	0.249
	site:depth	11	0.198	0.018	1.449	0.150
	Residuals	321	3.985	0.012		
<i>Pharia pyramidata</i>	site	11	0.113	0.010	2.332	0.009
	depth	1	0.002	0.002	0.349	0.555
	site:depth	11	0.171	0.016	3.537	< 0.001
	Residuals	321	1.411	0.004		
<i>Phataria unifascialis</i>	site	11	0.630	0.057	4.968	< 0.001
	depth	1	0.003	0.003	0.289	0.591
	site:depth	11	0.097	0.009	0.764	0.677
	Residuals	321	3.701	0.012		
<i>Asteropsis carinifera</i>	site	11	0.132	0.012	2.846	0.001
	depth	1	0.001	0.001	0.353	0.553
	site:depth	11	0.043	0.004	0.935	0.507
	Residuals	321	1.355	0.004		

The two types of sea star abundance surveys – counts in 60 m² transects and 150 m² video recorded plots – revealed several similar patterns of abundance (Fig. 2, Supplementary Fig. 1, Table 2,

Supplementary Table 4) even though abundance was sampled differently and the habitats were adjacent to each other. For example, both indicated that *P. cumingi* and *N. armata* were the most abundant species and that there was significant site variation in abundance for *P. cumingi*, *N. armata* and *P. unifascialis* (Supplementary Table 4). Results of both surveys suggested that the highest densities of *N. armata* occurred at RC (at 15 m Fig. 2B, Supplementary Fig. 1) and that *P. unifascialis* densities were high at BAL (at 6 m Fig. 2B, Supplementary Fig. 1).

3.2. Feeding

Our analyses of feeding observations for six sea star species indicate that roughly half of all sea stars were feeding at any given time during the diurnal period, with species-specific rates varying between 35% (*A. carinifera*) and 68% (*N. armata*; Table 3). The six species had distinct diets, with select food items restricted to single or few sea star species. In particular, *P. cumingi* was the only species feeding on a mobile benthic invertebrate, the pencil urchin *E. galapagensis*, which comprised 8.1% of its diet across sites (Fig. 5). *P. cumingi* and *N. armata* were both frequently recorded with stomachs everted on crustose coralline algae (CCA, Fig. 5), leaving behind bleached white patches on the substrate (Fig. 4c). However, this behavior was more common in *N. armata*, as CCA composed 52.8% of its diet. With the exception of *A. carinifera*, the diets of all of the sea stars contained low proportions of sessile invertebrates as well as algae and diatoms (Fig. 5). Within this group, it appears that *N. armata* is primarily herbivorous (Fig. 5).

Table 3
Percentage feeding and size of the six most abundant species of sea stars. Mean size is radial length (R) from the oral cavity to the tip of the longest arm in cm. For further information on size structure, see Supplementary Fig. 3.

Species	Total observations	% Feeding	Mean size (R in cm)
<i>Nidorellia armata</i>	388	68.80	7.82
<i>Pentaceraster cumingi</i>	462	51.48	13.85
<i>Mithrodia bradleyi</i>	35	51.43	13.15
<i>Phataria unifascialis</i>	60	49.15	10.27
<i>Pharia pyramidata</i>	26	44.00	16.72
<i>Asteropsis carinifera</i>	15	35.71	11.61

The multi-dimensional scaling analysis of food items revealed that sea star diets varied by species (Supplementary Table 5, PERMANOVA $F_{[4]} = 3.19$; $R^2 = 0.32$; $P = 0.001$) although considerable overlap was present among some species (Fig. 6). *N. armata* was strongly associated with CCA, as this food item explained approximately 30% of the variation in diet differences from the other species analyzed (Supplementary Table 5). *P. pyramidata* was significantly associated with sessile invertebrate prey, as this food category was responsible for approximately 30% of diet differences. This analysis also provided additional evidence that *P. cumingi* was unique in its consumption of *E. galapagensis* pencil urchins. Substantial overlap in diet was particularly evident for *M. bradleyi* and *P. unifascialis*, which also had the

most generalized diets (Fig. 6). The dispersion analysis of diet breadth indicated that *P. cumingi* had the narrowest diet, followed by *N. armata* (Supplementary Table 5), and both had significantly narrower diets than *M. bradleyi*.

3.3. *P. cumingi* prey selection experiment

Results of the prey selection experiment indicated that *P. cumingi* preferred small *E. galapagensis* urchins over large ones during each time interval of the experiment, as all selectivity coefficients (W_i) for small urchins were >0.5 , indicating preference (Table 4).

Table 4. Results of *Pentaceraster* prey selection experiments with large and small pencil urchin prey. Values of Vanderploeg and Scavia’s (1979) selectivity coefficients for this experiment, $W_i > 0.5$, indicate preference, while W_i values < 0.5 indicate avoidance. The coefficients were calculated over each time interval that the experiment was censused. The results indicate selective predation on small urchins during each of the 3 time periods.

Time interval	W_i Small urchins	W_i Large urchins
0 – 20 hours	0.750	0.240
20 -24 hours	1.00	0
24 – 90 hours	0.775	0.530

3.4. *N. armata* feeding experiment

A comparison of final benthic biomass on recruitment plates from control and inclusion cages with *N. armata* indicated that the presence of *N. armata* led to a significant reduction in biomass of healthy (non-bleached) CCA ($W= 32, P< .0001$) and macroalgae ($W= 35, P= 0.042$) and in total benthic biomass ($W= 731, P= 0.025$; Fig. 7). The presence of *N. armata* did not, however, result in a significant decrease in the biomass of sessile benthic invertebrates ($W= 42, P= 0.29$; Fig. 7).

4. Discussion

4.1. Abundance and distribution

Of the nine sea star species recorded in our surveys of subtidal rocky reefs in the Galápagos, *N. armata* and *P. cumingi* were the most abundant, with all sea stars varying significantly in abundance across sites. Two sites – RC and RB – were identified as persistent “abundance hotspots” *sensu* Hazen et al. (2013) for all sea stars. The video-recorded data reinforced the characterization of RC as an abundance hotspot for sea stars. We observed higher sea star abundances for most species at sites with pronounced terraces (e.g., RC, RB), where sediment tends to collect and horizontal surfaces provide a broad range of

food for several species. These factors may also apply at the LC and BAL sites where *P. pyramidata* and *P. unifascialis* were most abundant, characterized by heterogeneous bottom topography with short walls, large boulders, and rock ridges surrounded by sandy bottom. In contrast, sea star abundances were lower and we observed fewer species at vertical wall sites (e.g. CHE, DM), where food and topographic complexity may be lower than at sites with terraces.

The abundance of sea stars in Galápagos has previously been described as varying spatially between islands and bioregions (Gómez Alfaro 2010). Several of the species that were common in our surveys, including *N. armata*, *P. unifascialis*, and *P. pyramidata* are associated with the colder Elizabethan and Western biogeographic provinces of the Galápagos (Edgar et al. 2004). In contrast, *P. cumingi* is characteristic of the southeastern region where our study largely took place (Edgar et al. 2004). Gómez Alfaro's (2010) study also identified *P. cumingi* and *N. armata* as the most abundant sea star species, though their abundance values were an order of magnitude higher than our observations, reaching up to around 12 individuals per 100m² for both species. This is probably due to habitat preferences, as our transects were primarily on steeply sloping walls and the Charles Darwin Research Station monitoring data – on which Gómez Alfaro (2010) and Edgar et al. (2004) were based – also cover many flat sites. Our findings indicate these sites may be more hospitable for sea stars; at several of our sites (e.g., LC, BAL), we often observed sea stars, especially *P. cumingi*, on nearby sediment-covered flat rock and sandy substrates. This particular habitat was sampled more extensively in the video-recorded 150 m² plots which revealed higher densities of *P. cumingi* and *N. armata* than the wall transects, underscoring the important influence of habitat variation on sea star abundance. Our observed densities were also low in comparison to other observations of sea star densities in sandy and rocky intertidal areas worldwide, indicating subtidal rock walls may be less densely populated than flatter areas in general (Scheibling and Metaxas 2008; Martinez et al. 2016).

Sea star abundances in the Galápagos are likely to be driven by food availability, in addition to other factors such as larval dispersal (Witman et al. 2003), temperature preferences (Edgar et al. 2004) and possibly by predators (Rogers and Elliott 2013). Predation of sea stars in the Galápagos is thought to be rare, with few consumers observed feeding on sea stars (Glynn et al. 2017). This could make them something of a trophic dead end. However, we have observed several sea stars with missing arms and entire bodies regrown from single arms. We also observed a blunthead triggerfish (*Pseudobalistes naufragium* feeding on *N. armata* (J. Witman, personal observation) and several species of damselfish (*Stegastes* spp.) biting at the tube feet of both *N. armata* and *P. cumingi* (R. Lamb, personal observation), and Edgar et al. (2010) interpreted damaged sea stars as indicative of sea lion predation or play. In concert, these observations add to the list of potential asteroid predators and may indicate greater trophic connectivity than has been previously assumed. More information is needed to fully understand the role of sea stars and their predators in the Galápagos subtidal food web.

Baseline data on sea star abundance and feeding patterns in the Galápagos rocky subtidal may become particularly valuable in light of the numerous threats affecting sea star populations worldwide, including disease (Harvell et al. 1999; Menge et al. 2016), the aquarium trade (Micael et al. 2009) and ocean

acidification (Appelhans et al. 2014). Ocean acidification has been identified as a particular threat to juvenile sea stars as it may impede their feeding and growth (Appelhans et al. 2014). Due to the major traffic of tourists on terrestrial and marine systems in Galápagos, the introduction of pathogens is also a concern that should be taken seriously and incorporated into protocols for marine tourism.

4.2. Diet breadth

Our analyses indicate there is substantial variation among sea stars in the Galápagos rocky subtidal in terms of diet and trophic position, with *P. cumingi* and *N. armata* exhibiting the narrowest diets. As facultative herbivores (Martinez et al. 2017), most of the Galápagos sea star species are omnivorous, with a guild of generalists consisting of four species (*A. carinifera*, *M. bradleyi*, *P. unifascialis* and *P. pyramidata*), one specialist invertivore-herbivorous species (*P. cumingi*) and the largely herbivorous *N. armata*. Results suggest *N. armata* can be classified as an obligate herbivore while the majority of the sea stars are facultative herbivores, which are herbivores that also feed on animal derived material (Martinez et al. 2017). *P. cumingi* was the lone sea star predator of *E. galapagensis* pencil urchins, and *N. armata* was strongly associated with CCA.

The majority of the sea stars we surveyed appeared to be grazing on foliose or crustose algae, which aligns with Gómez Alfaro's (2010) assertion that herbivory is common in Galápagos sea stars. In their review of sea star herbivory, Martinez et al. (2017) found most were feeding on soft structured macroalgae such as *Ulva* sp. and filamentous algae. This corresponds to our qualitative observations as nearly all of the sea star feeding on non-crustose algae was on filamentous algae (J. Witman, unpublished observations). The Galapagos marine ecosystem is relatively warm, with an average sea surface temperature ranging from 23–26°C, which is believed to facilitate herbivory in potentially omnivorous ectotherms (Zhang et al. 2020). Algal substrates, especially CCA, are also the most abundant benthic prey available in the archipelago (Tompkins 2017). Whether sea stars such as *N. armata* are targeting the algae itself or associated microbial films and epibionts would be an interesting direction for future research.

Previous observations of predation by *P. cumingi* on *E. galapagensis* pencil urchins (Dee et al. 2012) were confirmed in this study through field-based and experimental evidence as well as observations in the field (N. Low, personal observations). In addition, *P. cumingi* displayed strong selectivity for small sized *E. galapagensis*. Along with the significant association of *P. pyramidata* with sessile invertebrate prey, this indicates that sea stars in the Galápagos may play an important predatory role. *M. bradleyi* and *P. unifascialis* were also frequently observed consuming sessile invertebrates, particularly ascidians and sponges. Only one species (*Heliaster* sp.) was found feeding on barnacles (J. Witman: unpublished data) and no other species was found to exploit barnacles as a major prey item, even though barnacles are abundant in the Galápagos subtidal (Witman et al. 2010) and have been identified as a major prey item for sea stars in other temperate systems (Mauzey et al. 1968).

Our findings on diet breadth confirm that sea stars in the Galápagos occupy multiple trophic levels in the subtidal food web (Menge 1982) and are generally “polyphagous” (Tokeshi et al. 1989) which is in line

with observations of sea stars in other systems. However, there were striking dietary differences between species and some unique feeding relationships, such as that of *P. cumingi* feeding on *E. galapagensis* pencil urchins and the widespread consumption of CCA by *N. armata*. This trophic specificity and our finding of narrower niches for *P. cumingi* and *N. armata* than the rest of the sea stars surveyed suggest that previous groupings of sea stars (Okey et al. 2004) and echinoderms in general (Wolff et al. 2012) as ecologically equivalent in trophic models in Galápagos may not be appropriate.

4.3. Ecological impact of sea stars in Galápagos subtidal ecosystems

The functional impact of herbivory and predation by sea stars in the Galápagos subtidal zone is likely to be larger and more diverse than previously realized, varying by species according to distinct diets. Herbivory by Galápagos sea stars has the potential to directly limit primary productivity and percent cover of live CCA. At the same time, *P. cumingi* is a common predator of *E. galapagensis* pencil urchins, with the possibility of inducing trophic cascades by reducing the grazing capacity of this important herbivore (Witman et al. 2017). While our study focused on characterizing diets and abundances across sea star species, intra- and inter-specific behavioral interactions may also shape their aggregate ecological impact (Gaymer et al. 2002; McClintock et al. 2008).

The incidence of feeding we observed (57.6% of surveyed individuals across species) was in line with Gómez Alfaro's (2010) observation that the proportion of Galápagos sea stars with stomachs everted was between 50–60% of sampled individuals. It also echoes findings by Navarrete & Manzur (2008) along the coast of Chile, which indicated seasonal variation with 51% – 55% of *H. helianthus* feeding, and the results of Dayton et al. (1974) who reported feeding rates from 20–61% in the Antarctic subtidal. It will be important to monitor sea star feeding rates over time as they can mediate the strength of ecological impact and may be impacted by wider processes such as ocean acidification (Appelhans et al. 2012). Gómez Alfaro (2010) noted that the formation of sea star aggregations or fronts, which has been observed in Galápagos, could magnify the effects of their feeding and lead to significant ecological changes as with “urchin barrens” created by urchins including the pencil urchin *E. galapagensis* (Edgar et al 2010). Warmer temperatures are predicted to increase the metabolic rate and feeding of sea stars, which could lead to a sizable impact on prey and cause community-wide changes (Sanford 2002). An elevated seawater temperatures of 28°C yielded significantly higher feeding rates in another Galápagos echinoid, the green urchin *Lytechinus semituberculatus*, and may produce similar increases in sea star foraging rates (Carr and Bruno 2013).

The disproportionately high abundance and unique feeding habits of *P. cumingi* and *N. armata* indicate that among the sea stars examined, these two are the most likely to impact the benthic community, either through local cropping of small sea urchins (in the case of *P. cumingi*) or through focused grazing on CCA (in the case of *N. armata*). As sea stars were confined with their prey during feeding experiments, data from these experiments represent maximal rates of predation or consumption rather than averages. *P. cumingi* has previously been recorded as feeding on algae, sponges, sea urchins, and coral (Glynn et al.

2016), and we observed *P. cumingi* feeding on *E. galapagensis* pencil urchins approximately 8.0 % of the time in the field, which is comparable to the estimation of Dee et al. (2012) of 6.3%. In limited surveys of sea star feeding at 3 sites in the Galápagos, Dee et al. (2012) found that *P. cumingi* has a unique role as an occasional predator of *E. galapagensis*, but the generality of this interaction is unknown. The interpretation by Dee et al. (2012) that *P. cumingi* preyed on tethered *E. galapagensis* was questioned by Martinez et al. (2017), who raised the possibility that the sea stars in this experiment may have been feeding on moribund urchins attacked by other predators.

The results of the prey selection experiment suggest that the sea star *P. cumingi* is a size-selective predator of *E. galapagensis*, a key grazing and bioeroding sea urchin which is extremely abundant throughout the archipelago and is believed to cause urchin barrens (Edgar et al. 2010). Few predators can consume large *E. galapagensis* adults, so in concert with predation by hogfish (*Bodianus diplotaenia*) this size-selective predation could contribute to the localized cropping of small *E. galapagensis* (Witman et al. 2017). Since predatory fishes are unable to access most small urchins when they are hidden in reef cracks and among rubble during the day, *P. cumingi* may have a predatory advantage due to its flexibility and use of non-visual prey sensing. These combined multiple predator effects (Sih et al. 1998; Siddon and Witman 2004) may in situations of high predator density impede the progression of young cohorts into larger, older urchin size classes. This process is likely to be due to mediated habitat heterogeneity given that small urchins often take refuge in rubble and avoid predators through nocturnal activity (Dee et al. 2012). We did not measure sea star feeding at night so we do not know whether nocturnal predation is occurring, but some sea star species such as *Acanthaster* sp. are known to feed nocturnally (Chesher 1969).

The observation of *N. armata* leaving bleached CCA feeding patches in the field prompted us to investigate the impacts that its feeding was having on benthic community structure. Glynn & Wellington (1983) reported that *N. armata* fed on the coral *Pavona clavus* and left behind small feeding scars. In his detailed observations of *O. reticulatus* in the Caribbean, Scheibling (1982) describes the discoloration of macroalgae after stomach eversion events and occasional eversions on coral rubble, hypothesizing that it was “apparently digesting organic films and/or encrusting coralline algae on the rubble surface” (p. 505). Gómez Alfaro’s (2010) description of fluorescent pink feeding scars left behind by *P. cumingi* is highly similar to the appearance of fresh feeding scars we observed in the field, which we believe then bleached and turned white since we saw many of the same sea star-shaped bleached feeding scars caused by this species. The feeding scars we observed were mostly created by *N. armata*, so the chemical process underlying their creation is likely similar to that of *P. cumingi*. It is possible that sea stars are feeding on associated biofilms, as indicated by Martinez et al. (2017); however it was impossible to tell the difference using our methods, and further analysis, perhaps with isotopes, would be necessary to provide a conclusive response to this question. Krutwa (2014) carried out an isotope analysis, which indicated that the sea star *N. armata* took on a similar trophic role to *E. galapagensis* in the Galápagos Islands. Glynn & Wellington (1983) refers to *E. galapagensis* pencil urchins feeding on CCA, but makes no mention of *N. armata* doing the same, so we hypothesized that the creation of these small dead patches of coralline algae could open up local colonization sites for benthic invertebrates and

algae. In this way, the feeding scars of varying sizes we observed on CCA could be changing the availability of space and affecting the composition in benthic communities.

The results of our feeding experiment supported the hypothesis that *N. armata* grazing has the potential to alter benthic community structure via reduction in biomass of CCA and macroalgae. The rate of feeding outstripped the rate of recruitment or replacement of algae, as live coralline algal cover decreased over the course of the 4-month experiment despite the open design of the experiment that allowed colonization of algae to continue. The significant reduction in healthy CCA and its transition to bleached CCA suggests that *N. armata* feeds on CCA and negatively affects the abundance of living CCA crusts. This could have important effects on benthic ecosystems since CCA is an important substrate for settlement and recruitment of larvae of various sessile invertebrates including corals (Steneck 1986; Doropoulos et al. 2012). Reduced calcification and health of CCA is predicted to disrupt closely paired relationships with corals (Doropoulos et al. 2012); however, sea star feeding could also be contributing to the process of “deep-layer sloughing” which generates new tissue in some *Lithophyllum* species (Fujita 1999). Our finding that *N. armata* feeding causes abundant bleached patches in CCA parallels reports of other feeding scars on CCA caused by other sea stars species, such as *Parvulastra exigua* in Australia and South Africa and *Asterina pectinifera* in Japan (Fujita 1999; Martinez et al. 2016). It is likely that synergistic effects of *N. armata* and *P. cumingi* feeding, urchin grazing (Witman et al. 2017) and El Niño associated benthic cyanobacterial mats (Beltram et al. 2019) are affecting the distribution of CCA in the Galápagos benthic ecosystem. This may have long-term effects on succession and the diversity of Galápagos rocky subtidal communities if other species colonize the bleached patches and the facilitation of coral settlement on CCA is reduced.

As a baseline, our study has characterized feeding and abundance across 12 sites for six commonly observed sea star species in the Galápagos. This ecologically important group shows affinity for subtidal habitats with flat or gently sloping reef substrata that allow for accumulation of sediment and growth of algae. Galápagos sea stars appear to be largely facultative herbivores, and yet the varied diets and occasionally high rates of predation on both sessile and mobile invertebrates suggest resource partitioning. Due to their high densities and broad feeding relationships, and in light of our experimental evidence, we believe sea stars are likely to influence the diversity and abundance of benthic organisms in the Galápagos rocky subtidal zone. Sustained ecological research on this important group could reveal how their ecological roles change in a warming ocean.

Declarations

- *Funding(information that explains whether and by whom the research was supported)*

This work was funded by the United States National Science Foundation (Award Numbers OCE-1061475, OCE-1450214 and OCE-1623867), and by an award from the Galápagos Conservancy, Inc. to J. D. Witman. It was also supported by an award from the Brown International Scholars Program to N. Low.

- *Conflicts of interest/Competing interests(include appropriate disclosures)*
The authors have no conflicts of interest to declare that are relevant to the content of this article.
- *Ethics approval(include appropriate approvals or waivers)*
All experimental work was conducted in the field with invertebrate species with permits from the Galápagos National Park.
- *Consent to participate(include appropriate statements)* N/A
- *Consent for publication(include appropriate statements)* N/A
- *Availability of data and material(data transparency)*
All data and custom code for analysis will be stored in Dryad upon acceptance of the article.
- *Code availability(software application or custom code)*
All data and custom code for analysis will be stored in Dryad upon acceptance of the article.
- *Authors' contributions(optional: please review the submission guidelines from the journal whether statements are mandatory)*
The manuscript was primarily written by SCT, with edits from JW, RL, NL and MB; research was designed by JW, NL, SCT and RL; data collection was undertaken by JW, NL, SCT, RL and MB; and data analysis was undertaken by JW, NL, RL and SCT.

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Figures

Figure 1

Common sea stars surveyed for feeding in Galápagos. Clockwise, from top left: a) *Asteropsis carinifera* (Lamarck 1816), b) *Mithrodia bradleyi* (Verrill 1867), c) *Pharia pyramidata* (Gray 1840), d) *Pentaceraster cumingi* (Gray 1840), e) *Nidorellia armata* (Gray 1840) and f) *Phataria unifascialis* (Gray 1840). Photo credits: J. D. Witman.

Figure 2

A) Map of the study region, indicating location of 12 study sites in the central Galápagos Islands and B) mean abundance for the six most abundant species of sea stars. Data are shown for shallow (6m – left) and deep (15m - right) transects for each species at each site compiled across eight years of survey data (2006-2014). Sites comprising terrace habitats (Islote Champion – CHA, Rocas Beagle – RB, Guy Fawkes – GF, and Roca Cousins – RC) are in black; mixed habitats: substrate of boulders, small walls, rubble, and

sand (Las Cuevas – LC, La Botella – LB, Pinzón – PIN, and Baltra Norte – BAL) are in light grey; and wall habitats (Daphne Menor – DM, Rocas Gordon – GOR, Cuatro Hermanos – CHE, and Islote Gardner – GAR) are labeled in white. Baltra Norte (BAL*) is marked with an asterisk as it is the site where feeding experiments occurred. White circles represent sites with wall habitat, grey sites represent mixed habitat sites, and black circles represent terrace habitat sites (for examples of habitat types see Figure 3).

Figure 3

Example photographs of the three habitat types assessed for sea stars. Counter-clockwise from top left: a) terrace habitat at the Guy Fawkes site (GF); b) mixed habitat (substrate of boulders, small walls, rubble, and sand) at Las Cuevas (LC); c) wall habitat at Rocas Gordon (RG). Photos: J. D. Witman.

Figure 4

Photos of feeding behavior in the field and experimental setups with *P. cumingi* and *N. armata*. Clockwise from top left-: a) *P. cumingi* (16.0 cm radius) feeding on a pencil urchin *E. galapagensis* (5.0 cm) in natural subtidal habitats at the Baltra site; b) View of a 0.95 m² predator inclusion cage with *P. cumingi* and *E. galapagensis* pencil urchin prey; c) View of a *N. armata* inclusion treatment where a single sea star was enclosed with 2 plexiglas plates colonized by varying amounts of potential prey (CCA, macroalgae, sessile invertebrates). The cage was removed for the photograph. Controls lacked sea stars. Plexiglas plates were 100 – 144 cm² area; d) Observation of *N. armata* feeding on CCA in natural habitats with conspicuously bleached patches indicating where *N. armata* had been.

Figure 5

Feeding observations for the six most abundant sea stars in Galápagos (N = 1,066). In some cases, sea stars were recorded as feeding on up to two food categories if their cardiac stomachs were everted on both prey. CCA: Crustose Coralline Algae.

Figure 6

Multidimensional scaling plot of sea star diets. X- and Y-axes represent the first and second dimensions of a multi-dimensional scaling performed using Bray-Curtis dissimilarity on arcsin-square root transformed data. Each point represents the proportion of diet corresponding to different prey types for a single sea star species at a single site (*Asteropsis carinifera* was not considered in this analysis due to limited feeding data for this species). Colored polygon hulls enclose all points for each species of sea star, and the location in multivariate space of each prey type is also labeled. CCA: crustose coralline algae (primarily *Lithophyllum* sp.).

Figure 7

Final benthic biomass for potential prey items on recruitment plates for *N. armata* inclusion cages and controls. Light blue boxes (left) indicate control treatments, and darker blue boxes (right) indicate treatments containing *N. armata*. CCA = crustose coralline algae. Healthy CCA represents un-bleached CCA. The upper and lower limits of the box represent the 75th and 25th percentiles of the data, respectively, the whiskers (lines) extend to ± 1.5 the interquartile range, the horizontal bar is the median, and points are outliers beyond the whisker range. Asterisks represent significant differences between cage and control treatments in a Mann Whitney U / Wilcoxon Ranked Sum non-parametric test.

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