



Trophic ecology of an abundant kelp forest echinoderm, the bat star *Patiria miniata*

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ABSTRACT: Echinoderms often play key roles in structuring marine ecosystems. The bat star *Patiria miniata* is an abundant echinoderm in the kelp forests of the northeastern Pacific coast whose trophic ecology has been understudied. Understanding the trophic role of *P. miniata* is important given the recent declines of many sea star populations due to wasting disease. *Patiria miniata* was largely unaffected by these outbreaks and could potentially fill the trophic niches left by other ecologically important sea star species. In this study, we used a combination of feeding experiments and stable isotope analysis to provide new insights into the trophic ecology of *P. miniata*. Given that *P. miniata* is considered an omnivorous generalist, we conducted a series of feeding experiments in which we quantified consumption rates for a wide range of reported prey items. Consumption rates were highest for different types of carrion, lower for sessile invertebrates, and negligible for all species of macrophytes. In a series of follow-up experiments, we found that food deprivation did not lead to demonstrable consumption of macrophytes by *P. miniata*, but that the presence of epiphytes significantly increased consumption rates (presumably of the epiphytes plus incidental consumption of macrophytes). Finally, we compared the isotopic niche of *P. miniata* with that of a carnivore (the giant sea star *Pisaster giganteus*), an herbivore (the purple sea urchin *Strongylocentrotus purpuratus*), and a detritivore (the warty sea cucumber *Parastichopus parvimensis*) and found that *P. miniata* occupied the highest relative trophic level and was isotopically most similar to *P. giganteus*. Altogether, our results suggest that the diet of *P. miniata* is narrower and more carnivorous than previously expected.

KEY WORDS: Trophic ecology · Sea star · Kelp forest · Stable isotopes

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1. INTRODUCTION

Keystone species have a disproportionate effect on community structure and functioning, and thus their removal from communities often results in significant ecological change (Mills et al. 1993). The keystone species concept was first introduced by Paine (1966) to describe how predatory sea stars shaped rocky intertidal communities by preferentially consuming dominant competitors for space. Many subsequent

studies have found that sea stars and other echinoderms have a strong influence on community structure and ecological processes in marine ecosystems. For example, sea urchins can facilitate phase shifts from kelp forests to rocky barrens through intensive overgrazing (Steneck et al. 2004, Harrold & Reed 1985), and sea cucumbers can improve water quality and promote biogeochemical cycling by consuming sediment and detritus (Bonham & Held 1963, Wolfe et al. 2018). Still, these examples involve only a small

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portion of all known echinoderm species. Most echinoderms are understudied, and their importance to ecosystem functioning remains unknown.

In 2013, an outbreak of sea star wasting disease decimated sea star populations from Alaska to Baja California (Stokstad 2014). The cause of this mass mortality event remains unresolved (Aquino et al. 2021), but over 20 sea star species suffered population declines, including many carnivorous sea stars such as the sunflower star *Pycnopodia helianthoides* and ochre star *Pisaster ochraceus*, which play important roles in structuring kelp forests (Duggins 1983) and intertidal ecosystems (Paine 1974). The loss of these predators has led to trophic cascades in some regions (Schultz et al. 2016). Interestingly, some sea star species experienced only minor declines in abundance after the outbreak (Stokstad 2014). Understanding whether and how these species can fill the trophic niches left by other sea star species requires knowledge of their functional roles in these communities, especially as revealed by their dietary patterns; yet we lack information on the feeding ecology of many species.

One such species is the bat star *Patiria miniata*, which is found in subtidal environments from Alaska to Baja California and is particularly common in the kelp forests of Monterey Bay, California (Morris et al. 1980). Little attention has been paid to the trophic ecology of *P. miniata*, especially compared to larger sea stars such as *P. helianthoides* and *P. ochraceus*. Unlike these carnivorous species, bat stars have been described as omnivorous generalists, detritivores, and scavengers. Their diets reportedly include kelp, algae, surfgrass, bryozoans, colonial tunicates, sponges, biofilms, detritus, and carrion (Morris et al. 1980, Day & Osman 1981, Farias et al. 2012). Unlike other sea stars, which use their strong arms to capture or pry open their prey, *P. miniata* has short, weak arms, and feeds by covering prey with its voluminous cardiac stomach and digesting it externally (Anderson 1959). Despite its ostensibly broad diet, the few studies that have examined the trophic ecology of *P. miniata* have focused on their consumption of single prey species, such as bryozoans (Day & Osman 1981), sea urchins (Schroeter et al. 1983), and juvenile kelp (Leonard 1994), without consideration of their broader effects on the larger kelp forest ecosystem. Understanding the trophic ecology of *P. miniata* has become increasingly relevant, given the declines of other ecologically important sea stars due to the wasting disease.

In this study, we used a combination of feeding experiments and stable isotope analysis to provide

new insights into the trophic ecology of *P. miniata*. Given this species' reputation as an omnivorous generalist, we initially conducted a series of feeding experiments in which we quantified rates of consumption for a variety of reported prey items. After noting negligible consumption rates on all species of macrophytes, we conducted a series of follow-up experiments testing the effects of food deprivation and the role of epiphytic communities on the consumption of macrophytes by *P. miniata*. To determine whether the diet of *P. miniata* was more carnivorous than previously recognized, we conducted a stable isotope study comparing the isotopic niches of bat stars with a carnivorous sea star (*Pisaster giganteus*), an herbivorous sea urchin (*Strongylocentrotus purpuratus*), and a detritivorous sea cucumber (*Parastichopus parvimensis*), which occupy distinct trophic niches (Morris et al. 1980, Page et al. 2013) against which we could infer the role of *P. miniata* in the ecosystem.

2. MATERIALS AND METHODS

2.1. Feeding experiments

2.1.1. Study site

Feeding experiments were conducted during June–August of 2016 and September of 2017. *Patiria miniata* and their potential prey species were collected by divers and snorkelers from subtidal kelp forests and *Phyllospadix* seagrass beds off Hopkins Marine Station, Pacific Grove, CA, USA. Collected specimens were kept in large saltwater aquaria within a shaded pavilion, to recreate the low light conditions common in kelp forests. Each tank received a constant flow of filtered seawater from Monterey Bay. Water temperatures ranged from 12.1 to 15.8°C over the course of the experiments, reflecting natural variation in temperature conditions in Monterey Bay. The bat stars and their potential prey were maintained in separate tanks, and the bat stars were starved for 24 h before being used in a feeding trial. Each individual was only used once.

2.1.2. Expt 1: feeding rates on single prey species

We conducted 16 feeding trials to quantify the rates at which *P. miniata* consumed different prey types. We tested potential prey from 3 distinct groups that were chosen based on observations of *P. miniata*

in the field and reports of their diets from the literature: carrion (goldfish *Carassius auratus*, California market squid *Loligo opalescens*, and purple shore crab *Hemigrapsus nudus*), sessile invertebrates (elephant ear tunicate *Polyclinum planum*, orange puffball sponge *Tethya aurantia*, lacy ball sponge *Leucosolenia eleanor*, fluted bryozoan *Hippoporina insculpta*, and the bryozoan *Celleporina robertsoniae*), and macrophytes (Pacific rose seaweed *Rhodymenia* sp., giant kelp *Macrocystis pyrifera*, splendid iridescent seaweed *Mazzaella splendens*, articulated coralline algae *Calliarthron tuberculosum*, and surfgrass *Phyllospadix* sp.). All prey were cleaned of any epiphytes. Each trial consisted of 4 replicates of each of 2 treatments ('bat star', which contained a bat star and the prey, and 'control', which contained only the prey) for the given prey species. We conducted 1 trial for each prey species, with the exception of *H. nudus*, *Rhodymenia* sp., and *M. pyrifera*, for which we conducted 2 trials (designated, for example, as *Hemigrapsus* 1 and *Hemigrapsus* 2).

Experiments were conducted in 5.7 l plastic storage containers. Three holes were drilled in the lids of each container: one allowed filtered seawater to flow into the container via an attached tube, and the other 2 allowed water to flow out. The chambers were arranged in rows of 8 and placed under a shaded tarp to simulate natural, low-light conditions (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m696p057_supp.pdf). If microalgae were observed growing on the walls of the containers, those chambers were cleaned before proceeding with the experiment.

For a trial, each container was randomly assigned to one of the 2 treatments (i.e. bat star or control). Potential prey items were weighed before being placed in their designated chamber. To ensure consistent masses, a salad spinner was used to remove excess water from the macrophytes (Bickel & Perrett 2016), and paper towels were used to blot dry the sessile invertebrates and carrion. A single *P. miniata* was then placed in each of the 'bat star' chambers and the trial was allowed to begin.

Due to the wide variety of prey items used in this experiment, the initial prey masses and duration of the trials varied between prey species (see Table S1 in the Supplement). This was done to account for differences in handling time and to ensure that at least 40% of the prey remained at the end of each trial. We did not require minimum levels of consumption since not all prey species were eaten by *P. miniata*. Feeding periods were longer and initial masses were

greater for prey species requiring more handling time; this increased our ability to measure consumption rates. However, the duration of the feeding trial remained consistent within a given prey species, as did the initial prey mass (to within ~0.4 g).

At the end of each trial, we took the remaining prey items from their chambers, removed excess water, and determined their final mass. We then removed the bat stars from their chambers, blotted them dry with paper towels, and weighed them. The average mass of each *P. miniata* was 99.2 g, with a standard deviation of 28.2 g (range = 53.1 to 192.2 g). Each *P. miniata* was only used once in the feeding experiments.

2.1.3. Calculating consumption rates

Changes in prey mass are driven by 3 processes: consumption by *P. miniata*, growth of living prey, and decomposition or other losses of prey. Growth and other losses both are likely best modeled with an exponential model. Consumption by bat stars might also be expressed as an exponential (if bat stars are primarily search time limited) or linear (if primarily handling time limited) decay, although linear is more likely in these experiments. Given the possibly different dynamics of prey in response to these processes, there was no simple way to combine data from the 2 treatments. Thus, we undertook 2 analyses to infer consumption rates of bat stars: one based on exponential changes in prey mass and one based on linear changes. Because log-response ratios (based on exponential growth) are commonly used in ecology and have been applied to consumer-resource interactions (Osenberg et al. 1997), we present those results in the main text, and provide results based on a linear model in the Supplement (Table S2). Both analyses yielded similar conclusions. All analyses were conducted in R (version 4.1.2).

We first calculated the rate of change in prey mass, R , for each replicate in each treatment, as the log-response ratio of the final and initial prey masses (M_F and M_0 , respectively), divided by the duration of the trial (t) in days:

$$R = \frac{\ln\left(\frac{M_F}{M_0}\right)}{t} \quad (1)$$

$R < 0$ indicates prey mass was reduced through time; $R > 0$ indicates net growth. Because the bat star and control replicates were not paired during this experiment (nor in our other experiments), we were unable

to calculate individual consumption rates for each bat star replicate, and instead compared prey growth rates. Preliminary analyses using ANCOVA did not find a significant effect of *P. miniata* mass (nor an interaction between mass and prey species) on $R_{\text{bat star}}$, so we did not include *P. miniata* mass in our final analyses. Because the data did not meet the assumptions of normality and homogeneity of variances required for parametric tests, we used a non-parametric approach (aligned rank transformation ANOVA with fixed effect of prey species, bat star treatment [i.e. bat star or control], and their interaction) to compare prey growth rates (i.e. R from Eq. 1) (Wobbrock et al. 2011). We also used post hoc Mann-Whitney tests to compare $R_{\text{bat star}}$ and R_{control} for specific prey species (we did not correct for multiple comparisons).

To facilitate the presentation of data, we calculated the average consumption rate of *P. miniata* as the difference between the mean prey growth rate without *P. miniata* (\bar{R}_{control}) and the mean rate of change in prey mass with *P. miniata* ($\bar{R}_{\text{bat star}}$):

$$c = \bar{R}_{\text{control}} - \bar{R}_{\text{bat star}} \quad (2)$$

We estimated the variance of c as the sum of the 2 variances:

$$V(c) = V(\bar{R}_{\text{control}}) + V(\bar{R}_{\text{bat star}}) \quad (3)$$

2.1.4. Expt 2: effects of food deprivation on *Rhodymenia* sp. consumption

Experiment 2 was designed to determine whether a prolonged period of food deprivation could increase the consumption rate of *Rhodymenia* sp., a benthic red alga commonly reported in the diet of *P. miniata* (Morris et al. 1980), but not readily consumed in Expt 1. A total of 18 bat stars (6 replicates for each of 3 treatments) were isolated without food in aquaria for periods of 1 d (as in Expt 1), 7 d, and 14 d. At the beginning of the experiment, 5 g of *Rhodymenia* sp. (with epiphytes removed) was placed in each of 36 chambers. The 18 bat stars were then placed in their respective chambers, while the remaining 18 chambers, containing only *Rhodymenia* sp., were designated as controls. The experiment lasted 3 d to give *P. miniata* ample time to consume the *Rhodymenia* sp.; all other aspects of the experiment were the same as in Expt 1. We calculated the prey growth rate (R) for each experimental replicate (Eq. 1), as well as the average consumption rate for each

food deprivation treatment (Eq. 2). Since the data were not normally distributed, we analyzed prey growth rates (R) using an aligned rank transformation ANOVA (with main effects of food deprivation treatment and bat star treatment, as well as their interaction). A significant interaction would indicate that the difference between the treatment with *P. miniata* and the treatment without *P. miniata* (i.e. the consumption rate) was affected by the length of food deprivation. Again, for presentation purposes we applied Eqs. (2) and (3).

2.1.5. Expt 3: clean versus encrusted macrophytes

Many of the macrophytes species described in the diet of *P. miniata* support rich communities of epiphytes that may provide nutritional value separate from the macrophytes themselves (Currin et al. 1995, Borowitzka et al. 2007). *Rhodymenia* sp., for example, is often overgrown by the white sponge *L. eleanor*, and is home to a variety of other sponges, tunicates, and bryozoans. Similarly, *Phyllospadix* sp. is often covered by the soft, reddish-brown algae *Smithora naiadum* (see Fig. S2). To determine the dietary importance of these epiphytic communities, we compared the feeding rates of *P. miniata* on macrophytes with versus without epiphytes.

We compared 2 treatments (clean and encrusted) for 2 species of macrophytes: *Rhodymenia* sp., a red alga, and *Phyllospadix* sp., a seagrass. In the 'clean' treatment, all epiphytes were manually removed from the macrophyte (as in Expts 1 and 2). In the 'encrusted' treatment, the macrophytes were left encrusted with epiphytes (mainly *L. eleanor* for *Rhodymenia* sp., and *S. naiadum* for *Phyllospadix* sp.). We conducted 3 trials for *Rhodymenia* sp. in August 2016, and 3 trials for *Phyllospadix* sp. in September 2017 (i.e. the 2 macrophyte species were tested separately). Each trial lasted 3 d and included 5 replicates for each of 4 treatments (clean–bat star, clean–control, encrusted–bat star, and encrusted–control) for the given macrophyte species. For each replicate in each treatment, we calculated the rate of change in prey mass (R , Eq. 1) and then, since the data were not normally distributed and variances were unequal, we used an aligned rank transformation ANOVA to evaluate the effects of epiphyte status and bat star treatment, as well as their interaction. We analyzed *Phyllospadix* sp. and *Rhodymenia* sp. separately because trials were conducted in separate years (hence, effects of species and years could not be decoupled).

2.2. Stable isotope analyses

Stable isotope analyses of consumers collected in the field, where a wide array of prey species is available, can complement short-term laboratory feeding experiments by quantifying dietary patterns over longer temporal scales (Peterson & Fry 1987, Thompson et al. 2005, Newton 2010). Ratios of ^{15}N to ^{14}N reflect the trophic position of a given consumer (e.g. discriminating between herbivores and carnivores) while ratios of ^{13}C to ^{12}C provide information on the sources of dietary carbon (e.g. discriminating carbon derived from the pelagic habitat from that derived from the kelp forest) (DeNiro & Epstein 1978, 1981). Here, we used stable isotopes to determine how the diet of *P. miniata* compared to those of 3 other kelp forest echinoderms whose diets are better resolved: a carnivore (the giant sea star *Pisaster giganteus*), an herbivore (the purple sea urchin *Strongylocentrotus purpuratus*), and a detritivore (the warty sea cucumber *Parastichopus parvimensis*).

2.2.1. Sampling

Echinoderms were collected from the kelp forest off Hopkins Marine Station in July and August of 2016. In total, divers collected 38 bat stars *P. miniata* (size range: 42.5–153.7 g), 33 purple sea urchins *S. purpuratus* (size range: 26.6–94 g), 29 giant sea stars *P. giganteus* (size range: 161.4–702.4 g), and 6 warty sea cucumbers *P. parvimensis* (size range: 214.8–647.8 g). All echinoderms were kept without food in recirculating saltwater aquaria for at least 2 d prior to tissue collection (to allow time for depuration).

Just before tissue collection, each animal was blotted dry with paper towels and weighed to the nearest hundredth of a gram. For the 2 sea star species, we sampled tube feet and ampullae; for sea urchins, we sampled muscle surrounding the Aristotle's lantern; and for the sea cucumbers, we used tissue from the papillae (Newsome et al. 2009). Samples were frozen before being placed in a drying oven at 50°C for at least 1 d, after which we homogenized each sample into a fine powder. Approximately 500 µg of powder from each sample was then sealed in tin boats and analyzed using a Carlo Erba NA 1500 Series 2 Elemental Analyzer interfaced with a Finnigan Delta+ stable isotope ratio mass spectrometer (SIRMS) at Stanford University, USA. USGS-40 and acetanilide were used as standards, and results were expressed as deviations from the standards.

2.2.2. Data analysis

To evaluate differences in the relative trophic levels and sources of dietary carbon for the 4 echinoderm species, we analyzed the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, respectively, for each species using an aligned rank transformation ANOVA (since the data did not meet the assumptions of parametric ANOVA) and an aligned rank transformation analogue of Tukey's HSD test (Mansouri 1998). To compare isotopic niche breadth, we used the Stable Isotope Bayesian Ellipses in R (SIBER) package to calculate the corrected standard ellipse area (SEA_C) for each species group (Jackson et al. 2011). We also analyzed the Euclidean distances of each sample from its species centroid using an aligned rank transformation ANOVA (since data were not normally distributed) and an aligned rank transformation analogue of Tukey's HSD test (Layman et al. 2007). All statistical comparisons were conducted with $\alpha = 0.05$ and a Bonferroni correction. We then measured the overall dietary similarity of each species relative to *P. miniata* by calculating the Euclidean distance from each group's centroid to the centroid for *P. miniata*, and by calculating the overlap between the 95% prediction ellipses for *P. miniata* with each of the other 3 echinoderm species (using the SIBER package in R; Jackson et al. 2011).

3. RESULTS

3.1. Feeding experiments

3.1.1. Expt 1: feeding rates on single prey species

All prey species had R_{control} values close to zero. By contrast, $R_{\text{bat star}}$ values were negative for some prey species, and close to zero for others. Accordingly, there was a significant interaction between prey species and bat star treatment (i.e. bat star versus control) on the rate of change in prey mass (R) ($F_{15,95} = 13.35$, $p < 0.01$), demonstrating that consumption rates varied among prey species (Fig. 1).

The largest consumption rates (c , i.e. differences between R_{control} and $R_{\text{bat star}}$; Eq. 2) were observed for prey in the carrion group (e.g. *Carassius auratus*, *Loligo opalescens*, and *Hemigrapsus nudus*). *C. auratus* and *L. opalescens* each had significant differences between $R_{\text{bat star}}$ and R_{control} ($p = 0.03$ for *C. auratus*, and $p < 0.03$ for *L. opalescens*) and the highest consumption rates of all the prey species we

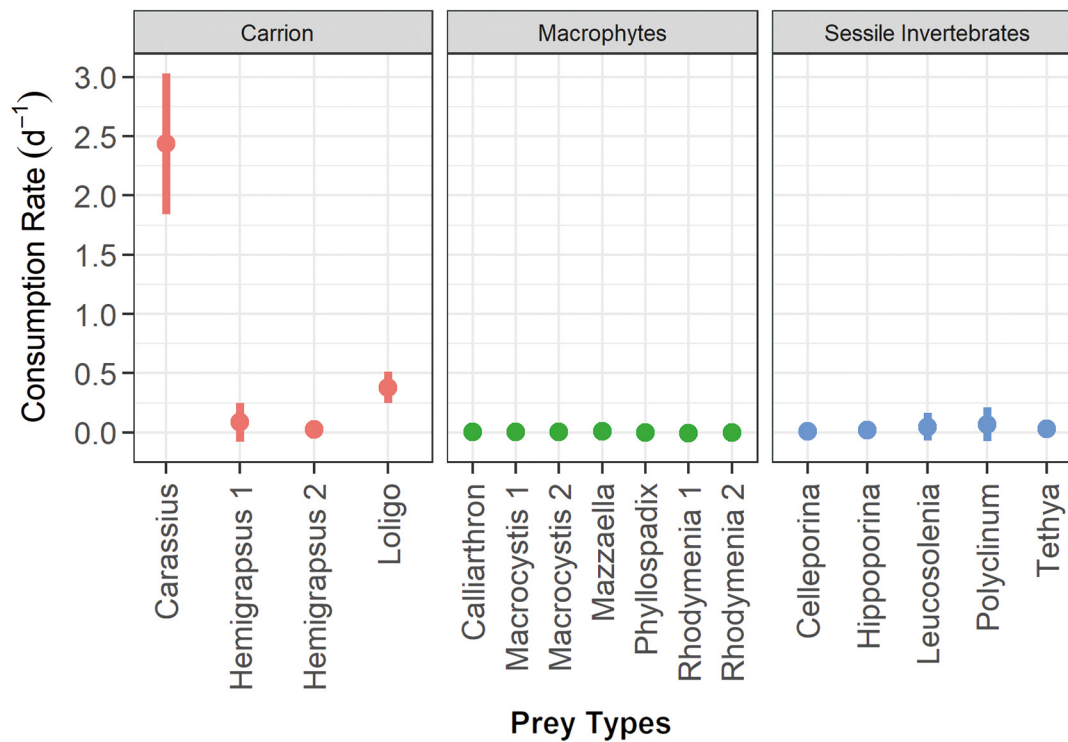


Fig. 1. Bat star *Patiria miniata* consumption rates (d^{-1} ; mean \pm SE) for single prey types. Prey are designated as either carrion (red), macrophytes (green), or sessile invertebrates (blue). Positive values indicate net prey consumption

tested, $2.44 d^{-1}$ and $0.37 d^{-1}$, respectively (Fig. 1). By contrast, $R_{bat\ star}$ and $R_{control}$ were not significantly different for the 2 *H. nudus* trials ($p = 1.0$ for *Hemigrapsus* 1, $p = 0.2$ for *Hemigrapsus* 2) and consumption rates were thus lower ($0.09 d^{-1}$ for *Hemigrapsus* 1, and $0.02 d^{-1}$ for *Hemigrapsus* 2).

Consumption rates on sessile invertebrates were relatively low ($c < 0.05 d^{-1}$), with only *Hippoporina insculpta* having a significant difference between $R_{bat\ star}$ and $R_{control}$ ($p = 0.03$). Consumption rates on macrophytes were even lower ($c < 0.008 d^{-1}$), and no species showed a significant difference between $R_{bat\ star}$ and $R_{control}$ ($p > 0.05$).

3.1.2. Expt 2: effects of food deprivation on *Rhodymenia* sp. consumption

There was no significant interaction between food deprivation treatment and bat star treatment on the rate of change in *Rhodymenia* sp. mass, R ($F_{2,30} = 0.354$, $p = 0.70$) (Fig. 2), nor was there a significant main effect of the food deprivation treatment ($F_{2,30} = 0.354$, $p = 0.70$), suggesting that consumption was not affected by the duration of food deprivation. The main effect of the bat star treatment on *Rhodymenia*

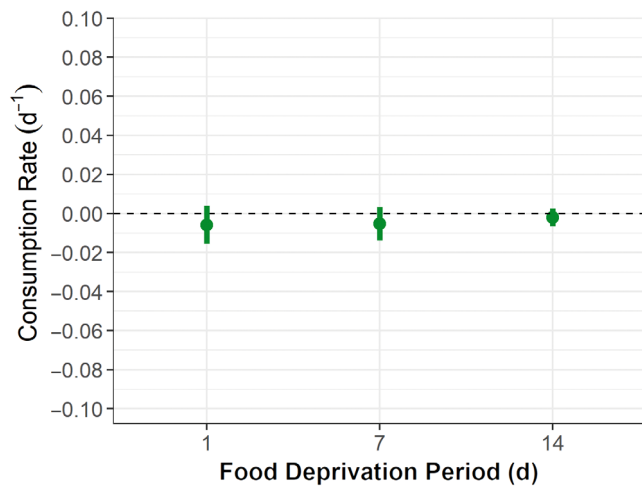


Fig. 2. Bat star *Patiria miniata* consumption rates (d^{-1} ; mean \pm SE) for *Rhodymenia* sp. after different food deprivation periods (Expt 2). Food deprivation periods are for 1, 7 and 14 d. Negative values indicate net prey growth in the presence of bat stars (not consumption)

sp. growth was significant ($F_{1,30} = 6.00$, $p = 0.02$), although the effect was in the opposite direction than expected: the algae increased in mass more in the presence of *P. miniata* ($R_{bat\ star} > R_{control}$), leading to negative consumption rates for each food deprivation

treatment (-0.006 d^{-1} for 1 d, -0.005 d^{-1} for 7 d, and -0.002 d^{-1} for 14 d) and suggesting that *P. miniata* facilitated the growth of *Rhodymenia* sp. Although the overall effect of bat stars was significant, none of the individual food deprivation treatments showed a significant effect of bat stars.

3.1.3. Expt 3: clean versus encrusted macrophytes

There was a significant interaction between epiphyte status and bat star treatment on the rate of change in prey mass (R) for both *Rhodymenia* sp. ($F_{1,56} = 9.96$, $p < 0.01$) and *Phyllospadix* sp. ($F_{1,56} = 20.26$, $p < 0.01$). Consumption rates (c) were greater on 'encrusted' than on 'clean' macrophytes for both *Rhodymenia* sp. and *Phyllospadix* sp. (Fig. 3). *Patiria miniata* consumed 'encrusted' *Phyllospadix* sp. at a rate of 0.04 d^{-1} but only consumed 'clean' *Phyllospadix* sp. at a rate of $-1.9 \times 10^{-4} \text{ d}^{-1}$. Similarly, *P. miniata* consumed 'encrusted' *Rhodymenia* sp. at a rate of 0.02 day^{-1} but only consumed 'clean' *Rhodymenia* sp. at a rate of $-3.0 \times 10^{-3} \text{ d}^{-1}$. Post hoc Mann-Whitney tests revealed significant differences in 'bat star' and 'control' growth rates for 'encrusted' macrophytes ($p < 0.01$ for *Phyllospadix* sp., $p = 0.04$ for *Rhodymenia* sp.), but insignificant differences in 'bat star' and 'control' growth rates for 'clean' macrophytes ($p = 0.9$ for *Phyllospadix* sp., $p = 0.05$ for *Rhodymenia* sp.).

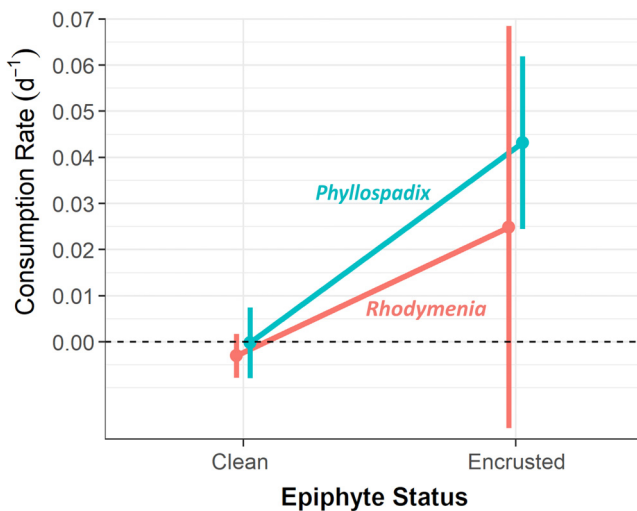


Fig. 3. Bat star *Patiria miniata* consumption rates (d^{-1} ; mean \pm SE) on clean versus encrusted macrophytes (Expt 3). Macrophytes are classified as either 'clean' (epiphytes removed) or 'encrusted' (epiphytes attached). *Rhodymenia* sp. is shown in red, and *Phyllospadix* sp. is shown in green. Positive values indicate net prey consumption; negative values indicate net prey growth in the presence of bat stars

3.2. Stable isotope study

The 4 species of echinoderms varied significantly in their nitrogen ($F_{3,102} = 101.78$, $p < 0.01$) and carbon ($F_{3,102} = 20.90$, $p < 0.01$) isotope ratios (Fig. 4). *Patiria miniata* had the highest average $\delta^{15}\text{N}$ value (14.54‰), followed by *Pisaster giganteus* (14.10‰), *Parastichopus parvimensis* (12.11‰), and finally *Strongylocentrotus purpuratus* (11.06‰). Differences in $\delta^{15}\text{N}$ values were statistically significant for all species pairs, except *P. parvimensis* and *S. purpuratus* ($p = 0.12$, Tukey's HSD test). Of the 4 species, *P. parvimensis* had the lowest average $\delta^{13}\text{C}$ values (-15.61‰), followed by *P. miniata* (-14.33‰), *S. purpuratus* (-13.83‰), and finally *P. giganteus* (-13.59‰). Differences in $\delta^{13}\text{C}$ values were statistically significant for all species pairings, except for *P. giganteus* and *S. purpuratus* ($p = 0.17$) according to Tukey's HSD test.

Overall, *P. miniata* exhibited low variability in its carbon and nitrogen isotope ratios (Fig. 4). *Patiria miniata* had the lowest isotopic niche breadth ($\text{SEA}_C = 0.53\text{‰}^2$) of the 4 echinoderm species, followed by *S. purpuratus* (0.83‰^2), *P. giganteus* (0.88‰^2), and *P. parvimensis* (1.83‰^2). Overall, there were statistically significant differences in dietary breadth (as measured by the distance to the species' centroid) for the 4 echinoderm species ($F_{3,102} = 4.20$, $p = 0.01$); however, the only significant pairwise comparison was between *P. miniata* and *P. parvimensis* (0.49 versus 1.07 ; $p = 0.01$).

Finally, the isotopic signature of *P. miniata* was more similar to that of *P. giganteus* than it was to that of *P. parvimensis* or *S. purpuratus*. *Pisaster giganteus*

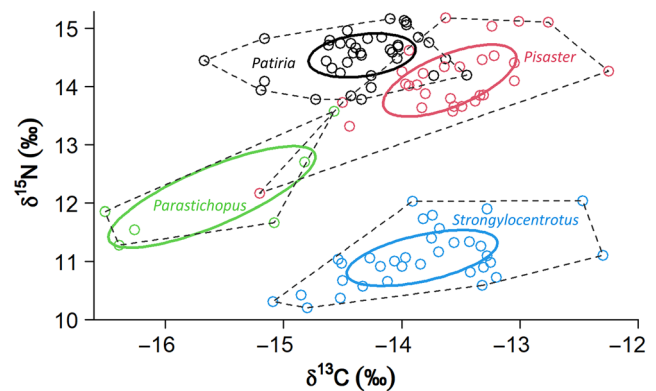


Fig. 4. Isotope ratios of 4 kelp forest echinoderms. Bat stars *Patiria miniata* are shown in black, giant sea stars *Pisaster giganteus* are shown in red, purple sea urchins *Strongylocentrotus purpuratus* are shown in blue, and warty sea cucumbers *Parastichopus parvimensis* are shown in green. Dashed lines mark the convex hulls for each group; solid, colored lines define the standard ellipses for each group

had the shortest distance to *P. miniata*'s centroid (0.86) and the highest proportional ellipse overlap with *P. miniata* (0.23). The distance from *Parastichopus parvimensis* and *S. purpuratus* to *P. miniata*'s centroid was 3 and 4 times greater than for *P. giganteus*, and their proportional ellipse overlaps were similarly reduced (0.23 for *P. giganteus*, 0.07 for *P. parvimensis*, and 0 for *S. purpuratus*) (Fig. 4).

4. DISCUSSION

4.1. Feeding experiments

The feeding experiments on single prey species yielded several interesting results, some of which confirmed previous ideas about the trophic ecology of *Patiria miniata*, and some of which challenged these notions. Perhaps the least surprising results were the high consumption rates recorded for *Carassius auratus* and *Loligo opalescens* (dead fish and squid, respectively). These soft-bodied carrion are high in energy and easily digested (Moleón et al. 2019). In contrast, results from the other carrion prey (dead shore crabs) did not provide concrete evidence of consumption during our experimental timeframe, even though bat stars were observed with their stomachs extended over them, seemingly in a state of active feeding. Unlike the squid and fish, the shore crabs are covered in a hard shell that resisted degradation (despite *P. miniata*'s attempts at feeding). If *P. miniata* had more time to feed, or if the crabs were already partially decomposed, there may have been a significant change in prey mass. Other studies have recorded *P. miniata* consuming dead crabs, but only after their exoskeletons had been crushed, allowing access to the underlying soft tissue (reviewed by Araki 1964). A limitation of these feeding experiments is that they represent a specific condition in which prey is always present and readily abundant. Consumption rates in the field are likely much lower for prey species where abundances are relatively low and search times high. This is especially true for carrion, which represents a valuable yet ephemeral resource for *P. miniata*, subject to intense competition by a suite of opportunistic scavengers (Britton & Morton 1994). Accordingly, it is still unclear how much carrion contributes to the overall diet of *P. miniata*.

Of the sessile invertebrates, *P. miniata* only consumed *Hippoporina insculpta* (the fluted bryozoan). The absence of demonstrable consumption of the other prey warrants some qualification. For example,

one bat star did consume *Polyclinum planum*, while the others ignored this potential prey. Thus, *P. planum* can be consumed by *P. miniata*, but the high inter-individual variation among bat stars led to an uncertain average consumption rate. Although consumption of *Tethya aurantia* (the orange puffball sponge) and *Celleporina robertsoniae* (another bryozoan species) was not significantly different from zero, we did observe some *P. miniata* with their stomachs extended over these invertebrates, and at the end of the trial some individuals appeared faded in color. Previous studies of the predation of *P. miniata* on bryozoans demonstrated that *P. miniata* significantly reduced the cover of live bryozoan colonies but left their skeletons clean and intact (Day & Osman 1981). Our reliance on mass-based techniques may underestimate the consumption rates on heavily calcified organisms (such as bryozoans and possibly crabs), whose inedible, calcified exoskeletons account for the majority of their overall body mass. These calcified species may also have handling times that were longer than the duration of the feeding trials. If consumption rates could be calibrated to only consider changes in soft tissue, *P. miniata*'s consumption rates of calcified organisms would likely be higher. Unfortunately, we did not distinguish between the consumption of hard- versus soft-bodied tissues for the different prey species. Overall, none of the consumption rates on sessile invertebrates, hard- or soft-bodied, approached those seen for *L. opalescens* and *C. auratus*. This is likely due to the lower nutritive value and greater handling time of these invertebrate species relative to the soft-bodied carrion. Still, sessile invertebrates are a more consistent food source in the kelp forest than carrion, and may constitute a greater portion of the overall diet of *P. miniata*.

The most surprising result of the feeding experiments was the consistent lack of consumption of clean macrophytes, given that the literature consistently describes *P. miniata* as an omnivore, with accounts of it eating kelp, surfgrass, and a variety of other macrophyte species (Morris et al. 1980, Day & Osman 1981, Farias et al. 2012). Yet in all 7 trials, none of the macrophyte species were consumed. A notable limitation of these experiments was that we only tested consumption rates on fresh macrophytes. In the kelp forest, *P. miniata* encounters macrophytes in various states of decomposition. Older, decaying tissues may be more easily digested than fresh tissues and could thus yield higher consumption rates. Nevertheless, our results directly contradict the literature, suggesting a more limited trophic role for

P. miniata than has been previously reported. Resolving this paradox became the focus of our remaining feeding experiments.

Increased food deprivation did not elicit consumption of *Rhododymenia* sp. Furthermore, our results suggested that *Rhododymenia* sp. benefited from the presence of its putative consumer, further casting doubt on the importance of *P. miniata* as a consumer of macrophytes. One potential explanation for these patterns is that nutrient excretion from *P. miniata* benefited the algae more than any harm imposed by consumption. In other aquatic systems, animal-derived nutrient inputs can create local hotspots of enhanced algal growth (Burkepile et al. 2013, Childress et al. 2014). Alternatively, if *P. miniata* was feeding on cryptic epiphytes (those that remained on *Rhododymenia* sp. despite our attempts to remove them), it is possible that this selective feeding could promote the growth of the underlying algae by increasing the availability of light and oxygen. Ultimately, these results indicate that food deprivation alone cannot explain the disparities between our field observations of *P. miniata* in association with and seemingly consuming macrophytes, and laboratory feeding experiments that did not support this assumption.

In some systems, it is the epiphytes, and not their host plants, that form the base of the local food web (Kitting et al. 1984, Klumpp et al. 1992, Moncreiff & Sullivan 2001, Zheng et al. 2015). If epiphytes represent a trophic resource for *P. miniata*, rather than the macrophytes on which they grow, it could explain the reporting of *P. miniata* as a consumer of macrophytes. Much of our understanding of the trophic ecology of *P. miniata* comes from field observations, in which any organism observed beneath *P. miniata*'s extended stomach is assumed to be prey. Unfortunately, this visual method cannot distinguish between the consumption of epiphytes and the underlying macrophyte. Epiphyte consumption could also potentially explain the slight positive effects of *P. miniata* on *Rhododymenia* sp. in our food deprivation experiment if the reduction of epiphytes promotes algal growth. Results from Expt 3 clearly indicated that *P. miniata* was primarily consuming epiphytes and not the host macrophytes (*Rhododymenia* sp. or *Phyllospadix* sp.). Interestingly, in Monterey Bay, *Phyllospadix* sp. is often covered by the soft red algae *Smithora naiadum*, thus *P. miniata*'s consumption of encrusted *Phyllospadix* sp. constitutes the only conclusive demonstration of *P. miniata* feeding on macrophytes; in this case the macrophyte is *S. naiadum*, the epiphytic algae growing on *Phyllo-*

spadix sp. *S. naiadum* is soft and fleshy, and evidently one of the few macrophytes capable of being digested by *P. miniata*. Altogether, these findings support our conclusion that *P. miniata* often feeds on epiphytes, but not on the underlying macrophytes themselves. This could have significant implications for the effects of *P. miniata* on benthic community structure. By selectively feeding on epiphytes, *P. miniata* may indirectly benefit the underlying macrophytes, as has been observed for other invertebrate species (Hughes et al. 2010). While feeding on epiphytes, *P. miniata* may incidentally digest some of the underlying macrophyte, but the negligible consumption of macrophytes lacking epiphytes still suggests that the importance of macrophytes in the diet of *P. miniata* is largely overstated.

Patiria miniata did not consume any macrophytes in our feeding trials, except for the epiphytic algae *S. naiadum*, which is easily digested. The diet of *P. miniata* may be constrained by the strength of its digestive enzymes, whose effects are limited to the area directly beneath its cardiac stomach and which are rapidly diluted in the surrounding seawater (Araki 1964). Many macrophyte species may be able to resist degradation by *P. miniata*'s digestive enzymes, thereby excluding those species from its diet. This idea is supported by a previous study that showed that *P. miniata* could feed on kelp sporophytes, but once the algae grew larger than 1 cm, it reached a size refuge (Leonard 1994). Such size refuges from herbivory are common among primary producers in marine and terrestrial ecosystems and are driven by ontogenetic changes in the plant's physical and chemical defenses (Cronin & Hay 1996, Barton & Koricheva 2010).

4.2. Stable isotope analysis

The results of our stable isotope analysis further support the conclusion that *P. miniata* is a predominantly carnivorous species, and not a generalist omnivore. If *P. miniata* were omnivorous, and macrophytes composed a substantial part of its diet, its average $\delta^{15}\text{N}$ value should be intermediate between that of *P. giganteus* (a carnivore) and *S. purpuratus* (an herbivore), and similar to that of *P. parvimensis* (a detritivore). Yet, *P. miniata* had an average $\delta^{15}\text{N}$ value that was significantly higher than that of all the reference species, including *P. giganteus*, suggesting it occupied the highest relative trophic level. Our findings agree remarkably well with a previous study (Page et al. 2013) of several consumers in a southern California

kelp forest, which found that *S. purpuratus* and *P. parvimensis* had average $\delta^{15}\text{N}$ values of approximately 11‰ and 12‰, respectively, meaning they occupied the first trophic level above primary producers (i.e. herbivores), while *P. miniata* and *P. giganteus* had average $\delta^{15}\text{N}$ values of approximately 14‰, meaning they occupied the second trophic level above primary producers (i.e. carnivores) (Page et al. 2013). These values are nearly identical to what we found in our study. Caution should be taken when interpreting this similarity in isotopic values, as baseline isotope ratios can vary between different systems, and it is impossible to know an organism's exact trophic level without knowing the isotopic baseline for resources (Kristensen et al. 2016). Still, the consistent alignment of the isotopic pattern of *P. miniata* with that of other known carnivores strongly suggests that its diet is more carnivorous than generally appreciated. Page et al. (2013, p. 184) also noted the unusually high $\delta^{15}\text{N}$ values for *P. miniata*, remarking, 'the bat star...is reported as an omnivore, but the N isotope data suggest that it feeds primarily as a carnivore on the study reefs.'

The isotopic signature of *P. miniata* was closest to that of the giant sea star *P. giganteus*, though isotopic similarity does not necessarily imply trophic similarity. Two species with distinct diets can have similar isotope ratios if their prey have the same collective isotopic composition (Layman et al. 2012). Indeed, although *P. miniata* and *P. giganteus* occupy similar trophic levels, there may be important differences in the specific diets of these 2 species. On average, *P. miniata* had more depleted $\delta^{13}\text{C}$ values than *P. giganteus*, and the area of overlap between the 2 species was still only a fraction of their total isotopic niche space. One potentially important difference in the 2 species' diets is that *P. giganteus* feeds on several species of live mollusks, such as mussels, clams, and turban snails, while such behavior has not been reported for *P. miniata* (Landenberger 1968, Vance 1978, Harrold & Pearse 1980). Also, although *P. miniata*'s consumption of macrophytes seems to be largely overstated in the literature, *P. miniata* did consume the epiphytic algae *Smithora naiadum*, growing on *Phyllospadix* sp. By contrast, *P. giganteus* has not been reported feeding on macrophytes or their epiphytes. These dietary differences likely account for many of the differences in the isotopic signatures of each species.

Finally, *P. miniata* had the smallest among-individual variation in isotopic niche breadth of the 4 echinoderm species (Fig. 4). These diversity metrics (Layman et al. 2007, Jackson et al. 2011) are typically higher for generalist species, especially those feed-

ing across trophic levels, due to their greater dietary plasticity (Van Valen 1965, Bolnick et al. 2003). One important limitation of these metrics is that they only reflect isotopic variation among individuals, and not within individuals (Matthews & Mazumder 2004, Newsome et al. 2012, Matich et al. 2021). If all individuals in a generalist population shared similar diets, they could have similar isotopic values, and score low on these trophic diversity metrics (despite their broad diets at the individual level). This is especially true if individuals are sampled within a relatively short timeframe, as was the case in our study. Thus, the small standard ellipse area and distance to the centroid of *P. miniata* suggest limited dietary plasticity at the population level but does not necessarily imply a narrow dietary breadth at the individual level.

4.3. The trophic ecology of *P. miniata*

By combining different methodological approaches (e.g. field observations, laboratory experiments, and stable isotope analyses), our study reveals novel insights into the role of *P. miniata* in the kelp forest ecosystem of the northeastern Pacific coast. Specifically, our results suggest that *P. miniata* has a narrower diet than previously expected, acting primarily as a benthic scavenger and predator of epiphytic invertebrates, with limited effects on most macrophytes. *Patiria miniata* shares a similar isotopic niche and trophic level with *P. giganteus*, but there are key differences between the diets of the 2 species (e.g. only *P. giganteus* consumes live mollusks, and only *P. miniata* feeds on algal detritus) (Landenberger 1968, Vance 1978, Harrold & Pearse 1980). Due to these dietary differences, *P. miniata* and *P. giganteus* likely play different roles in shaping benthic community structure. Future studies should use field experiments to directly compare the effects of *P. miniata* and *P. giganteus* on benthic algal and invertebrate communities. This would allow us to understand the broader trophic roles of *P. miniata* and *P. giganteus* in the northeastern Pacific kelp forest community and help quantify the extent of niche overlap between the 2 species. Doing so would also provide us a greater understanding of the complex trophic dynamics that govern kelp forest ecosystems.

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