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Parasite and host biomass and reproductive output in barnacle populations in the rocky intertidal zone

Research Article

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Abstract

The rocky intertidal zone has a long history of ecological study with barnacles frequently serving as a model system to explore foundational theories. Parasites are often ignored in community ecology studies, and this particularly holds for true for the rocky intertidal zone. We explore the role of the isopod parasite, *Hemioniscus balani*, on its host, the acorn barnacle, *Chthamalus fissus*. We use the currencies of biomass and reproduction measured at the individual level, then applied to the population level, to evaluate the importance of this parasite to barnacle populations. We found *H. balani* can comprise substantial biomass in 'apparent' barnacle populations, sometimes even equaling barnacle biomass. Additionally, parasite reproduction sometimes matched barnacle reproduction. Thus, parasites divert substantial energy flow from the barnacle population and to near-shore communities in the form of parasite larvae. Parasites appeared to decrease barnacle reproduction per area. Potentially, this parasite may control barnacle populations, depending on the extent to which heavily infected barnacle populations contribute to barnacle populations at larger scales. These findings regarding the importance of a particular parasite for host population dynamics in this well studied ecosystem call for the integration of disease dynamics into community ecological studies of the rocky intertidal zone.

Introduction

The rocky intertidal zone is an iconic ecosystem in which the impacts and consequences of parasitism are understudied. Whether this is the absence of evidence or evidence of absence remains to be determined. This is striking because ecologists have long used this ecosystem to develop a foundational theory (e.g. Connell, 1961*a*, *b*; Paine, 1966; Dayton, 1971; Gaines and Roughgarden, 1985). Barnacles, in particular, have a long history of ecological study and have been a model organism for evaluation of key processes such as competition (Connell, 1961*a*; Menge, 1976), predation (Connell, 1961*b*), disturbance (Sousa, 1979) and recruitment dynamics (Gaines and Roughgarden, 1985; Menge, 2000). However, the role of parasitism in barnacle population performance has been generally ignored (with some interesting exceptions, see Blower and Roughgarden, 1987; Harley and Lopez, 2003). In fact, in his classic 1961 *Ecology* paper on competition, Connell remarked that *Semibalanus balanoides* had an isopod parasite that could impact growth rate. He chose to ignore that interaction, yet noted the parasite may be able to regulate the outcome of competition by diminishing the ability of *S. balanoides* to outcompete *Chthamalus stellatus*, which had not been reported as infected. Currently, when searched as a topic, Web of Science recovers 369 items for the genus *Chthamalus,* but only 13 for its parasite, *Hemioniscus*. Concealed within the host, parasites are often excluded from ecological consideration. However, the importance of the rocky intertidal zone to ecology, particularly its barnacles, calls for an evaluation of the effects of parasitism on these model organisms in this model ecosystem.

Hemioniscus balani is a globally distributed isopod parasite that castrates its barnacle host (Caullery and Mesnil, 1901; Crisp, 1960; Goudeau, 1970). Parasitic castrators use a consumer strategy in which a single infecting parasite eliminates host reproduction (Kuris, 1974; Lafferty and Kuris, 2009; Lafferty *et al.*, 2015). *Hemioniscus balani* enters the barnacle test and attaches to the ovaries, draining ovarian fluid and rendering the barnacle unable to reproduce as a female. After the isopod matures, it releases its offspring and dies. Following infection, barnacles recover female reproductive function. Hence, *H. balani* is an ephemeral, semelparous parasite that temporarily blocks female reproduction (most castrators are long-lived and iteroparous). Consequently, *H. balani* has the potential to substantially impact the ecology of its barnacle hosts.

Ecologists use standing-stock biomass and reproductive output to estimate the importance and contribution of different populations to communities, ecosystems and ecological processes. Examples include competition (Wilson and Tilman, 1991; Fong and Fong, 2018), trophic dynamics (Lindeman, 1942; Power, 1992; Wilmers *et al.*, 2012), stability (Tilman, 1996; Borer *et al.*, 2012), carbon fixation (Wilson and Tilman, 1991; Wilmers *et al.*, 2012) and nutrient cycling (Odum and Odum, 1955; Odum, 1971; Metcalfe *et al.*, 2014).

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Infectious agents have generally been ignored in these studies, likely because they were assumed to have negligible biomass and productivity (e.g., Loreau et al., 2005). However, parasite biomass can be substantial, exceeding the biomass of top predators and major groups of free-living organisms in estuarine and pond ecosystems (Kuris et al., 2008; Preston et al., 2013). However, because of the challenging logistics of studying the effects of parasitism, the generality that parasites are important to population, community and ecosystem processes is still in question.

Here, we provide an initial insight into the role of parasites in rocky intertidal communities by examining how *H. balani* impacts *Chthamalus fissus* hosts and populations using the currencies of biomass and reproduction. *Chthamalus fissus* is a simultaneously hermaphroditic acorn barnacle susceptible to parasitism by *H. balani* that inhabits the high rocky intertidal zone. We first documented the relationship between body size and reproductive output for both individual hosts and parasites. We then applied these relationships to natural barnacle populations from 12 localities throughout Southern California, allowing us to express the impacts of parasitism at the population-level in terms of host and parasite standing-stock biomasses and reproductive outputs.

Methods

Individual estimates

We collected naturally infected and uninfected barnacles from the field to quantify individual barnacle and parasite tissue weight and reproductive output. Barnacles were collected from Miramar Beach in Santa Barbara, CA, USA between September 2013 and September 2015 (see Fong et al., *in revision* for methods). Barnacles were processed in the laboratory to quantify the relationships between size and reproductive rates for both barnacle hosts and isopod parasites. We ensured each dissected barnacle belonged to the genus *Chthamalus* based on plate arrangement. While we cannot exclude the possibility that other similar *Chthamalus* species (e.g., the rarer *Chthamalus dalli*) were included in our samples, *C. fissus* is the most common *Chthamalus* species in southern California (Newman and Abbott, 1980; Ricketts et al., 1985, Newman, personal communication). Both species are similar in size, biology and ecology (Newman and Abbott, 1980) and *H. balani* infects both species (Blower and Roughgarden, 1988), making accidental inclusion relatively unimportant. Hence, we refer to the host as *C. fissus* in this study.

For each barnacle, we measured maximum basal diameter to the nearest ¼ mm and determined whether it was infected or uninfected. For infected barnacle weight, we only used hosts with mature infections (when the parasite had eggs) to minimize variation in weight due to parasite developmental stage. For uninfected barnacles, we classified individuals as brooding or non-brooding where non-brooding barnacles had fully deflated ovaries while brooding barnacles had oviposited eggs (embryos). We only included brooding barnacles because as the ovary inflates, it goes from a negligible weight to a fully developed ovary that can comprise 70% of barnacle total weight (Hines, 1976). We separated and weighed the barnacle body, parasite body and barnacle egg mass using an analytical balance.

To relate barnacle size to barnacle egg production, we used GetData (www.getdata.com) to digitize graphs from the unpublished thesis of Hines (1976) that provided egg counts *vs* barnacle basal diameter. This data come from the same species of host, just north of the geographic range covered in our study.

To relate host barnacle size to parasite egg production, we measured maximum host base diameter to the nearest ¼ mm and counted the number of eggs (embryos) in the marsupium of the parasite within the host. We only used gravid parasites because eggs could be easily counted and to minimize variability due to development. We excluded barnacles with more than one parasite (<5% of infections across all sites) to minimize variation due to competition among parasites for host resources (Fong et al., 2017).

To estimate the total volume of parasite and barnacle eggs, we used published measurements of parasite and barnacle egg length and width (Goudeau, 1976, Hines, 1978). We calculated egg volume as a prolate spheroid and calculated the total biovolume of eggs produced by individual parasites and barnacles by multiplying the number of eggs by individual egg volume.

For these individual data, we collected a total of 142 barnacles ranging from 1.75 to 5.50 mm long. All of the barnacles were collected from Miramar Beach in Santa Barbara, CA, USA. We processed 60 infected, 28 uninfected/brooding and 54 uninfected/non-brooding barnacles. From the 60 infected barnacles, we counted the eggs produced by the parasite for 25 individuals ranging in size from 2.00 to 5.25 mm.

Population estimates

We applied the weight relationships described at the individual level to these field samples to estimate population standing-stock biomass and standing-stock reproductive output for barnacle and parasite. We surveyed 12 barnacle populations along the Southern California Bight to quantify population standing-stock biomass for uninfected barnacles, infected barnacles and parasites (see Fong et al., *in revision* for descriptions of field sampling, collection, dissection and SOM). Briefly, we surveyed 6 sites with 2 habitats per site – natural rock and pier pilings. Sites ranged from Gaviota to San Diego (SOM Fig. 1). To characterize each population, we used 10 replicate cores to quantify barnacle population density, size-frequency distribution, brooding frequency and infection prevalence (percentage of hosts infected). We dissected every *C. fissus* individual ≥1 mm collected to characterize the barnacle population. Population estimates of biomass and reproduction included uncertainty from individual measurements and population samples, so we estimated the combined uncertainty using standard rules of error propagation (Taylor, 1982; Lehrter and Cebrian, 2010). We estimated the total error originating from the regressions by propagating the standard error of the regression [root of $(SSE/(N-2))$], first among individuals within each core, then among cores before dividing by sample size. We then added in quadrature standard error from the individual regressions to the standard error from the population density estimates. Hence, standard errors for estimates of population biomass and reproduction include both sources of uncertainty.

We then determined the relationship between parasite prevalence and number of barnacle and parasite eggs per cm^2 across the 12 localities surveyed. To do this, we used the relationships between barnacle body size and egg production, barnacle body size and parasite egg production and applied these relationships to the population estimates from our survey data.

Statistical analysis

We used a combination of linear and non-linear models to analyse the data using the statistical package JMP v. 12.0. We ensured data met assumptions of homogeneous variance and normality. When appropriate, we used a model selection approach where we compared AICc scores to choose the most appropriate model using the model selection platform in JMP.
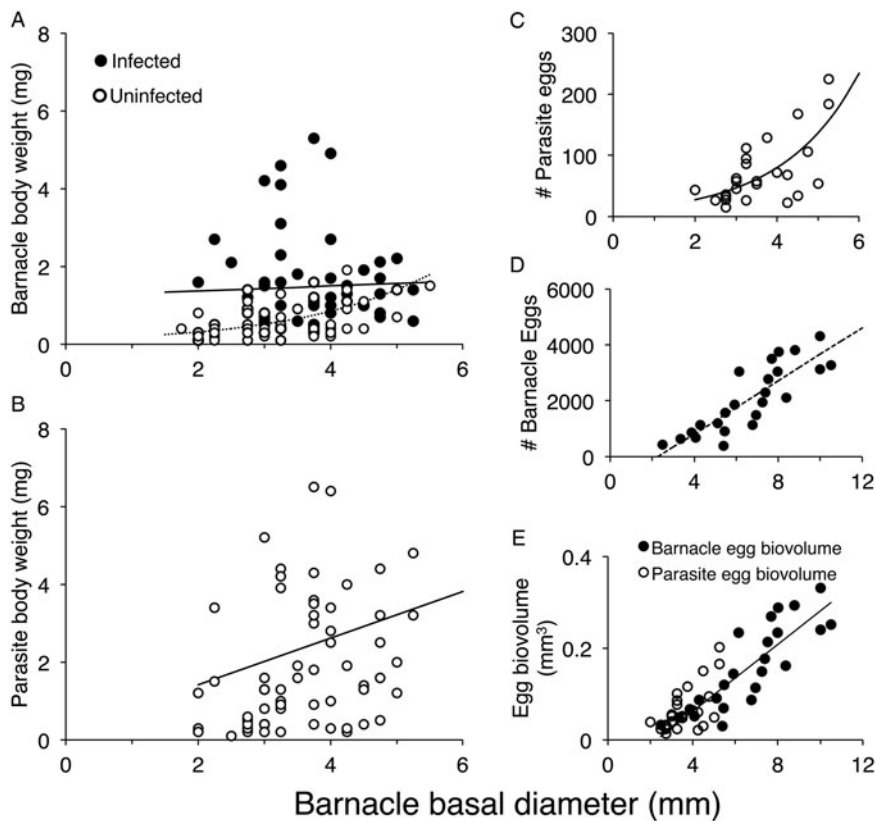
Fig. 1. (A) Relationship between barnacle body weight and barnacle test basal diameter. The dashed line represents the positive exponential relationship between uninfected barnacle weight and basal diameter, while the solid line represents the non-significant linear relationship between infected barnacle weight and basal diameter. (B) The relationship between isopod parasite body weight and barnacle host basal diameter. (C) Dependence of the number of isopod parasite eggs on barnacle basal diameter, (D) the number of barnacle eggs in relation to barnacle basal diameter, and (E) the biovolumes of parasite and barnacle eggs produced in relation to barnacle basal diameter.

Results

Individual estimates

The best-fit model for predicting individual barnacle body weight included infection status and barnacle length, but not barnacle brooding status (Table S1). We used a follow-up model selection approach to determine what type of regression (i.e. linear, exponential, log, etc.) best explained the relationship between length and weight for infected and uninfected barnacles. For infected barnacles, although a linear relationship between basal diameter and weight had the lowest AICc, the fit was not substantially better than the exponential fit and the relationship was not significant ($P = 0.42$). Overall, the mean weight of infected barnacles was $1.47 \pm$ s.e. 0.15 μg. An exponential relationship best described the positive relationship between tissue weight and test diameter for uninfected barnacles (uninfected weight = $0.1^{0.5*\text{length}}$, $P = $, Fig. 1A). Thus, the tissue weight of uninfected barnacles increased exponentially with test diameter. Hence, uninfected barnacles weighed less than infected barnacles for all but the largest size classes (Fig. 1A).

Parasite body weight was best explained by a linear relationship with a basal diameter (Table S1, Fig. 1B). As basal diameter increased, parasite weight increased ($y = 0.22 + 0.60*\text{length}$). Thus, while infected barnacle body weight did not vary with basal diameter, parasites grew larger in larger barnacles.

Barnacle eggs are $65 \times 47.5 \times 47.5$ μm and 7.68×10^{-14} m^3 while *H. balani* eggs are $190 \times 95 \times 95$ μm and 8.97×10^{-13} m^3. Hence, a parasite egg is ~$11.7 \times$ the size of barnacle eggs.

Egg number increased with barnacle basal diameter exponentially for parasites and linearly for barnacles (Fig. 1C and D). Thus, parasites in larger barnacles produced eggs exponentially (Table S1, Fig. 1C, $y = 9.4^{0.54x}$) while the barnacle itself produced linearly more eggs with increased size (Table S1, Fig. 1D, $y = 475.3x-1090.3$). However, the relationship between barnacle length and egg biovolume did not differ in either slope or intercept between parasite eggs and barnacle eggs (Table S1,

Fig. 1E). Thus, a barnacle produced an equivalent biovolume of eggs, whether parasite or barnacle.

Population estimates

To estimate standing-stock biomass and egg production at the population level, we processed 6381 barnacles collected from 12 sites along the Southern California Bight. Barnacles at the 12 sampled sites ranged in size from 1 to 13.5 mm and the overall prevalence of *Hemioniscus balani* was 5.7%. Of the uninfected barnacles, 28% were actively reproducing as females.

Across all sites, estimated average standing-stock biomass of uninfected barnacles ($2.10 \pm$ s.e. 0.28 mg per cm^2) was significantly greater than that of infected barnacles ($0.61 \pm$ s.e. 0.14 mg per cm^2), which in turn was greater than that of the parasites ($0.41 \pm$ s.e. 0.10 mg per cm^2) (Fig. 2A).

Mean standing-stock biomass of uninfected barnacles ranged from $1.11 \pm$ s.e. 0.19 to $2.81 \pm$ s.e. 0.91 mg per cm^2, infected barnacles from 0.00 to $2.97 \pm$ s.e. 0.71 mg per cm^2, and parasites from 0.00 to $1.69 \pm$ s.e. 0.30 mg per cm^2. Site 7 had the highest parasite prevalence (Fig. 2A), and infected barnacle standing-stock biomass was ~$1.3 \times$ the standing-stock biomass of uninfected barnacles while standing-stock biomass of parasite equaled that of uninfected barnacles.

Across sites, biovolume of barnacle eggs was ~$7 \times$ greater than parasite egg biovolume. Brooding barnacles produced an average of $0.09 \pm$ s.e. 0.02 mm^3 biovolume of eggs per cm^2 while parasites produced an average $0.01 \pm$ s.e. 0.00 mm^3 biovolume of eggs per cm^2. Egg production varied substantially among sites, and at one site (7), parasite egg biovolume production exceeded barnacle egg biovolume production (Fig. 2B).

Mean parasite egg production ranged from 0 to $0.05 \pm$ s.e. 0.01 mm^3 per cm^2 between sites while barnacle egg production per core ranged from $0.02 \pm$ s.e. 0.01 to $0.18 \pm$ s.e. 0.03 mm^3 per cm^2. At site 7, parasites and barnacles produced an equivalent
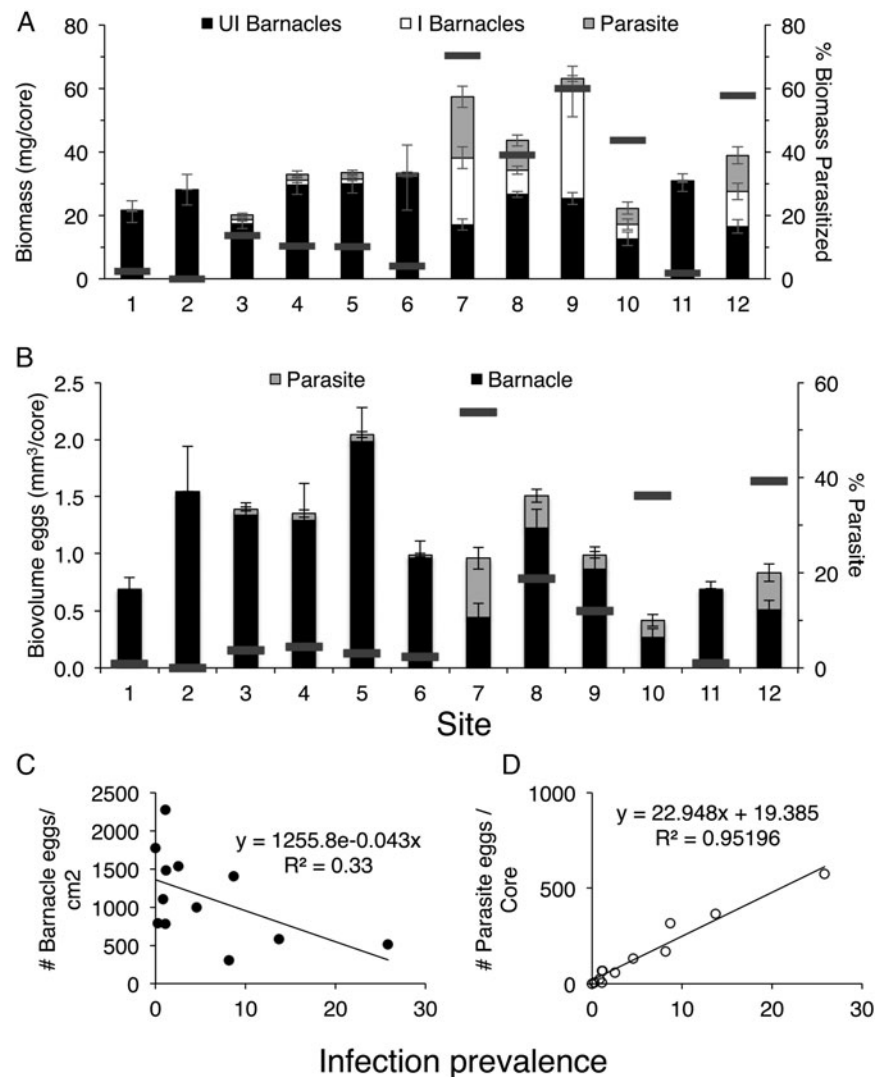
Fig. 2. (A) Average standing-stock biomass of barnacle hosts and isopod parasites in ten 11.34 cm² cores taken at each of 12 sites spread throughout southern California. Error bars represent ± 1 s.e., and include error propagated from both the replicate cores and the application of length-weight regressions. Horizontal bars indicate the percent of biomass at each site that is parasitized (parasite + infected barnacle biomass). (B) Average biovolume of barnacle host and isopod parasite eggs produced in 11.34 cm² for each of 12 sites. Ten cores were taken per site and estimated biovolume of egg production was averaged across cores. s.e. on means include error generated by both the core and the individual level count data. Horizontal bars indicate the percent of egg biovolume at each site that is parasite. (C) An average number of barnacle eggs produced and (D) average number isopod parasite eggs produced per 11.34 cm² core at each site as a function of infection prevalence at that site.

biovolume of eggs, with parasites producing 0.05 ± s.e. 0.01 mm³ and barnacles producing 0.04 ± s.e. 0.01 mm³ per cm².

There was a marginally significant negative linear relationship across sites between parasite prevalence and the estimated egg production density of the barnacle population (Fig. 2C, $P = 0.073$). This pattern reflected ∼50% reduction in barnacle population reproductive output as prevalence increased from 0 to 26% prevalence. Similarly, we found a strong, positive, linear relationship between prevalence and parasite egg productivity (Fig. 2D, $P < 0.0001$).

Discussion

Within apparent barnacle populations, *Hemioniscus balani* comprised a substantial component of its biomass, a common proxy for relative importance. Parasite standing-stock biomass, including the extended phenotype of the infected host (O'Brien and Van Wyk, 1985; Kuris *et al.*, 2008; Dawkins, 1982), was greater than or equal to uninfected barnacle standing-stock biomass at 25% of our sites. Although the relationship between host size and parasite size had much unexplained variation, the error in our population estimates far exceeded the error in our individual estimates, so this effect was predominantly driven by variation in parasite prevalence among sites.

Researchers have found parasites can comprise substantial biomass in Californian estuaries (Kuris *et al.*, 2008) and ponds (Preston *et al.*, 2013) and New Zealand lake (Lagrue and

Poulin, 2016) communities. We extend that finding to barnacle populations in the rocky intertidal zone, necessitating consideration of parasites in this iconic community.

We found parasite reproductive output could match that of barnacles. This needs to be assessed over time to consider the extent to which a barnacle population contributes more barnacle or parasite progeny to ecosystem energetics. This productivity has important implications for connectivity between populations and ecosystems. Predators often consume free-living parasites (e.g., Kaplan *et al.*, 2009; Orlofske *et al.*, 2012); in the rocky intertidal zone, in particular, intertidal anemones readily consume *H. balani* cryptonisci (Fong and Kuris, 2017). Parasite larvae are substantially larger than barnacle larvae and may be consumed by different species of predators, which may influence food web dynamics. Further, both barnacle and parasite offspring are resource subsidies (Yang *et al.*, 2008) from intertidal to nearshore subtidal/pelagic marine communities. However, the nature of these subsidies is likely quite different – barnacle larvae disperse far and spend considerable time in the water column; in contrast, *H. balani* larvae attach to copepod intermediate hosts and likely stay near shore. By diverting and repackaging a substantial fraction of host productivity, *H. balani* may alter energy flows, and the perception of relative sources and sinks for barnacle recruitment to adult populations, within and between near-shore marine communities.

Hemioniscus balani may have the potential to control *C. fissus* barnacle populations by suppressing barnacle reproduction. The

number of barnacle eggs produced per area decreased with increasing parasite prevalence. Models indicate that the high prevalence of *H. balani* can regulate host populations (Blower and Roughgarden, 1987). Some anecdotal evidence supports population regulation as well – Perez (1923) reported an outbreak of *H. balani* in *Balanus improvisus* populations lasting several years, after which the barnacle population was almost completely eradicated. Hence, there is evidence that this parasitic castrator can regulate barnacle host populations by suppressing barnacle reproduction and ultimately recruitment. Here we show a significant and substantial diversion of productivity from barnacle to parasite that varies among sites (Blower and Roughgarden, 1988; Fong et al., in revision). This study suggests *H. balani* may strongly influence the metapopulation dynamics of *C. fissus*. In particular, the parasite-host dynamics may control relative sources and sinks for barnacle reproductive productivity and recruitment to adult populations. Further analyses of barnacle population biology should assess the impacts of these parasites.

We documented substantial variation in parasite prevalence among our sites. While we cannot currently provide a definitive driver for this spatial variation, we provide two hypotheses. One possible mechanism is the differences in food availability. Increased food availability increases barnacle female reproductive productivity (Hines, 1978). For example, the fraction of barnacles brooding eggs can be 5 times higher at sites with higher near-shore primary productivity (Leslie *et al.*, 2005). Thus, if food availability varies amongst sites and sets barnacle reproduction, this might in turn control resource availability for the parasite. Another possibility has to do with predators on parasite infective stages. For example, anemones consume *H. balani* infective stages and reduce fine-scale parasite prevalence (Fong and Kuris, 2017). Thus, spatial differences among sites in levels of predation on parasites may also explain the strong variability in levels of parasitism among sites.

Barnacles in the rocky intertidal zone have been used as a model system for understanding basic ecological processes. However, the foundational studies did not evaluate parasitism (e.g. Connell, 1961*a*, *b*; Paine, 1966; Dayton, 1971; Menge, 1976, 2000; Sousa, 1979; Gaines and Roughgarden, 1985). How could parasitism be included in rocky intertidal zone ecosystem research? For example, consideration of parasitism may alter the interpretation of the classic study of competition and zonation in the rocky intertidal zone (Connell, 1961*a*). Only one species, the competitively dominant *Semibalanus balanoides*, was a documented host of *H. balani*. *Hemioniscus balani* likely reduces the growth rate in barnacles (Crisp, 1960). Hence, the extent of parasitism could alter competitive outcomes as barnacles compete by overgrowing or dislodging inferior space competitors. Parasitism could also influence predation rates on barnacles and thus zonation. Barnacle ovaries are predominantly lipid, a rich resource for predators and can comprise 70% of barnacle body weight (Hines, 1976). By consuming ovarian fluid and rapidly leaving, parasites may make recently infected barnacles a less desirable food source, reducing predation rates. Larval recruitment is a strong structuring force in the rocky intertidal zone (Gaines and Roughgarden, 1985; Menge, 2000). By depressing local reproduction, parasites may drive variability in barnacle recruitment rates in both space and time. This could further drive population and community responses to disturbances. Following disturbance, rocky intertidal communities undergo succession driven by recruitment (Sousa, 1979). If parasitism suppresses reproduction in source populations, then parasitism by *H. balani* may affect barnacle population recovery following disturbance. Our findings in this iconic system show a widespread distribution of this sometimes-abundant parasite and a substantial reduction in host reproductive productivity where it is prevalent. Its impacts on barnacle populations and rocky intertidal community structure may be substantial and are worthy of further study.

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