

Biotic interactions shift across temperature and ontogeny in an intertidal barnacle

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Abstract

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Natural systems provide beneficial goods and services to humanity. To maintain these benefits, modern science is tasked with predicting how natural systems respond to global change. Understanding the ecological processes that underly natural systems, such as interactions between organisms, can help improve such predictions and is thus a research priority. In this dissertation, I present novel findings on how ecological interactions vary across biotic and abiotic factors, and some potential consequences thereof.

The hallmark of global change is warming. Warming is important because temperature controls biology at all levels of organization. Many organisms are also shrinking. This is important because body size is a fundamental driver of ecological processes. From survival and growth to reproduction, organismal vital rates vary with ontogeny. Research over the past two decades emphasize that knowledge of the direct effects of temperature and body size on organisms is

inadequate to forecast community trajectories. Organisms do not exist in vacuum; they interact with neighbors and with predators. To improve understanding of how natural systems respond to global change, knowledge of the indirect effects – how biotic interactions change with temperature and body size – is required.

The rocky intertidal zone provides a valuable system in which to study the ecological impacts of global change. Sessile ectotherms in particular have been used to elucidate principles that now pervade ecology. For example, the acorn barnacle *Balanus glandula*, though mostly mute and wholly illiterate, tells excellent ecological stories. Seemingly shy in its “squatter’s nutshell”¹, a barnacle can reveal much about competition and facilitation given the right coaxing. Then there is the whelk *Nucella ostrina*. All who know them admire these “tiny wet beings straining calcium from the water and spinning it into polished dreams on their backs”². All except perhaps the barnacles, whom the whelks eat.

Using organisms in the rocky intertidal zone, this dissertation examines how biotic interactions shift across temperature and ontogeny. In Chapter 1, I examine how multiple physical drivers concurrently affect a consumer-resource interaction. Evidence suggests widespread non-additive effects between multiple drivers; most of this evidence, however, is based on species-level responses, which is problematic because community responses to environmental change also depend on species interactions. To address this knowledge gap, I experimentally manipulated two physical drivers fundamental in intertidal systems – air and water temperatures – and

¹ From “Mr Arthrobalanus” by Simon Carnell

² From *All the Light We Cannot See* by Anthony Doerr, Scribner: New York, 2014.

examined the responses of the predator–prey interaction between *B. glandula* and *N. ostrina*. I obtained two key findings. First, air and water warming non-additively affected interaction strength: warm water mitigated a decrease in mean whelk feeding rate caused by warm air. Second, air warming had contrasting effects on individual growth rates of predator and prey. While whelk growth decreased in warm air, barnacle growth increased. These findings suggest that combined air and water warming will benefit barnacle populations more than their whelk predators. This study highlights the value of integrating species performances and interactions to understand how multiple physical drivers may affect community structure.

In Chapter 2, I examine how environmental context governs trait-rate relationships. Trait and environmental controls on individual vital rates have been well documented, but the potential interactive effects between these controls have been less studied. This is problematic because global change often alters traits and environmental factors simultaneously; to predict the responses of systems, the interaction effects have to be understood. To investigate the links between traits, environmental factors, and demographic processes, I tested how the vital rates of *B. glandula* respond to the interactive effects of body size, temperature, and crowding. I found that body size and crowding interact to set barnacle survival and reproduction. In the field, crowding increased survival, an effect which became stronger with increasing body size. This effect was likely due to a shift in the balance of size-dependent competition and temperature-dependent facilitation. In mesocosms, crowding increased probability of being reproductive for smaller barnacles but decreased it for larger barnacles. I also found that warmer low tide temperatures decreased barnacle survival (field and mesocosms) and growth (mesocosms)

regardless of body size. These findings suggest that incorporating environmental context is necessary to predicting vital rates from traits in barnacles.

In Chapter 3, I examine how ontogenetic shifts in intraspecific interactions affect population dynamics. Compared to consumer-interactions, there is a dearth of information on how ontogenetic shifts in interactions within a trophic level affect population dynamics. This is problematic because interactions within a trophic level (e.g., competition and facilitation) are critical determinants of community structure. I used population models to investigate the conditions under which ontogenetic shifts in intraspecific interactions affect the population dynamics of *B. glandula*. I obtained two key findings. First, crowding modified the effect of body size in an important way: the direction of intraspecific interactions on barnacle growth shifted from negative to positive across size. At a small initial size, high crowding decreased barnacle growth. At a large initial size, however, crowding increased barnacle growth slightly. Second, populations modeled with theoretical crowding distributions showed differences in population growth rates consistent with the observed ontogenetic shifts. Populations with low crowding in established individuals and high crowding in recruits had the lowest population growth rate. Conversely, populations with high crowding in established individuals and low crowding in recruits had the highest population growth rate. This difference in population growth rate was mediated by changes in the population size distribution. These findings highlight the importance of considering how ontogenetic shifts in competition and facilitation alter population size structure and dynamics when predicting the responses of sessile ectotherms to global change.

The firmament of ecology is vast. Although this dissertation focuses on a small subset of ecology, it crosses levels of organization, drawing concepts from physiological, population, and community ecology. It also combines fieldwork in the spirit of my academic ancestors (including G.E. Hutchinson and R.T. Paine) with modern techniques in statistical analysis and mathematical modeling. Together, this dissertation contributes basic knowledge on how biotic interactions shift across temperature and ontogeny, and how the latter shift may scale up to population dynamics. In doing so, it bolsters the foundation on which science builds to address global change.

Note

My legal name is Tang-wei King. I publish as William King.

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Ryan Kelly helped me consider the details of barnacle biology while nudging me to think about the big picture of my research. He responded to my emails promptly and added a useful perspective to my committee meetings, all with good humor.

In some horrid alternate universe I would've had to do this PhD without my fellow marine ecology grad students in the Bio department. Fortunately, the configuration of this universe was a favorable one. These grad students (past and present) were especially helpful for their mentorship, friendship, willingness for physical labor, fun, understanding, and insight in all sorts of matters: Mo Turner, Molly Roberts, Hilary Hayford, Eliza Heery, Alex Lowe, Katie Dobkowski, and Chris Wells.

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Chapter 1

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Title

Non-additive effects of air and water warming on an intertidal predator-prey interaction

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Abstract

Climate change alters multiple physical drivers that act concurrently on ecological communities. Evidence suggests widespread non-additive effects between multiple drivers; most of this evidence, however, is based on species-level responses, which is problematic because community responses to environmental change also depend on species interactions. To address this knowledge gap, this study experimentally manipulated two physical drivers and examined the responses of a predator-prey interaction. The two drivers tested are fundamental in intertidal systems: air and water temperatures. The two species were the intertidal dogwhelk, *Nucella ostrina*, and its barnacle prey, *Balanus glandula*. The objective was to test alternative hypotheses that air and water warming have additive vs. non-additive effects on the whelk-barnacle interaction. A 14 day mesocosm experiment was conducted in which animals were subjected to one of four temperature treatments: ambient (no temperature manipulation; water 12°C, air 13°C), warm water (15°C), warm air (27°C), or combined (water 15°C, air 27°C). There were two key findings. First, air and water warming non-additively affected interaction strength: warm water mitigated a 35% decrease in mean whelk feeding rate caused by warm air. Second, air warming had contrasting effects on individual growth rates of predator and prey. While whelk growth decreased by ~60% in warm air, barnacle growth increased by 47%. These findings suggest that combined air and water warming will benefit barnacle populations more than their whelk predators. This study highlights the value of integrating species performances and interactions to understand how multiple physical drivers may affect community structure.

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Introduction

Climate change affects biodiversity and ecosystem services by altering multiple physical drivers that act concurrently on ecological communities (Halpern et al. 2007; Crain et al. 2008; Gunderson et al. 2016). Modern ecology aims to understand how ecological communities respond to multiple drivers (Koussoroplis et al. 2017) in order to improve the accuracy of biological projections (Sala et al. 2000; Harley et al. 2006). Evidence suggests that interactive effects between multiple physical drivers are widespread (Paine et al. 1998; Folt et al. 1999; Harley et al. 2006; Crain et al. 2008; Darling and Côté 2008; Gunderson et al. 2016). Most of the evidence, however, is based on species-level responses (but see Cheng et al. 2016), which is problematic because community responses to environmental change also depend on interactions between species (Gilman et al. 2010; Kordas et al. 2011; Russell et al. 2012; Harley 2013). To address this important knowledge gap, this study experimentally tested the responses of a model predator-prey interaction to the combined effect of two physical drivers (air and water temperature).

Temperature is a fundamental driver of biological processes (Gillooly et al. 2001; Brown et al. 2004; Kordas et al. 2011). In the intertidal zone, air and water temperatures are different physical drivers that affect the physiology of intertidal organisms in distinct ways (Helmuth et al. 2006b; Koussoroplis et al. 2017). For example, intertidal organisms can undergo evaporative cooling when exposed to air, preventing thermal stress (Porter and Gates 1969; Bell 1995; Helmuth 1998). Desiccation stress associated with warmer temperatures occurs only in air. Furthermore, most intertidal animals respire aerobically in one medium but anaerobically in the other, leading to different effects of temperature changes on organism oxygen and energy balances in air and water (McMahon 1988; Somero 2002; Sokolova and Pörtner 2003).

As both air and water temperatures continue to increase with climate change (IPCC 2014), intertidal organisms may face increased combined effects of these two drivers. A useful conceptual framework for considering such effects is thermal performance curves (TPCs), which describe organism performance (e.g., growth) as a function of body temperature (Huey and Stevenson 1979). Most ectotherms have unimodal TPCs (Dell et al. 2011), which means the direction of the effect of temperature change will depend on where the organism is currently on its TPC (Figure 1). The unimodal shape of TPCs informs predictions of how intertidal organisms will potentially respond to climate warming (assuming no adaptation or acclimation), which is likely to occur faster in the air than in the water due to water's high heat capacity (IPCC 2014). Since many intertidal species already live at the upper edges of their thermal tolerances during emersion (Tomanek and Helmuth 2002; Gilman et al. 2015;), further air warming may bring them to the falling portions of their air TPCs and decrease performance (Figure 1f). For example, studies have found that air warming decreased survival, growth, and feeding rates of intertidal whelks and sea stars, potentially due to the energetic costs of preparing for and recovering from thermal stress (Menge et al. 2002; Pincebourde et al. 2008; Yamane and Gilman 2009; Pincebourde et al. 2012; Vaughn et al. 2014). In contrast, water warming may bring intertidal organisms to the rising portions of their water TPCs and increase performance (Figure 1a). Previous studies have found that warm water increased feeding rates of whelks and sea stars, although growth may decrease depending on the energetic costs of faster metabolic rates under warmer body temperatures (Sanford 1999, 2002a, b; Yamane and Gilman 2009; Pincebourde et al. 2012; Miller 2013; Fakhoury and Gosnell 2014). Thus, intertidal organisms may respond differently to air and water warming under future climates (e.g., Yamane and Gilman 2009; King et al. 2017).

The combined effect of air and water warming will depend on the timing and intensity of each driver, which will determine whether the drivers are additive or non-additive (Gunderson et al. 2016; Koussoroplis et al. 2017). When air and water warming are additive, their combined influence will be the algebraic sum of the effect of each driver alone. When air and warming are non-additive, their combined effect will be different than the sum of the effect of each driver alone (covariance of co-limiting factors; see theory in Koussoroplis et al. 2017). Several categories of non-additive effects are known (Koussoroplis et al. 2017). Growing evidence indicates that air and water warming can have non-additive effects for intertidal predators and prey at the species level (Pincebourde et al. 2012; Schneider et al. 2012; Seabra et al. 2016), raising the question: how do intertidal predator-prey interactions respond to combined warming?

This study examined the combined effects of air and water warming on the species interaction between the dogwhelk, *Nucella ostrina*, and its barnacle prey, *Balanus glandula*. In the Northeast Pacific, *B. glandula* is an abundant ecosystem engineer (Barnes 2000). *N. ostrina* eat barnacles, altering barnacle abundance and distribution (Connell 1970; Dayton 1971). Both species respond to air or water warming (Yamane and Gilman 2009; Nishizaki and Carrington 2014; Vaughn et al. 2014), making them a prime system to examine potential non-additivity between the two drivers. The objective of this study was to test the hypothesis that air and water warming have a non-additive effect on the strength of the interaction between *N. ostrina* and *B. glandula*. A mesocosm experiment increased air and water temperatures factorially and measured the individual growth rates of *N. ostrina* and *B. glandula*, and their interaction strength (whelk feeding rate). This paper presents findings that air and water warming have a non-additive effect on *N. ostrina* feeding rate upon *B. glandula*. Contrasting responses of predator and prey growth to air warming are also presented. Along with other recent studies, this

paper underscores the importance of considering species interactions in understanding how multiple physical drivers affect ecological communities.

Methods

Field temperature recordings

To understand the thermal context that whelks and barnacles may experience in nature, temperature loggers were used to measure field air and water temperatures at intertidal sites on San Juan Island, Washington, USA (Supplement Table S1). The four sites (Reuben Tarte, Colin's Cove, Friday Harbor Labs, and Cattle Point) were protected from full oceanic conditions; see Dethier and Williams (2009) for general site descriptions. At each site, two to three iButton temperature loggers (DS1921G-F5, Maxim Integrated; $\pm 0.5^{\circ}\text{C}$), wrapped in parafilm and embedded in marine epoxy (Z-Spar Splash Zone A-788), recorded approximate rock temperatures in the barnacle zone on vertical walls and boulder faces (+0.94 to +1.91 m) hourly from late May to mid August 2017. Temperature recordings were categorized as emersion or immersion based on predicted tidal elevations (<http://tbone.biol.sc.edu/tide/> [accessed August 2017]).

Collection and preparation of organisms

N. ostrina were collected from Eagle Cove (48°27'N 123°01'W) on San Juan Island in early September 2016. San Juan Island experiences warm summer temperatures that coincide with daytime low-tides, making it a “hot spot” for climate warming (Helmuth et al. 2006a). Only whelks showing recent shell growth were used. To minimize the confounding effects of body

size, whelks were selected within a narrow size range (mean shell length \pm SD; 2.27 ± 0.07 cm, $n = 48$).

B. glandula on the valves of mussels (*Mytilus trossulus*) were collected from a pier at Jackson Beach (48°31'N 123°00'W) on San Juan Island in early September 2016. Mussels were killed and the valves separated from each other. Mussel valves with barnacles were glued to plastic disks (similar to Vaughn et al. 2014). Barnacles with operculum length > 1 mm were used (mean barnacle operculum length \pm SD; 3.24 ± 0.74 mm, $n = 1,327$).

To give replicate whelks and barnacles similar thermal histories, animals were acclimated in outdoor tanks at Friday Harbor Laboratories (FHL) for one to two weeks before the experiment. Barnacles were continuously submerged in running seawater ($\sim 12^\circ\text{C}$). Whelks experienced the ambient tidal cycle (air $\sim 13^\circ\text{C}$, water $\sim 12^\circ\text{C}$) and were fed *B. glandula* from the same population as those used in the study *ad libitum*.

Temperature treatments

To quantify how air and water temperatures affect the whelk-barnacle interaction, animals were subjected to one of four treatments manipulating air and water temperatures factorially: ambient (no temperature manipulation; water 12°C , air 13°C), water warming (15°C), air warming (27°C), or combined (water 15°C , air 27°C). These temperatures were chosen based on previous studies which found that warm water increased whelk (12°C , Sanford 2002a; 13.5°C , Yamane and Gilman 2009) and barnacle (14°C , Nishizaki and Carrington 2014) performance and warm air decreased whelk performance (28°C , Yamane and Gilman 2009; Vaughn et al. 2014). The water warming treatment was expected to be on the rising portions of

the TPCs for both species whereas the air warming treatment was expected to be on the falling portion for whelks.

Since physiological processes depend on body temperatures, which can differ from environmental temperatures (Helmuth et al. 2006b), biomimetic sensors were used to estimate body temperatures in each treatment. *N. ostrina* biomimetics were thermocouples (Type T, OMEGA Engineering, Inc.) inserted into empty *N. ostrina* shells flooded with clear epoxy (Gilman et al. 2015). *B. glandula* biomimetics were made of thermocouples embedded in ~1 cm diameter balls of white epoxy (modified from Gilman et al. 2015). Biomimetics placed in the centers of eight separate mesocosms estimated body temperatures for each species and treatment. A central datalogger (21X Micrologger, Campbell Scientific, Inc.) recorded biomimetic temperatures every 3 min throughout the experiment.

Mesocosm set-up

The 14 day experiment was conducted outdoors at FHL in September 2016. An opaque canopy shaded the set-up such that animals experienced indirect but naturally varying light. Clear plastic tanks (946 mL) with plastic mesh lids served as mesocosms (Supplement Figure S2). Four mesocosms were randomly assigned to each treatment. Plastic mesh divided each mesocosm into two compartments: one with barnacles and whelks and one with only barnacles. The barnacles in the two compartments were used to determine interaction strength (amount of predation) and barnacle performance (growth in the absence of predation) respectively. Barnacle density in the latter compartment was manipulated by removing neighboring individuals so that barnacles could grow without crowding. Free water movement between the compartments allowed barnacles to experience whelk presence, including potential chemical cues, without

being eaten. Each mesocosm started with 10-20 barnacles without whelks and 40-50 barnacles with 3 whelks (enough for whelks to feed on for at least a week), all randomly assigned.

All mesocosms experienced the same tidal regime. Mesocosms were subject to one low tide per day, approximating the ambient tidal regime at +1.0 m in the intertidal zone on San Juan Island during the study period (total emersion duration mean \pm SD; 6.1 ± 1.8 h). Tidal regimes were simulated using separate aquarium pumps (#VS-HG16-2, VicTsing) that continuously circulated seawater between mesocosms and clear storage tanks. At low tide the aquarium pumps turned off and water drained back into the storage tanks. To maintain water quality, a trickle of new seawater continuously fed each storage tank and all water was changed every 2-3 days. Every mesocosm had its own storage tank.

During immersion, separate aquarium heaters (#GH200, Aquatop) increased water temperature in each storage tank of mesocosms assigned to the warm water treatment. Temperature controllers (True Temp #JB1235, JBJ Lighting) for each aquarium heater continuously sensed and adjusted water temperatures in storage tanks by turning aquarium heaters on or off. During emersion, separate ceramic heat lamps (#LF-15, Zoo Med) raised air temperatures in each mesocosm assigned to the warm air treatment (including nighttime low tides). Separate temperature controllers continuously sensed and adjusted air temperatures in each mesocosm by turning heat lamps on or off. Heat lamps turned on 1 h into each low tide (Pincebourde et al. 2012) to allow organisms to adjust to aerial exposure. Timers (#FD60-U5, Titan Controls) automatically switched temperature controllers for heat lamps and aquarium pumps on or off. All mesocosms had lamps hanging directly above them; lamps in mesocosms without warm emersion remained off to control for potential effects of lamp presence on the animals.

Predator and prey growth rates

To examine how whelk growth responded to temperature treatments, absolute changes in shell height, total mass, and shell lip were measured for each whelk. Change in total mass (body and shell together) was measured as the blotted wet mass of whelks immediately before and after the experiment (following Palmer 1982). The lip (apertural growing edge) of each whelk shell was painted with nail polish at the start of the experiment. Photos of each whelk were taken at the start and end of the experiment and analyzed to determine change in shell lip (degrees of new shell extending beyond the nail polish line) and change in shell height (distance from apex to edge of siphonal canal).

To examine how barnacle growth responded to temperature treatments, absolute change in operculum length was measured from photos of each barnacle taken at the start and end of the experiment. All photo analyses in this experiment were conducted using ImageJ v1.48 (Schneider et al. 2012).

Predation rate

To examine how the interaction strength between whelks and barnacles responded to temperature treatments, whelk feeding rates were measured. Whelks were given a fresh set of barnacles each week. Number of barnacles eaten in each mesocosm was counted after days 7 and 14. Barnacles were considered eaten if their opercular plates split when gently tapped and their tests were empty. Counts from days 7 and 14 were summed to calculate the total number of barnacles eaten in each mesocosm.

Per capita feeding rates were calculated by dividing the total number of barnacles eaten by the number of whelks in each mesocosm. For the mesocosms where whelks died during the experiment (3 deaths total in two mesocosms), the numbers of whelks used in the denominators were calculated by summing the products of the number of whelks present and the fraction of days in which that number of whelks was present.

Statistical analysis

To test the effects of air and water warming on the whelk-barnacle interaction, linear models were developed for each response variable. All models had air warming, water warming, and their interaction as categorical fixed effects. For whelk and barnacle growth, separate linear mixed effects models with Gaussian response distribution and identity link function were used, with mesocosm as a random effect. Gaussian response distribution was chosen to accommodate negative values in response variables. Statistical significance of fixed effects in these models were determined using type III F-tests with Satterthwaite approximated degrees of freedom.

For whelk feeding rate, a generalized linear model with a Gamma response distribution and inverse link function was used. Here gamma response distribution was chosen because it is useful for positive continuous values and inverse link function was chosen because it is useful for bounded data (where the upper limit of feeding rate was the number of barnacles available; Faraway 2006). Statistical significance of fixed effects in this model were determined using t-tests. Switching the order of terms in the model did not change interpretation of results. Post-hoc pairwise comparisons (using the same linear models) were only conducted if an interaction between fixed effects was detected. Residuals were visually inspected to check that response distributions and link functions for all models were reasonable. All tests used $\alpha = 0.05$. Statistical

tests were conducted using R v3.3.1 (R Core Team 2016) and the R packages lme4 (Bates et al. 2015) and lmerTest (Kuznetsova et al. 2016).

Results

Field and mesocosm temperatures

A wide range of emersion and immersion temperature combinations were observed in the field (Figure 2). Daily median emersion temperatures were generally warmer than immersion temperatures due to summer daytime low tides. Field emersion temperatures ranged 10-35°C, with 90 records $\geq 25^\circ\text{C}$. Field immersion temperatures ranged 10-17°C, with 27 records $\geq 15^\circ\text{C}$. In the mesocosm experiment, emersion and immersion temperature combinations for all treatments were within the range of the field observations (Figure 2). Biomimetic temperatures were influenced by cool air during nighttime low tides, but were $\sim 3^\circ\text{C}$ warmer in water and $\sim 11^\circ\text{C}$ warmer in air when comparing warmed vs. ambient treatments (Table 1; Figure 2; Supplemental Figure S1).

Predator and prey growth rates

Warm air reduced whelk growth rates. Compared to whelks that did not experience any warm air, whelks that did experience warm air added 55% less shell lip (Figure 3), grew on average 54% less in shell height, and added 77% less body mass (Supplement Figure S3). No effects of warm water nor of the interaction between warm air and warm water were detected on whelk growth rates (Table 2; Supplement Table S2).

In contrast to whelks, warm air increased barnacle growth rates, as did warm water (Figure 3). Compared to barnacles that did not experience any warm air, barnacles that did

experience warm air increased mean operculum length by 47% (Table 2; Supplement Table S3). Similarly, compared to barnacles that did not experience any warm water, barnacles that did experience warm water increased mean operculum length by 36%. No interaction effect was detected between warm air and warm water on barnacle growth.

Predation rate

Warm air reduced mean whelk per capita feeding rate by 35% compared to whelks that did not experience any warm air (Table 3). However, there was no effect of warm water. There was a significant interaction between warm air and warm water; warm water mitigated the negative effects of warm air on whelk feeding rates (Figure 4). Post-hoc pairwise comparisons indicated that whelk feeding rates in combined warming were similar to those in the ambient and warm water treatments (Supplement Table S4).

Discussion

Evidence suggests that multiple physical drivers can have non-additive effects on individual species (Folt et al. 1999; Crain et al. 2008; Darling and Côté 2008; Gunderson et al. 2016); however, to better understand the community-level consequences of such effects, more information on the responses of species interactions is needed. Two findings from this study helped address this knowledge gap. First, air and water warming non-additively affected the strength of the whelk-barnacle interaction (Figure 4). Second, air warming had contrasting effects on whelk and barnacle growth (Figure 3). Together, these findings suggest that combined air and water warming under climate change will benefit barnacle populations more than whelks,

highlighting the value of using a multi-species perspective to examine how multiple drivers affect ecological communities.

Differences among species and studies in the consequences of intertidal warming

Differences between the responses of *N. ostrina* and *B. glandula* to warming in this study (Figure 3) emphasize that stress is species-specific (Maestre et al. 2009). The air warming treatment increased whelk and barnacle body temperatures similarly (Table 1) but was apparently only stressful to whelks. Other studies have also found that 25-28°C body temperature in air decreased *N. ostrina* growth and feeding (Yamane and Gilman 2009; Vaughn et al. 2014). Lower whelk growth rates under aerial warming in this study were likely caused by decreased energy intake (due to decreased feeding), increased energetic costs of heat stress response (Somero 2002), or both. Aerial stress affected whelk feeding rates even though whelks initiate feeding during immersion (Bertness and Schneider 1976) likely because thermal stress recovery took longer than the duration of aerial exposure (average 6 h). Heat shock protein expression in marine organisms may not peak until 15 h after stress exposure (Gunderson et al. 2016) and take days to return to baseline levels (Tomanek and Sanford 2003).

Warmer water may have increased barnacle growth by increasing their cirri beating rates and food capture efficiencies (Cole 1929; Southward 1955; Southward 1957; Nishizaki and Carrington 2014). It is also possible that warmer temperatures in the water storage tanks promoted plankton growth, leading to more food for barnacles. While it was known that warmer water (14-15°C) can increase barnacle growth rate (Figure 1a; Nishizaki and Carrington 2015), this may be the first study to find a similar effect of warmer air (Figure 1d). Increases in barnacle growth under air warming in this experiment were variable and slight overall; further tests are

needed to determine if this pattern is robust. Although barnacles feed only when underwater, higher body temperatures in air may have increased barnacle growth by increasing digestion efficiency (shown for other ectotherms, e.g., Harlow et al. 1976). More efficient digestion during emersion could have freed up stomach space for new food and allowed barnacles to allocate more energy to growth during immersion. Higher barnacle body temperatures in air may have also increased underwater feeding rates (shown for sea stars exposed to acute aerial warming; Pincebourde et al. 2008). In the laboratory, warm emersion temperatures up to 30°C have been observed to stimulate *B. glandula* feeding rate upon submersion (Sarah Gilman pers comm).

This study did not find that water warming increased *Nucella* feeding rates (Figure 4), in contrast to other studies (Sanford 2002a; Yamane and Gilman 2009; Miller 2013; Fakhoury and Gosnell 2014). Differences between studies may be due to the different species and temperatures tested. Three of the studies (Sanford 2002a; Miller 2013; Fakhoury and Gosnell 2014) tested other *Nucella* species that have different distributions than *N. ostrina* and potentially different thermal performance across water temperatures. Yamane and Gilman (2009) tested *N. ostrina* feeding on *B. glandula* from San Juan Island in late summer to early autumn, similar to this study. However, Yamane and Gilman (2009) compared underwater body temperatures of 11°C vs. 13.5°C while this study compared 12°C vs. 15°C. If 15°C is near the peak of the *N. ostrina* water TPC, then it is possible that Yamane and Gilman (2009) examined a part of the TPC with steep increases in performance (Figure 1a) while this study examined a part with little or no change in performance (Figure 1b). Even if there was a subtle change in feeding rate near 15°C, this study probably lacked the power to detect it ($n = 4$). Furthermore, body temperatures in this study (Figure 2; Supplement Figure S1) were more variable than in Yamane and Gilman (2009),

and magnitude of temperature variation can affect physiological performance and feeding rates (Pincebourde et al. 2012; Dowd et al. 2015).

Non-additivity in response to air and water warming

Two physical drivers that are temporally separated can have non-additive effects if the responses of organisms to each driver overlap (Gunderson et al. 2016). Results from this study contribute to a growing body of evidence that air and water warming can have non-additive effects on intertidal organisms (Schneider 2008; Pincebourde et al. 2012; Seabra et al. 2016). In this study, whelk feeding rate responded non-additively to sequential air and water warming: air warming strongly decreased whelk feeding rate when the water was at ambient temperatures but had no effect when the water was warmed (Figure 4). This suggests that warmer water may have increased whelk tolerance to aerial heat stress. Generally, non-lethal warm temperatures can prime ectotherms for thermal stress by upregulating heat shock protein production (Schneider 2008 and references therein; Gunderson et al. 2016;). Warmer water may have increased the standing stock of heat shock proteins in whelks, allowing them to feed at normal rates (i.e., rates similar to those in ambient conditions). It is also possible that whelks in the warm air treatment experienced more thermal stress than those in the combined treatment due to slightly lower air temperatures in the latter (<1°C; Table 1).

In contrast to whelk feeding rate, whelk growth responded additively to combined warming: decreased whelk growth caused by warmer air was not “rescued” by warmer water (Figure 3). The energetic costs of dealing with aerial thermal stress (Somero 2002) apparently overwhelmed energy intake from normal feeding rates. In general, warmer body temperatures increase metabolic rates, which can increase energy demand (Gillooly et al. 2001; Brown et al.

2004; but see Marshall and McQuaid 2011). Studies on sea stars and other whelks have found that decreased feeding in cooler water may be balanced by decreased metabolic costs (Sanford 2002a, b; Pincebourde et al. 2008) and that lower metabolic rates may contribute to rescuing sea stars from aerial thermal stress (Pincebourde et al. 2012). In this study, however, there was no evidence for the increased metabolic costs of warmer water because whelks in the warm water treatment grew at similar rates as those in the ambient treatment. Fine scale TPC measurements will help clarify how changes in body temperatures can alter the relationships between *N. ostrina* metabolic, growth, and feeding rates.

The limitations of this study temper its conclusions and point out valuable questions for future study. First, this study used mesocosms that enforced body temperatures, focusing on the physiological rather than behavioral responses of whelks and barnacles to warming. *Nucella*, however, are known to behaviorally adjust their environment (Berlow and Navarrette 1997; Hayford et al. 2015); thus, the non-additive effects of air and water warming on *Nucella* predation observed in this study establishes a null expectation against which future studies can test the effects of combined warming in the field, where whelks can thermoregulate. Second, in this study body temperatures of animals in treatments with air warming were more variable than in other treatments because aerial warming sometimes occurred during nighttime low tides (Table 1; Supplement Figure S1), and the results should be interpreted in this context. Future studies examining temperature variation between and within aerial and aquatic environments will contribute to the growing demand for understanding how changes in temperature mean and variation affect ecological systems (Pincebourde et al. 2012; Dillon et al. 2016; Koussoropolis et al. 2017). Lastly, while this study focused on organismal responses to changes in air and water body temperatures, other factors may have impacted performance. For example, humidity and

desiccation affect performance of *Balanus* (Barnes et al. 1963; Foster 1971) and *Nucella* (Stickle et al. 2017), and can alter the aerial thermal tolerances of intertidal invertebrates (as shown for limpets, Miller et al. 2009). Mesocosms in this experiment had open tops and humidity was not measured. Complementary tests are needed to tease apart the direct and interactive effects of changes in temperature, desiccation, and respiration on organismal responses to intertidal warming.

Community-level responses to multiple drivers

This study demonstrates that using a multi-species perspective to examine the consequences of multiple drivers yields useful information worth the logistical challenges. Using only whelk growth and feeding rates, it could be inferred that combined air and water warming might decrease whelk populations, potentially benefitting barnacle populations (Yamane and Gilman 2009); however, combined warming could also decrease barnacle growth. Using only barnacle growth rates, it would be unclear whether combined warming would also strengthen whelk predation upon barnacles, mitigating the direct benefits of warming on barnacle populations. Synthesizing the whelk and barnacle perspectives in this study suggests that combined warming may allow barnacles to more quickly reach size escape from whelk predation and, all else being equal, would lead to increased barnacle populations under projected climate warming. Simultaneously examining within and between species responses allowed this study to provide a more complete picture of the consequences of intertidal warming for this interacting pair. Future studies may also benefit by integrating species performances and interactions (Harley et al. 2006; Gilman et al. 2010; Kordas et al. 2011) to examine how multiple drivers affect ecological communities under global change.

Compliance with Ethical Standards

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. Animals were collected with permission of Friday Harbor Laboratories. The authors declare no conflict of interest.

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Figures

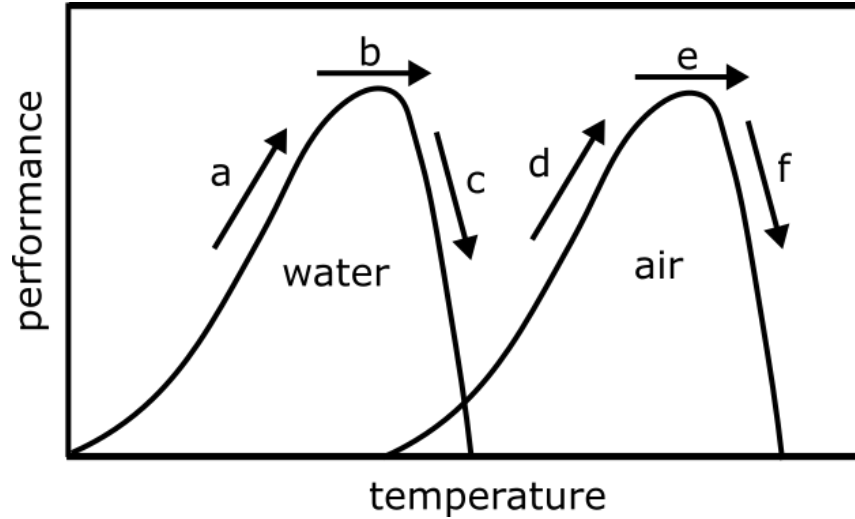


Fig. 1 General thermal performance curves (TPCs) of an intertidal ectotherm in air and water. Air and water TPCs likely have different shapes and locations. Performance (e.g., growth rate) can increase (a, d), decrease (c, f), or remain the same (b, e) with warming. Warming is not necessarily stressful; all nine combinations of a-f are possible even without considering potential non-additivity. Overall organism performance depends on both air and water temperatures, which may have non-additive effects

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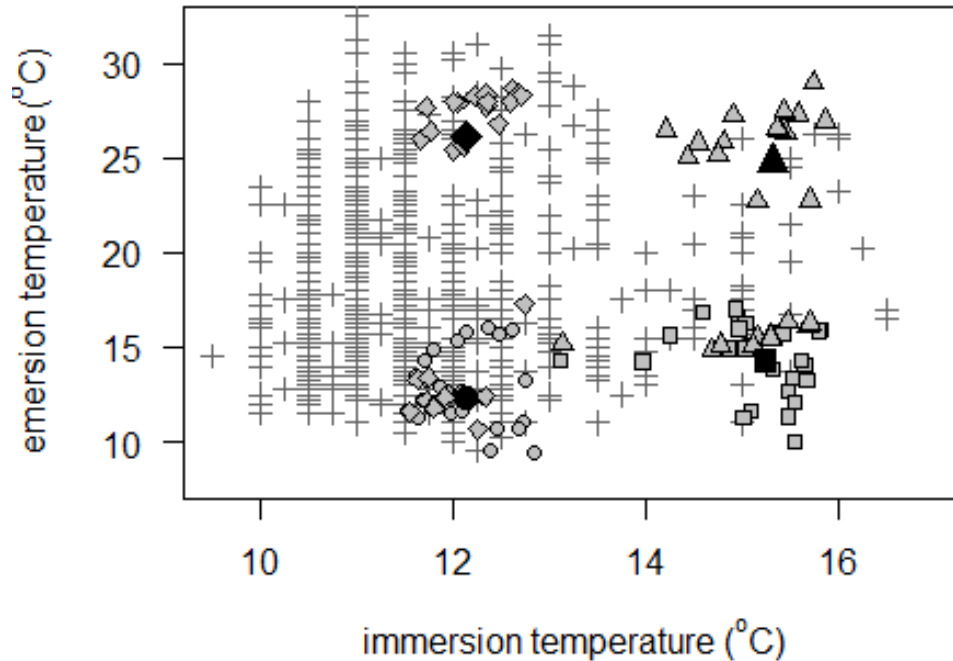


Fig. 2 Median emerged temperature during low tide compared to median immersed temperature during high tide in the field (crosses) and in the mesocosm experiment (points). In the field, iButton dataloggers measured summer temperatures in the barnacle zone at 4 intertidal sites ($n = 742$ records total). In the mesocosm experiment, biomimetic dataloggers estimated whelk and barnacle body temperatures (aggregated across species) in each treatment: ambient (circles), warm water (squares), warm air (diamonds), and combined (triangles). Crosses and grey points indicate median temperatures for a given day in the field and in the mesocosm experiment respectively. Black points indicate median temperatures for each treatment in the mesocosm experiment overall

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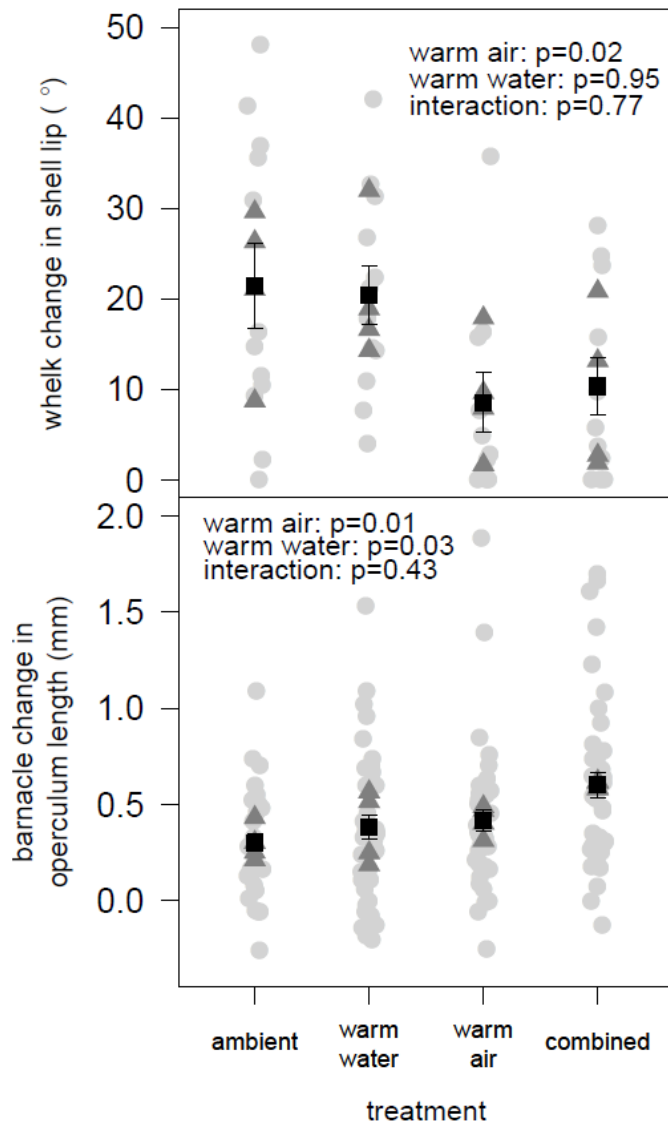


Fig. 3 *N. ostrina* (top) and *B. glandula* (bottom) growth after the 14 day experiment. P-values listed are for each fixed effect, where “interaction” indicates the statistical interaction between warm air and warm water, based on linear mixed effects models. The statistical tests used Satterthwaite approximated denominator $df = 12.20$ and 141 for change in whelk shell lip and barnacle operculum length respectively. Circles indicate individual animals, triangles indicate mesocosm means, and squares indicate treatment means. Bars indicate standard errors. Note different y-axes

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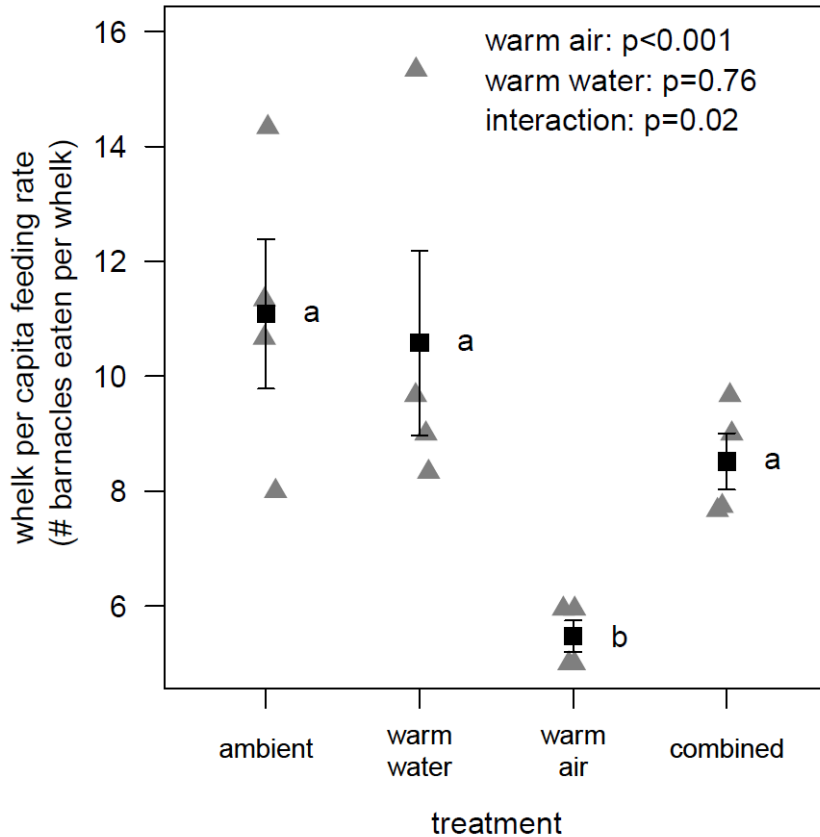


Fig. 4 *N. ostrina* per capita feeding rate on *B. glandula* over the 14 day experiment. $n = 4$ mesocosms per treatment (triangles). P-values listed are for each fixed effect, where “interaction” indicates the statistical interaction between warm air and warm water. Different letters indicate significantly different means (squares) based on pairwise comparisons. Bars indicate standard errors

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Tables

Table 1 Body temperatures of barnacles *B. glandula* and whelks *N. ostrina* in experimental treatments estimated using biomimetics for the mesocosm experiment overall

Treatment	Species	immersed (°C)			emersed (°C)		
		median	mean	sd	median	mean	sd
ambient	barnacle	12.2	12.5	1.0	12.3	13.9	3.9
	whelk	12.0	12.2	0.7	12.3	13.4	3.2
warm water	barnacle	15.4	15.3	0.7	15.1	15.7	3.5
	whelk	15.0	14.9	0.9	14.0	14.3	2.8
warm air	barnacle	12.0	12.2	0.7	26.1	20.8	7.9
	whelk	12.2	12.5	0.9	26.2	21.6	7.6
combined	barnacle	15.5	15.3	0.9	23.4	21.6	5.6
	whelk	15.2	15.0	0.7	25.4	21.9	6.1

Table 2 Summary of model results for whelk and barnacle growth. Bold indicates statistically significant p-values

Variable	MS	F	P
Whelk change in shell lip		den.df ^a = 12.2	
warm air	1114.42	7.54	0.017
warm water	0.59	0.0040	0.95
warm air*warm water	13.00	0.088	0.77
Barnacle change in operculum length		den.df ^a = 141	
warm air	1.01	6.68	0.0079
warm water	0.63	4.19	0.034
warm air*warm water	0.095	0.63	0.43

^aDenominator degrees of freedom

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Table 3 Summary of model results for *N. ostrina* per capita feeding rate on *B. glandula*. Bold indicates statistically significant p-values

Source	Estimate	SE	t	P
warm air	0.092	0.021	4.39	8.75x10⁻⁴
warm water	0.0043	0.013	0.32	0.76
warm air*warm water	-0.070	0.026	-2.66	0.021
treatment pairwise comparisons (n = 4): (ambient = warm water = combined) > (warm air)				

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Supplementary Material

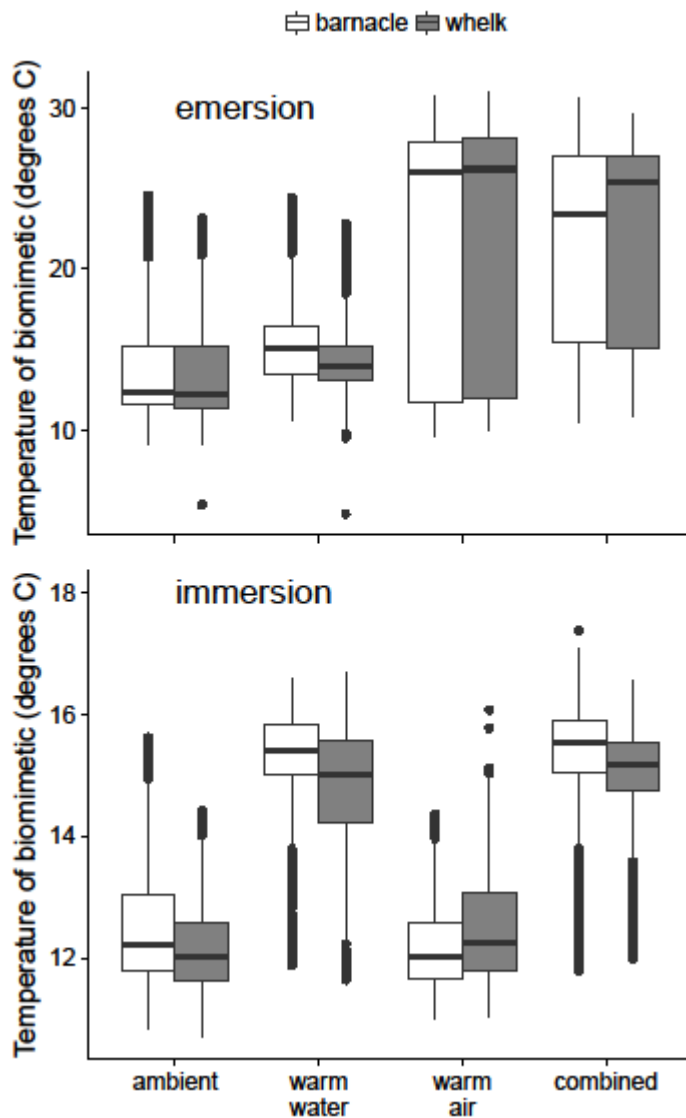


Figure S1 Body temperatures of *N. ostrina* and *B. glandula* during the 14 d experiment estimated using biomimetics. Boxplots indicate temperature minimum and maximum (vertical lines), first quartile, median, and third quartile (horizontal lines), and outliers (points). Note different y axes

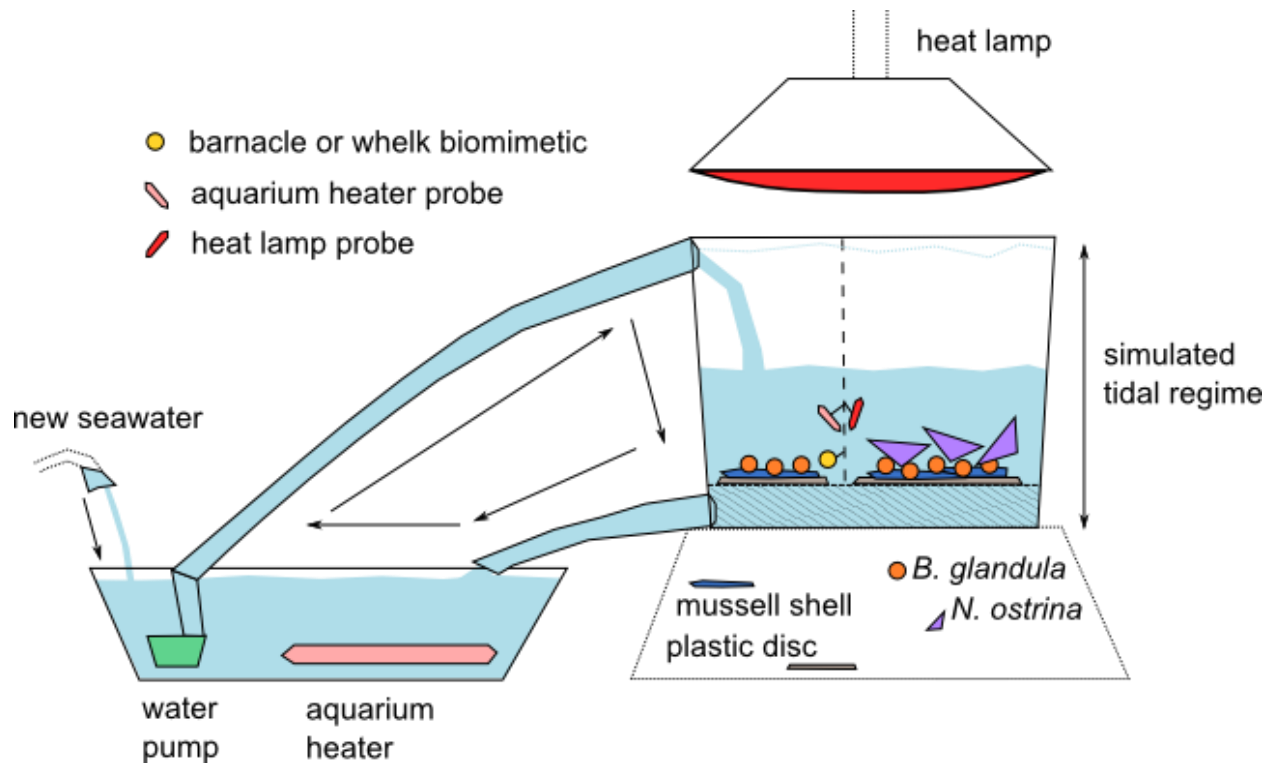


Figure S2 Schematic of mesocosm setup. Every mesocosm had its own set of water tank, water pump, aquarium heater, and heat lamp. Diagram is not to scale

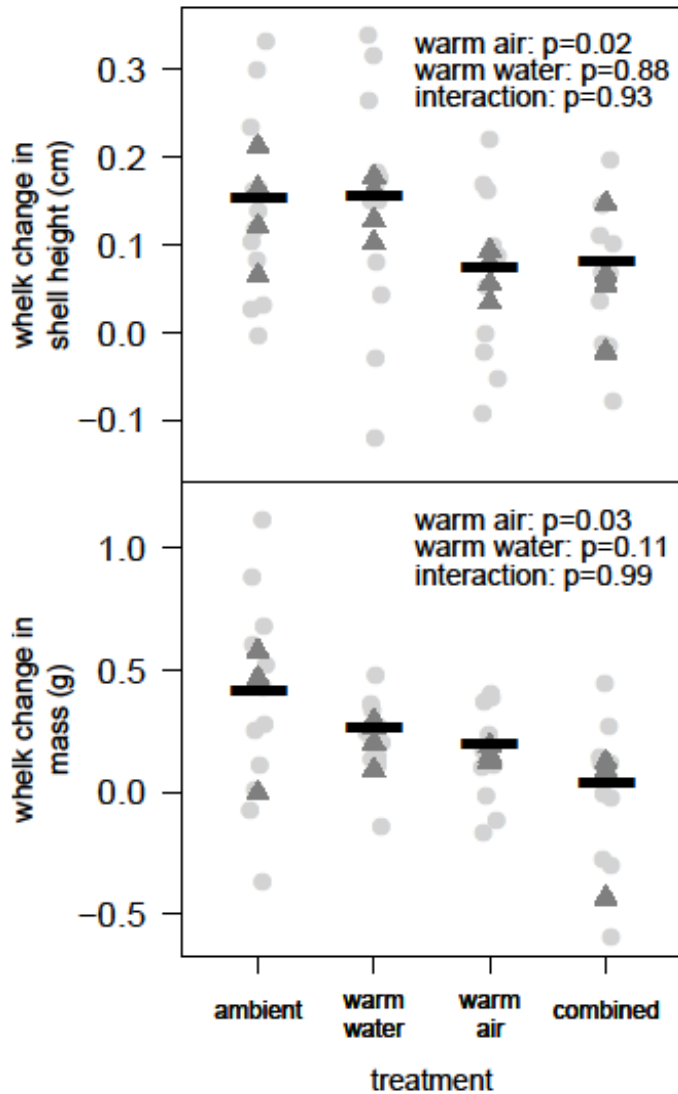


Figure S3 *N. ostrina* growth after the 14 day experiment using change in shell height (top) and mass (bottom) as metrics. P-values listed are for each fixed effect, where “interaction” indicates the interaction between warm air and warm water, based on linear mixed effects models. The statistical tests used Satterthwaite approximated $df = 41$ and 10.91 for change in shell height and mass respectively. Circles indicate individual animals, triangles indicate mesocosm means, and dashes indicate treatment means. Note different y-axes

Table S1 Locations of field iButton temperature loggers. See Dethier and Williams (2009) for general site descriptions

Site	Abbreviation	Coordinates N/W	Aspect	Tidal Elevation (m above MLLW)
Reuben Tarte	RT1	48°36'45.8"/123°05'53.1"	W	1.91
	RT2	48°36'45.0"/123°05'51.9"	SW	1.52
	RT3	48°36'42.1"/123°05'55.0"	NE	0.94
Colin's Cove	CC1	48°32'53.6"/123°00'24.1"	SE	1.12
	CC2	48°32'53.6"/123°00'24.1"	SW	1.12
Friday Harbor Labs ^a	FH1	48°32'45.4"/123°00'42.1"	NE	1.31
	FH2	48°32'45.4"/123°00'42.1"	SW	1.31
Cattle Point	CP1	48°27'16.5"/122°57'43.2"	SW	1.72
	CP2	48°27'18.6"/122°57'41.6"	N	1.29
	CP3	48°27'01.9"/122°57'54.9"	S	1.70

^aAt the old Cantilever Pier pilings, 290 m W of Pumphouse in Dethier and Williams (2009).

Table S2 Model coefficients for three metrics of whelk growth. The models were linear mixed effects models with warm air, warm water, and their interaction as fixed effects and mesocosm as a random effect. Denominator degrees of freedom were Satterthwaite approximated. Asterisk indicates interaction

Variable	SS	MS	Numerator DF	Denominator DF	F	P
Change in shell height						
warm air	0.065	0.065	1	41	5.48	0.024
warm water	2.69x10 ⁻⁴	2.69x10 ⁻⁴	1	41	0.0223	0.88
warm air*	8.90x10 ⁻⁵	8.90x10 ⁻⁵	1	41	0.0075	0.93
warm water						
Change in total mass						
warm air	0.50	0.50	1	10.91	6.10	0.031
warm water	0.24	0.24	1	10.91	3.00	0.11
warm air*	1.83 x10 ⁻⁷	1.83 x10 ⁻⁷	1	10.91	2.25x10 ⁻⁶	0.999
warm water						
Change in shell lip						
warm air	1114.42	1114.42	1	12.20	7.5433	0.017
warm water	0.59	0.59	1	12.20	0.0040	0.95
warm air*	13.00	13.00	1	12.20	0.088	0.77
warm water						

Table S3 Model coefficients for barnacle growth based on change in operculum length. The model was a linear mixed effects model. Warm air, warm water, and their interaction were the fixed effects and mesocosm was a random effect in the model. Denominator degrees of freedom were Satterthwaite approximated. Asterisk indicates interaction

Variable	SS	MS	Numerator DF	Denominator DF	F	P
warm air	1.01	1.01	1	141	6.68	0.0079
warm water	0.63	0.63	1	141	4.19	0.034
warm air*	0.095	0.095	1	141	0.63	0.43
warm water						

Table S4 Model coefficients for pairwise comparisons of *N. ostrina* per capita feeding rate on *B. glandula* across temperature treatments. Row and column headers indicate treatment. The model was a generalized linear model with Gamma error distribution and inverse link function

	ambient	warm air	warm water
warm air	estimate = -0.092 SE = 0.021 t = -4.39 P = 8.75x10⁻⁴		
warm water	estimate = -0.0043 SE = 0.013 t = -0.32 P = 0.76	estimate = -0.088 SE = 0.021 t = -4.15 P = 0.0013	
combined	estimate = 0.027 SE = 0.015 t = 1.78 P = 0.10	estimate = -0.065 SE = 0.022 t = -2.91 P = 0.013	estimate = 0.023 SE = 0.016 t = 1.47 P = 0.17

Chapter 2

Title

Temperature, crowding, and body size alter vital rates in a sessile ectotherm

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Abstract

Organisms vary in their vital rates—survival, growth, and reproduction—depending on their traits and environments. However, environmental context can also govern how trait-rate relationships vary among individuals. To investigate the links between traits, environmental factors, and demographic processes, we examined how the vital rates of a sessile marine ectotherm (acorn barnacle *Balanus glandula*) respond to the interactive effects of body size, temperature, and crowding. Our approach was to measure the individual vital rates of barnacles in response surfaces that varied in both body size and crowding, replicated across mean low tide temperature gradients in field surveys (~16-24°C) and a mesocosm experiment (20-34°C). We found that body size and crowding interact to set barnacle survival and reproduction. In the field, crowding increased survival, an effect which became stronger with increasing body size. This effect was likely due to a shift in the balance of size-dependent competition and temperature-dependent facilitation. In mesocosms, crowding increased probability of being reproductive for smaller barnacles but decreased it for larger barnacles. We also found that warmer low tide temperatures decreased barnacle survival (field and mesocosms) and growth (mesocosms) regardless of body size. These findings suggest that incorporating environmental context is necessary to predicting vital rates from traits in barnacles.

Key words: Traits; Demographic rates; Temperature; Intraspecific interactions; Acorn barnacles; *Balanus glandula*

Introduction

Organisms vary in their vital rates—survival, growth, and reproduction—depending on their traits and environments. In recent decades, ecologists have become more aware of the importance of intraspecific trait variation in controlling demographic and community processes (de Roos et al. 2003; Bolnick et al. 2011; Yang et al. 2018). Intraspecific variation in body size, for example, influences the vital rates of many taxa, including survival of birds (e.g., MacLeod et al. 2006) and fecundity of plants (e.g., Gross 1981; Aarssen and Taylor 1992). However, predictions of demographic rates using traits remain poor, possibly because trait-based approaches often ignore environmental factors that can alter trait-rate relationships (de Roos et al. 2003; McGill et al. 2006; Ehrlén et al. 2016; Yang et al. 2018). In the biotic environment, crowding by conspecifics can alter vital rates beyond what would be predicted from body size alone in plants (Yang et al. 2018) and sessile marine invertebrates (e.g., Levitan 1991). In the abiotic environment, temperature is a fundamental driver of the physiological processes that constrain traits and biotic interactions in ectotherms (Brown et al. 2004; Angilletta 2009). As body size and temperature distributions continue to shift under global change (Gardner et al. 2011; Ohlberger 2013), ecologists are challenged to understand how environmental context can govern variation in trait-rate relationships among individuals. To address this challenge, our study examined how body size, temperature, and crowding together affect the individual vital rates of a sessile ectotherm.

Crowding and body size have interactive effects on vital rates when competition is size-asymmetric. In the absence of biotic interactions, body size exhibits strong relationships with survival, growth, and reproduction in many organisms (Peters 1983). These relationships, however, can depend on size-asymmetric competition, in which larger individuals experience

weaker negative effects of crowding than smaller individuals (or vice versa). Studies define size-asymmetric competition differently (Rasmussen and Weiner 2017). Some explicitly incorporate resource exploitation (e.g., DeMalach et al. 2016) while others focus on competitive outcomes (e.g., Keddy and Shipley 1989). Here we take the latter approach because it is simpler and allows for the detection of size-asymmetric facilitation, which can also occur (e.g., nurse plants).

Temperature and crowding have interactive effects on vital rates when intraspecific interactions vary across thermal stress gradients. In the absence of biotic interactions, ectotherm survival, growth, and reproduction respond strongly to temperature (see Amarasekare and Coutinho 2014 and references therein). These relationships, however, can depend on crowding. Consider an ectotherm that experiences both intraspecific competition and facilitation. The facilitation occurs via habitat amelioration, in which organisms reduce the abiotic stress (in this case thermal stress) acting on their neighbors (Denny and Gaines 2007). Applied here, environmental stress theory from community ecology posits that the relative importance of competition decreases while the importance of facilitation increases with thermal stress (Bertness and Callaway 1994; Bruno et al. 2003). In a low thermal stress environment, temperatures optimal for survival, growth, and reproduction lead to high resource competition and overall negative effects of crowding (Amarasekare and Coutinho 2014). In a high thermal stress environment, habitat amelioration by neighbors leads to an overall positive effect of crowding. The balance of competition and facilitation depends on temperature.

Given that intraspecific crowding can have interactive effects with both body size and temperature, it is logical to suspect that the three factors together influence individual vital rates. Tests are relatively rare, however (Ehrlén et al. 2016; but see DeLong et al. 2014 and Lindmark et al. 2018). We examined the interactive effects of body size, temperature, and crowding on

vital rates (survival, growth, and reproduction) in a sessile marine ectotherm, the acorn barnacle *Balanus glandula*. The barnacle is a useful study organism because its vital rates depend on body size, it experiences strong environmental drivers, and it is experimentally tractable. Our objective was to test the hypotheses that 1) crowding alters the relationships between body size and vital rates and that 2) temperature influences the effect of crowding on vital rates. Our approach was to measure the individual vital rates of barnacles in response surfaces that varied in both body size and crowding, replicated across low tide temperature gradients in field surveys and a mesocosm experiment (Online Resource 1). This paper contributes a unique test in a sessile ectotherm that is useful for resolving environmental control on trait-rate relationships.

Methods

Study species

Sessile invertebrates of the rocky intertidal zone have proved useful for elucidating principles that now pervade ecology (e.g., Connell 1961a, b; Paine 1966; Dayton 1971). To test our hypothesis, we used acorn barnacles *Balanus glandula* (Darwin 1854). Barnacles are foundation species abundant in intertidal zones worldwide (Barnes 2000) whose vital rates vary with body size, temperature, and crowding. Body sizes of adult barnacles range widely within a species. Larger individuals are generally more fecund (Wetthey 1984a) and competitive (Wetthey 1983). Temperatures experienced by *B. glandula* can vary 30°C or more across time of day and microclimates (Gilman et al. 2015). Performance of barnacles (e.g., cirral beating rates: Cole 1929; Southward 1987) likely exhibit unimodal or left-skewed responses to temperature. *B. glandula* live under conditions that range from isolated to extremely crowded. The effect of

crowding can be positive (e.g., habitat amelioration: Bertness 1989) or negative (e.g., interference competition by undercutting and overgrowing: Connell 1961a, b; Dayton 1971).

Field surveys

Body size and crowding response surface

To investigate how crowding alters the effects of body size in barnacles, we surveyed individual *B. glandula* in the middle of the barnacle zone on San Juan Island, Washington, USA in June–August 2017. We aimed to capture a response surface of barnacles varying in both body size and crowding (Online Resource 1). Our metric for body size was initial operculum length (Lohse 1993; Gilman et al. 2013) for survival and growth and final shell volume for reproduction (see below). Our metric for crowding was the initial proportion of an individual’s shell perimeter directly touching alive conspecifics, which we measured using careful drawings and a protractor. As examples, crowding = 0 indicated isolation, crowding = 0.5 indicated half of the perimeter contiguous with conspecifics, and crowding = 1 indicated all of the perimeter contiguous with conspecifics.

We surveyed at multiple sites (see below). Each site had three horizontally adjacent (within 0.5 m) quadrats (10 x 10 cm) marked by epoxy dots on vertical boulders and rocky walls. To ensure a range of individual-level crowding, we first created a range of quadrat-level densities (~1, 3, and 6 individuals cm⁻²) by haphazardly removing individuals immediately before the first survey. Individuals of all crowding levels were sampled from all quadrats, so the quadrats were analyzed together. We photographed the quadrats every two weeks for 66-82 days (Online Resource 2) and analyzed these and all other photos in this study using ImageJ (Schneider et al. 2012). To focus on conspecific crowding, our analyses excluded *B. glandula*

that were mainly (~50% or more) crowded by heterospecific barnacles (*Chthamalus dalli* and *Semibalanus cariosus*). We also removed macroalgae (primarily *Fucus distichus*) at the start of the study to avoid confounding effects of their interactions with barnacles.

Study locations, site temperatures, and body temperatures

To investigate how temperature potentially alters the effects of body size and crowding, we surveyed size and crowding response surfaces at sites spanning a low tide temperature gradient. San Juan Island is a climate warming “hotspot” because summer low tides coincide with warm afternoon temperatures (Helmuth et al. 2002). We chose four locations on the island varying in low tide thermal regimes (Dethier and Williams 2009). Within each location, we chose two to three sites that differed in solar aspect (which affects barnacle body temperatures; Gilman et al. 2015) but had similar tidal elevations (total 10 sites; Online Resource 2). The sites thus spanned a range of mean low tide temperatures (~16-24°C; Online Resource 3) during the study period. Although locations varied in wave exposure, they were all protected from full oceanic conditions (Dethier and Williams 2009).

Substrate surface temperature is an important determinant of barnacle body temperatures (Bertness 1989). To characterize site thermal regimes, we tracked the temperature of the rock surface adjacent (< 0.5 m) to our survey quadrats at each site using digital loggers. Loggers were iButtons wrapped in parafilm and covered by marine epoxy (z-spar; dark gray-green color similar to rocks) that recorded temperatures hourly during the study period ($N = 15,360$). Predicted tidal elevations [<http://tbone.biol.sc.edu/tide/> (accessed August 2017)] categorized temperature recordings as emersed or immersed. Unless otherwise noted, all temperatures reported in this paper are emersed temperatures.

To determine how crowding affects barnacle body temperature, we separately surveyed individuals at six sites in 13 sessions during low tides May–July 2018. Sessions were conducted under sun ($N = 11$) or shade ($N = 2$). In each session, the body temperatures of individual barnacles ($N = 5-11$) with different crowding were measured by inserting a thermocouple (Omega HH603A with type T thermocouple) directly into their body cavities (Bertness 1989). We minimized potential confounding effects by choosing barnacles of similar body sizes (operculum length mean \pm SD; 3.52 ± 0.77 mm) and microclimate conditions (e.g., keeping to similar tidal elevations ≤ 0.3 m and avoiding crevices). For each session, we conducted a simple linear regression of individual body temperature as a function of crowding. The slope coefficients of these regressions were then plotted against mean body temperature per session to examine how thermal conditions affect the relationship between individual body temperature and crowding.

Mesocosm experiment

Body size and crowding response surface, animal collection

To investigate how crowding alters the effects of body size in mesocosms, we used *B. glandula* growing on mussel shells. Mussel shells (*Mytilus trossulus*) naturally varying in barnacle sizes and crowding were collected from a pier at Jackson Beach (48°31'N 123°00'W) on San Juan Island, WA, USA in June and July 2017. Separate mussel shells were glued to plastic disks (~5 shells per disk; ~30-60 barnacles per disk) to form a response surface varying in barnacle body size and crowding.

Temperature treatments

To investigate how temperature alters the effects of body size and crowding experimentally, we nested the body size and crowding response surface within manipulated temperature treatments. Our goal was to create gradient of low tide thermal stress. We subjected barnacles on the plastic plates to eight low tide temperature treatments, each varying from the next by 2°C in the range of 20–34°C (Online Resource 4), which is at the upper range of summer low tide temperatures that barnacles likely experience in the field on San Juan Island (Online Resource 3; Gilman et al. 2015). During high tide, barnacles in mesocosms experienced the ambient seawater temperature (~8–13°C). Barnacles were continuously submerged indoors with running seawater (~8–12°C) for two weeks before the experiment to give them similar thermal histories.

Experimental set-up

We conducted the 42-day experiment outdoors at Friday Harbor Laboratories on San Juan Island in June–August 2017. Clear plastic tanks (946 mL) with plastic mesh lids served as mesocosms. Two mesocosms were randomly assigned to each of the eight temperature treatments (Online Resource 5). Pumps controlling seawater levels in the mesocosms approximated the ambient tidal regime on San Juan Island at +1.0 m during the study period (duration of daily emersion mean \pm SD; 6.5 ± 1.6 h). Pumps filled and drained water from tanks that had a constant supply of fresh seawater. For equipment model numbers see King and Sebens (2018).

During emersion, heat lamps controlled by timers warmed the mesocosms (including nighttime low tides). Each mesocosm had an independent temperature controller that turned a heat lamp on or off to maintain the treatment temperature. We monitored mesocosm

temperatures sensed by the temperature controllers during low tides throughout the experiment ($N = 982$; Online Resource 4) and regularly checked them against body temperatures using barnacle biomimetics (King and Sebens 2018). Many barnacles died in the 32°C and 34°C treatments during week two, so we added new barnacles (~20-50 barnacles per tank) for all treatments on day 18 and analyzed them together. An opaque canopy shaded the set-up such that animals experienced indirect but naturally varying light throughout the experiment.

Vital rate measurements and analyses

Analytic approach

We explored how environmental factors alter trait effects on *B. glandula* vital rates using a generalized linear mixed model framework. To examine our hypothesis, we focused on testing the statistical significance ($\alpha = 0.05$) of the interaction effects between body size, temperature, and crowding (fixed effects) on each vital rate. Separate models were built for field and mesocosm data. For field data, we initially considered random intercepts for sites both nested and not nested within locations, and in each case random slopes for body size or crowding. For mesocosm data, we initially considered random intercepts for tanks. We did not examine random slopes because we had no biological reason to expect the effects of body size or crowding to differ among tanks.

Model selection followed the top-down strategy described by Zuur et al. (2009; page 120-128). First, we selected random structures for models with all fixed effects using AIC and BIC (Online Resource 6). Then, we selected fixed structures using F tests for models without random effects and Wald χ^2 tests for models with random effects (Bolker et al. 2009). Finally, we determined the most parsimonious models by excluding nonsignificant terms. These final models

were used for visualization. Models with full fixed effects (after selection of random structures) are reported in the results tables. To avoid confounding our inferences on interaction effects, we limited analyses to regions of the size and crowding response surfaces where both factors were reasonably well-sampled (Online Resource 7). Model residuals were checked visually throughout model selection. Analyses were conducted using R v3.5.1 (R Core Team 2018) and the packages lme4 (Bates et al. 2015), car (Fox and Weisberg 2011), lmerTest (Kuznetsova et al. 2017), MuMIn (Bartoń 2017) and merTools (Knowles et al. 2018).

Survival

Individual *B. glandula* were categorized as alive or dead at the end of each study. A barnacle was considered dead if its opercula were missing or collapsed, or if its shell was missing entirely. We examined field barnacles ($N = 286$) by analyzing photos and mesocosm barnacles ($N = 974$) by gently poking opercula. Two field sites (CP2 and RT3) were excluded from analysis due to insufficient variation in body size. We modeled the probability of survival following a binomial error distribution with logit link to accommodate the binary response variable (Online Resource 8).

Growth

The metric for *B. glandula* growth was absolute change in individual body size. Change in size was calculated as the difference between final and initial operculum lengths during the study period (Online Resource 2), as measured from photos of barnacles in the field ($N = 149$) and in mesocosms ($N = 533$). Two field sites (CP2 and RT3) were excluded from analysis due to insufficient variation in body size. Some change in size values were negative, probably due to

measurement error; we retained these values in the analysis to avoid bias towards higher values. We modeled growth (change in operculum length) following a Gaussian error distribution with identity link to accommodate positive and negative values of change in size (Online Resource 8).

Reproduction

Reproductive *B. glandula* are hermaphroditic and house their ovaries in their mantle cavity (Strathmann 1987). To determine whether individuals were reproductive, barnacles were dissected and scored for the presence of yolky ovarian tissue (Berger 2009) at the end of each study, resulting in binomial data. We dissected ~10 barnacles per field site ($N = 95$) and ~10-40 barnacles per mesocosm ($N = 455$). Field barnacles were collected from areas immediately adjacent to each quadrat and frozen at -20°C before dissection. Since body volume correlates with reproductive potential in acorn barnacles (Wethey 1984a), we used final volume as the metric for body size in the reproduction analyses. Final volume was estimated as: $\text{Volume} = \text{Basal diameter}^2 \times \text{Shell height}$, where basal diameter and shell height were maximum values per individual measured using digital calipers at the end of the studies. We did not use initial volumes because those measurements required dissection. We modeled the probability of being reproductive following a binomial error distribution with logit link to accommodate the binary response variable (Online Resource 8). Due to small sample size, we decided *a priori* to exclude temperature as a fixed effect from the field reproduction models. To check for temperature effects, we conducted a simple linear regression on the model residuals against site grand mean temperatures.

Results

Individual vital rates

Survival

Body size, crowding, and temperature all affected *B. glandula* survival, with evidence for an interaction effect between size and crowding in the field (Table 1). In the field, the direction and magnitude of the crowding effect on barnacle survival was mediated by initial body size (Fig. 1). Crowding increased barnacle probability of survival, and this effect became stronger with increasing body size. At 2 mm initial operculum length, crowding had a slightly negative effect on a barnacle's probability of survival. At 6 mm initial operculum length, however, crowding = 1 (completely surrounded) increased a barnacle's average probability of survival by ~60% compared to crowding = 0 (completely isolated). The mesocosm experiment detected a general increase in barnacle survival with body size but did not detect an interaction effect between size and crowding (Table 1). Raw data plotted as a size and crowding response surface are available in Online Resource 9.

B. glandula survival decreased with temperature (Fig. 2; Table 1). In the field, barnacles at the warmest site (average low tide temperature 22.8°C, Online Resource 2) survived with ~35% lower average probability than barnacles at the coolest site (16.0°C). In the mesocosm experiment, barnacles in the warmest treatment (34°C) had 100% lower average probability of survival than barnacles in the coolest treatment (20°C).

Growth

B. glandula growth (change in operculum length) decreased with temperature in the mesocosm experiment (Fig. 3; Table 1). Barnacles in the warmest treatment (34°C) grew ~0.4 mm less over 42 days than did barnacles in the coolest treatment (20°C). No effect of

temperature was detected in the field (Table 1). In both the mesocosm and the field, growth decreased with initial body size and no crowding or interaction effects were detected (Table 1).

Reproduction

Body size and crowding both affected *B. glandula* reproduction, with evidence for an interaction effect in the mesocosm experiment (Table 1). In the mesocosm experiment, the direction of the crowding effect on barnacle reproduction was mediated by final body size (Fig. 4b). Probability of being reproductive was weakly increased by crowding for smaller barnacles and weakly decreased for larger barnacles. At 150 mm³ final volume, crowding = 1 increased a barnacle's average probability of being reproductive by ~20% compared to crowding = 0. At 350 mm³ final volume, however, the pattern was reversed: crowding = 1 decreased a barnacle's average probability of being reproductive by ~30% compared to crowding = 0. In the field, crowding increased barnacle probability of being reproductive across body sizes (Fig. 4a). Raw data plotted as size and crowding response surfaces are available in Online Resource 9.

Crowding effects on body temperature

Low tide body temperatures of barnacles in the field decreased with crowding under warmer, sunny conditions (Fig. 5; Online Resource 10). The slope coefficients of the regressions between individual low tide body temperature and crowding were negative (except one) when mean body temperature was $\geq 24^{\circ}\text{C}$. Crowding did not decrease individual body temperatures under cooler or shade conditions.

Discussion

Although environmental factors can alter the effects of traits on vital rates in sessile organisms, tests of interaction effects between these factors are lacking (Ehrlén et al. 2016). The present study found support for the hypotheses that 1) crowding alters the relationships between body size and vital rates and that 2) temperature influences the effect of crowding on vital rates. Body size and crowding had an interactive effect: crowding benefitted survival of larger barnacles in the field. In mesocosms, crowding increased probability of being reproductive for smaller barnacles but decreased it for larger barnacles. Warmer low tide temperatures decreased barnacle survival (field and mesocosms) and growth (mesocosms) regardless of body size. Accordingly, intraspecific variation in traits cannot serve to indicate individual vital rates in these barnacles without also incorporating environmental context.

Environmental factors alter trait effects through intraspecific interactions

Our findings suggest that while general relationships exist between body size and vital rates (Table 1), these relationships can depend strongly on the balance between size-dependent competition and temperature-dependent facilitation. In the field, individuals with larger initial body size experienced higher rates of survival with increasing levels of crowding (Fig. 1). Crowding switched from having a slightly negative effect to having a positive effect at ~3 mm operculum length, the size beyond which barnacles were generally larger than their contiguous neighbors (Online Resource 11). Smaller barnacles experienced stronger negative effects of crowding than larger individuals, which suggests size-asymmetric competition. Intraspecific size-asymmetric competition has also been observed in a barnacle congener (Wetthey 1983), other marine invertebrates (Marshall and Keough 1994; Zilberberg and Edmunds 2001), and terrestrial plants (e.g., Weiner 1985; del Río et al. 2014).

Size-asymmetric competition alone cannot account for the increase in barnacle survival with crowding at larger sizes. Our results suggest that, with increasing body size, the effect of crowding shifted from competition toward temperature-dependent facilitation. Previous work found that crowding increased barnacle survival at hotter sites but not cooler sites (Bertness et al. 1999). In our study, the effects of crowding did not vary across sites with different temperature regimes (Table 1); however, crowding decreased barnacle body temperatures during warmer and sunny (potentially stressful) low tides (Fig. 5; Online Resource 10). Crowding ameliorates thermal stress in barnacles (Lively and Raimondi 1987; Bertness 1989; Bertness et al. 1999; Leonard et al. 1999) by decreasing substrate surface temperature (Bertness 1989), increasing retention of interstitial water between individuals (WK personal observation), and possibly other mechanisms. In this study, it is likely that smaller, crowded barnacles experienced amelioration of thermal stress, but the positive effects were overwhelmed by competition. In contrast, larger, crowded barnacles experienced relatively weak competition while also benefitting from thermal stress amelioration. Our results do not exclude the possibility that size-dependent facilitation, in which smaller barnacles experienced weaker thermal stress amelioration, also contributed to the observed pattern of survival.

Amelioration of thermal stress is a more likely mechanism for the observed positive crowding effects than mechanisms involving decreased predation or other types of facilitation. Increasing prey density can decrease per capita predation pressure *sensu* type II functional responses. However, for the slow-moving predators relevant to our study, predation would likely have increased with barnacle crowding (e.g., whelks: Dunkin and Hughes 1984; crabs: Leonard et al. 1999). Besides thermal stress amelioration, barnacles can facilitate each other by forming hummocks that decrease energy expenditure on shell formation or increase feeding efficiency

(Wu 1980; Wethey 1984b; Bertness et al. 1998). Both mechanisms appear unlikely for the barnacles in our study. In the former, decreased individual shell mass with crowding would indicate decreased energy expenditure on shell formation; individual shell mass did not vary with crowding in our study (Online Resource 12). In the latter, the shell morphologies observed in our study (height:basal diameter ≤ 1.2 ; Online Resource 12) were unlikely to have substantially increased feeding efficiency for crowded barnacles (compare to height:basal diameter $\sim 2-4$ in Bertness et al. 1998).

Vital rates respond to environmental factors differently

Our findings indicate that individual vital rates in the same species can respond to crowding differently, agreeing with previous studies (e.g., Wethey 1983; Leslie 2005). In mesocosms, crowding affected neither barnacle survival nor growth (Table 1). However, we detected a negative effect of crowding on the probability of being reproductive for larger barnacles (Fig. 4b; Table 1), which suggests that reproduction is especially sensitive to competition (Wu 1980; Wethey 1984a). Competitive effects may have been detected only in larger barnacles because smaller barnacles invested less in reproduction and were less affected by crowding based on that metric. In the field, we detected positive effects of crowding on reproduction regardless of size (Fig. 4a; Table 1) potentially because smaller barnacles experienced both amelioration of thermal stress and weak competition in terms of reproduction. We did not detect an interaction effect between crowding and body size on field reproduction, in contrast to survival. These results support the idea that crowding effects depend on the balance between competition and facilitation and that this balance can differ by vital rate.

Warmer temperatures decreased survival (Fig. 2) of barnacles regardless of body size or crowding (Table 1). Our mesocosm findings suggest that survival of *B. glandula* decreases with warming and reaches a threshold at ~30°C mean low tide temperature, beyond which survival is minimal, agreeing with previous field data in the region (Salt Spring Island, British Columbia, Canada; Kordas and Harley 2016). Barnacle survival appears to decrease monotonically with temperature in the range we studied. Barnacle growth, however, may be more unimodal. A previous mesocosm study on *B. glandula* growth found that increasing mean low tide body temperature from ~14°C to 20°C slightly increased growth (King and Sebens 2018). In the present study we found that increasing from ~20°C to 32°C slightly decreased growth (Fig. 3). For temperature effects in the field, we detected a weaker decrease in survival (Fig. 2a) and no change in growth (Table 1), potentially due to differences in field conditions among sites (e.g., thermal variability).

The limitations of this study offer at least three avenues of future study. First, we did not exclude mobile predators. Since field sites may have differed in predator abundance, it is possible that sites differing in temperature also differed in predation pressure. This would partially confound our inferences of site-level temperature effects on vital rates. Second, this study focused on low tide temperatures to examine barnacle responses to warming. However, barnacles also experience the effects of other physical drivers, including water temperature. The stressful air warming that decreased growth in this study could potentially be counteracted by increases in growth caused by water warming (King and Sebens 2018). Finally, our conclusions may only hold at the spatial and temporal scale of this study. For example, *B. glandula* shows genetic clines over latitude (Sotka et al. 2004) and may be locally adapted to different temperature regimes. The *B. glandula* used in this study were near the northern edge of their

range. Our results provide an expectation against which future studies can test how multiple physical drivers and evolutionary processes (e.g., local adaptation) influence ecological controls on the vital rates of barnacles.

Conclusions

This study shows the usefulness of incorporating environmental effects when using body size to predict the vital rates of a sessile ectotherm. Under complex field conditions, the models that included body size, temperature, and crowding were able to explain 13-62% of variation in the vital rates of barnacles (Table 1). Since adding explanatory variables typically increases the amount of variance explained, it is worth considering what was gained in understanding beyond fit to data. Our findings suggest that decreasing body sizes and increasing temperatures under global change (Gardner et al. 2011; Ohlberger 2013) will have direct negative effects on barnacle populations, but, critically, the steepness of these declines will depend on the indirect effects of crowding and local temperature conditions. Including environmental factors provided insight into barnacle vital rates beyond what was possible based on body size alone. Future studies may also benefit by integrating trait and environment effects on demographic processes.

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Conflict of interest: The authors declare that they have no conflict of interest.

Ethical approval: All applicable institutional and/or national guidelines for the care and use of animals were followed.

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TableTable 1. Results of models testing how body size, crowding, and temperature affect *Balanus glandula* individual vital rates

Effect	Field			Mesocosm		
	DF	χ^2	<i>P</i>	DF	χ^2	<i>P</i>
Probability of survival	<i>N</i> = 286 from 8 sites $R^2_m = 0.149, R^2_c = 0.240$			<i>N</i> = 974 in 16 tanks $R^2_m = 0.589, R^2_c = 0.800$		
Size	1	1.533	0.216	1	21.308	< 0.001
Crowding	1	8.487	0.004	1	2.984	0.084
Temperature	1	3.872	0.049	1	26.495	< 0.001
Size × Crowding	1	6.930	0.008	1	0.252	0.615
Size × Temperature	1	0.150	0.698	1	2.114	0.146
Crowding × Temperature	1	0.591	0.442	1	1.754	0.185
Size × Crowding × Temperature	1	0.124	0.724	1	0.219	0.640
Growth (change in operculum length)	<i>N</i> = 149 from 8 sites $R^2 = 0.127$			<i>N</i> = 533 in 16 tanks $R^2_m = 0.134, R^2_c = 0.330$		
Size	1	12.660	< 0.001	1	14.068	< 0.001
Crowding	1	0.985	0.322	1	1.941	0.164
Temperature	1	0.189	0.665	1	5.945	0.015
Size × Crowding	1	3.649	0.058	1	0.022	0.883
Size × Temperature	1	2.073	0.152	1	1.391	0.238
Crowding × Temperature	1	0.166	0.684	1	0.084	0.773
Size × Crowding × Temperature	1	1.260	0.263	1	1.753	0.185
Probability of being reproductive ^a	<i>N</i> = 95 from 10 sites $R^2 = 0.619$			<i>N</i> = 455 in 16 tanks $R^2_m = 0.509, R^2_c = 0.632$		
Size	1	43.819	< 0.001	1	55.458	< 0.001
Crowding	1	4.260	0.042	1	2.544	0.111
Temperature				1	2.920	0.087
Size × Crowding	1	0.363	0.548	1	8.771	0.003
Model residuals ~ Temperature	1	1.215	0.273			
Size × Temperature				1	0.090	0.764
Crowding × Temperature				1	0.000	0.987
Size × Crowding × Temperature				1	0.905	0.341

Size refers to body size as measured by initial operculum length (survival and growth) or final shell volume (reproduction). Temperature refers to site grand mean temperature (field) or temperature treatment (mesocosm). Sample size (*N*) refers to number of individuals. R^2_m and R^2_c indicate marginal (fixed effects only) and conditional (fixed and random effects) R^2 respectively. Bold indicates $P < 0.05$. ^aDue to small sample size, the model for field data only included Size and Crowding as fixed effects; the model residuals were tested against temperature to check for temperature effects.

Figure captions

Fig. 1 Probability of survival of *B. glandula* as a function of body size and crowding in the field after 66-82 days. Crowding is a continuous variable and we visualize predictions for three levels: 0 = isolated, 0.5 = half of perimeter contiguous with conspecifics, 1 = completely surrounded. Lines indicate model predictions based on observations of 286 individuals from eight sites. Shaded areas indicate 95% confidence intervals based on fixed effects, with darker regions indicating overlap. Points indicate observations, with darker colors indicating higher crowding

Fig. 2 Probability of survival of *B. glandula* as a function of temperature (a) in the field after 66-82 days and (b) in the mesocosm experiment after 42 days. Rock surface temperature indicates grand mean low tide temperature for each site during the study period (June-August 2017). Lines indicate model predictions based on observations of (a) 286 individuals from eight sites and (b) 974 individuals in 16 mesocosms. Triangles indicate observed survival frequencies and shaded areas indicate 95% confidence intervals (based on fixed effects for the mesocosm model). Abbreviations at the bottom of (a) indicate sites. Note different x-axes

Fig. 3 Growth of *B. glandula* as a function of temperature in the mesocosm experiment after 42 days. Line indicates model predictions based on observations of 533 individuals in 16 mesocosms. Shaded area indicates the 95% confidence interval based on fixed effects. Triangles indicate individuals

Fig. 4 Probability of being reproductive of *B. glandula* as a function of body size and crowding (a) in the field and (b) in the mesocosm experiment after 42 days. Crowding is a continuous variable and we visualize predictions for three levels: 0 = isolated, 0.5 = half of perimeter contiguous with conspecifics, 1 = completely surrounded. Lines indicate model predictions based on observations of (a) 95 individuals from 10 sites and (b) 455 individuals in 16 mesocosms. Shaded areas indicate 95% confidence intervals (based on fixed effects for the mesocosm model), with darker regions indicating overlap. Points indicate observations, with darker colors indicating higher crowding. Note different x-axes

Fig. 5 Effect of crowding on individual body temperature of *B. glandula* as a function of mean body temperature. Effect of crowding is the slope coefficient from the regression of individual body temperature vs. crowding, based on measurements in the field during 13 low tide sessions. Mean body temperature refers to the average body temperature across individuals of all crowding levels within a session. Points indicate regression slopes that are significantly different from zero (black) or not (white), based on sessions conducted in the sun (circles) or in the shade (triangles). Bars indicate standard errors

Fig. 1

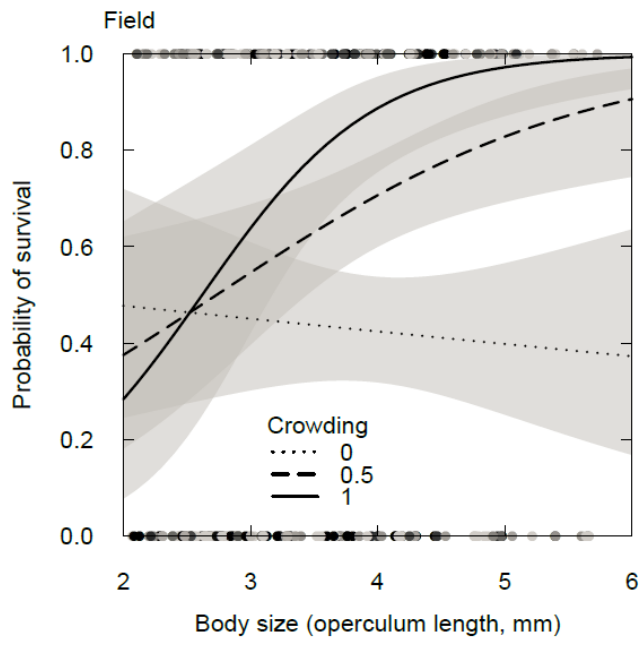


Fig. 2

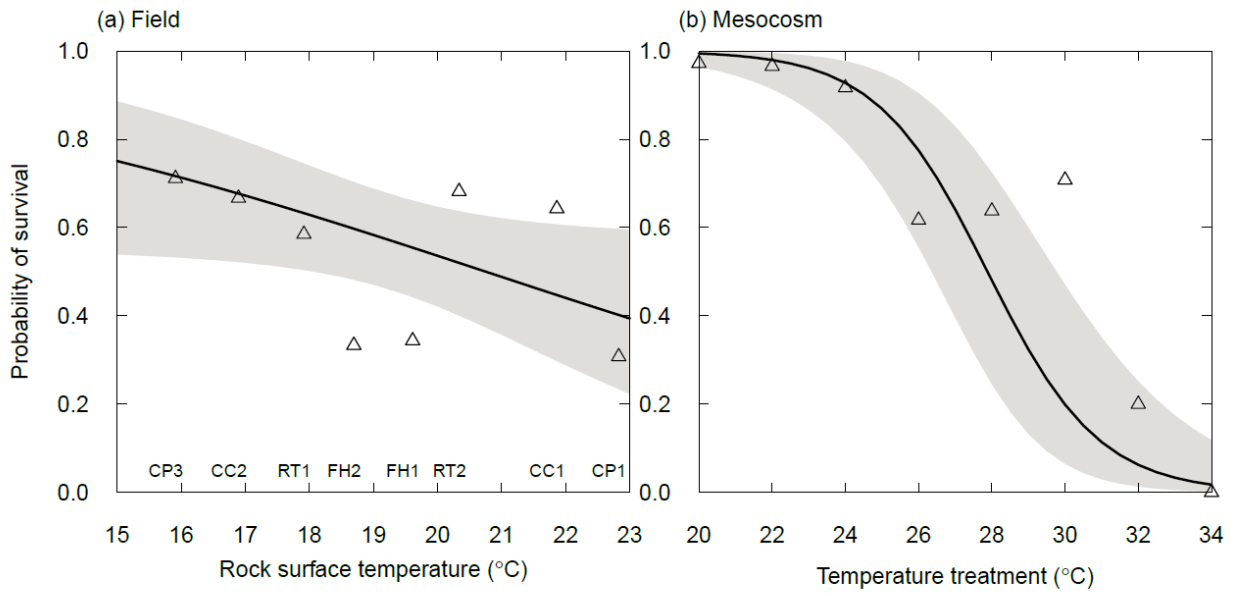


Fig. 3

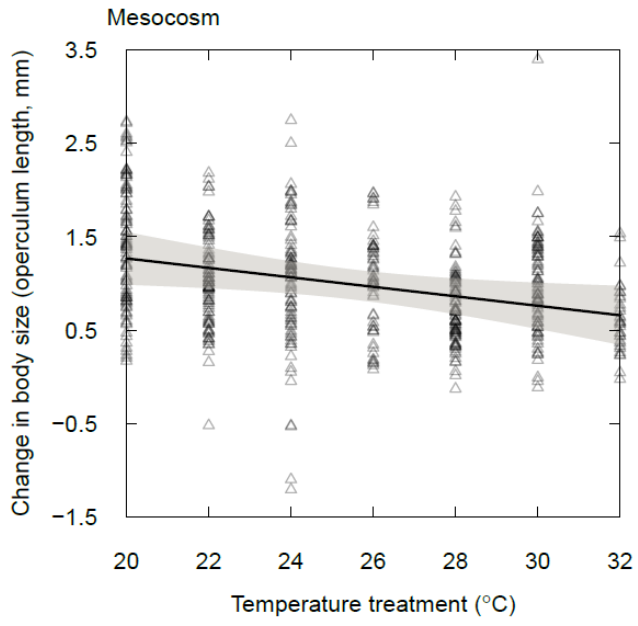


Fig. 4

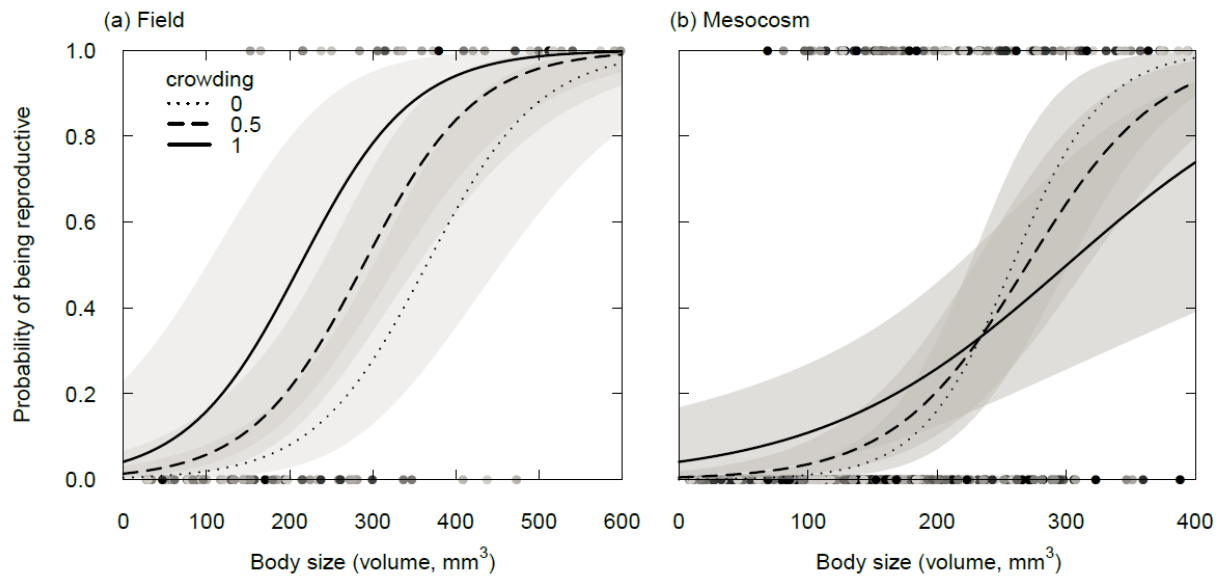
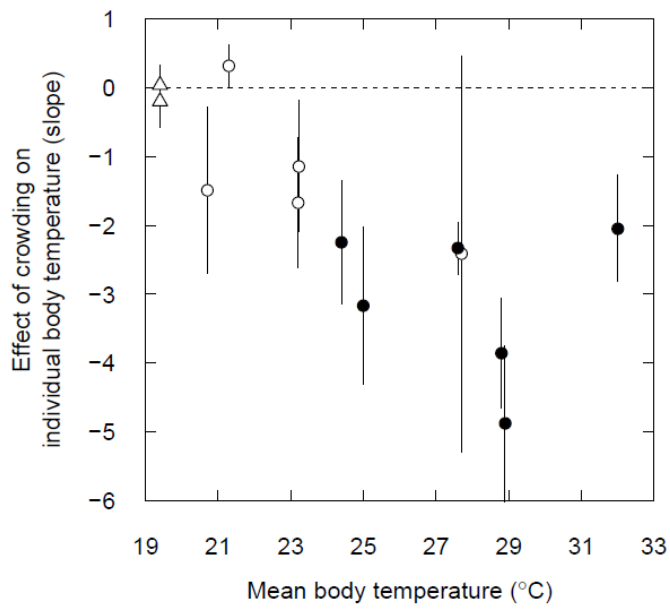


Fig. 5



Online Resource (Electronic Supplemental Material)

Title:

Temperature and crowding alter the effects of body size on vital rates in a sessile ectotherm

Authors:

William King^{a,b} and Kenneth P. Sebens^{a,b,c}

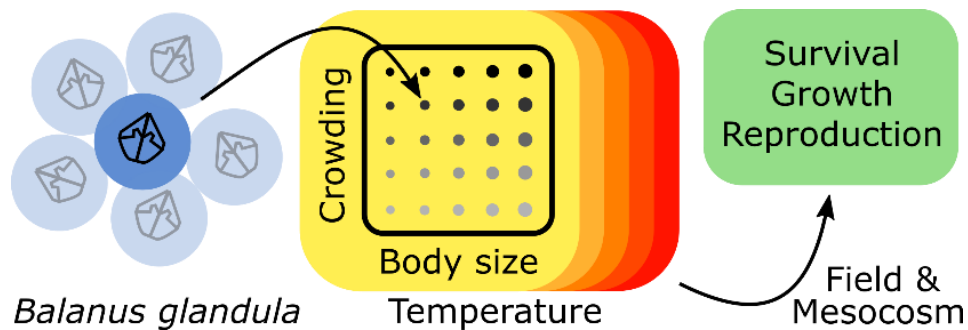
^aDepartment of Biology, University of Washington, Box 351800, Seattle, WA 98195, USA

^bFriday Harbor Laboratories, University of Washington, 620 University Rd, Friday Harbor, WA 98250, USA

^cSchool of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, WA 98195, USA

Online Resource 1

Schematic of study approach. Individual acorn barnacles *Balanus glandula* (sessile adults) undergo intraspecific interactions with contiguous neighbors (left). To test our hypothesis, we used a response surface design that varied in body size and crowding across a gradient of low tide temperatures (middle). We implemented this design in field surveys and a mesocosm experiment and measured individual vital rates (right).



Online Resource 2

Study locations and sites on San Juan Island, WA, USA. Duration refers to the number of days between the first and final photos taken of the quadrats at each location.

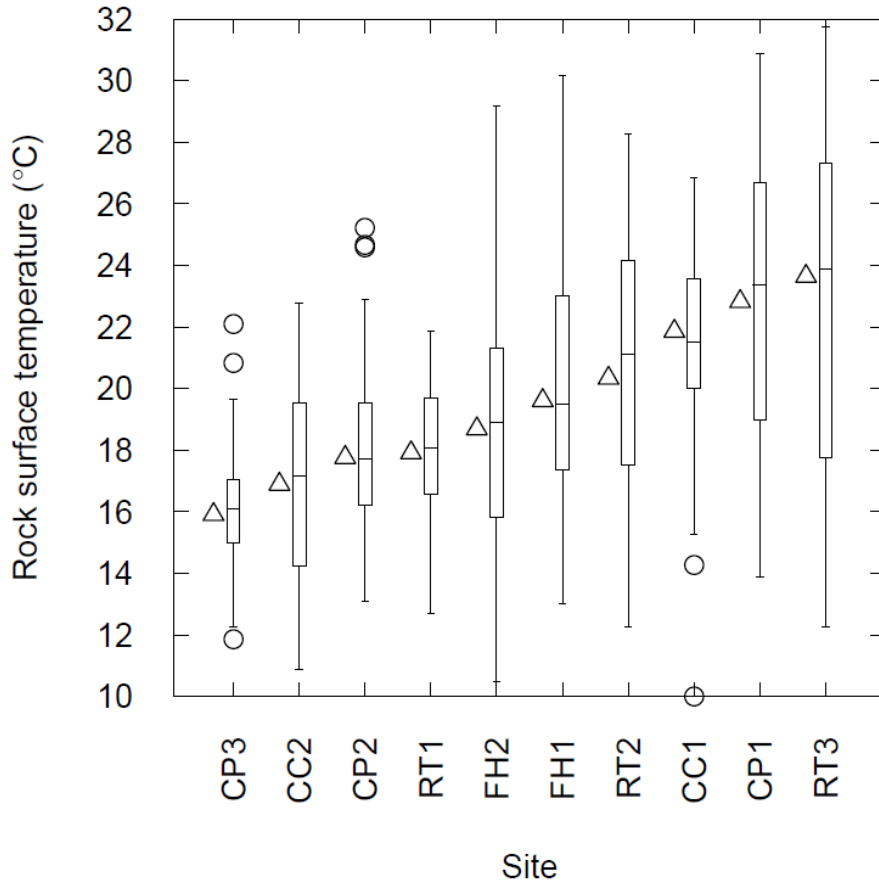
Location	Site	Coordinates N/W	Aspect	Tidal elevation (m above MLLW)	Duration
Reuben Tarte	RT1	48°36'45.8"/123°05'53.1"	W	1.91	70
	RT2	48°36'45.0"/123°05'51.9"	SW	1.52	70
	RT3	48°36'42.1"/123°05'55.0"	NE	0.94	70
Colin's Cove	CC1	48°32'53.6"/123°00'24.1"	SE	1.12	81
	CC2	48°32'53.6"/123°00'24.1"	SW	1.12	81
Friday	FH1	48°32'45.4"/123°00'42.1"	NE	1.31	82*
Harbor Labs	FH2	48°32'45.4"/123°00'42.1"	SW	1.31	82
	CP1	48°27'16.5"/122°57'43.2"	SW	1.72	66
Cattle Point	CP2	48°27'18.6"/122°57'41.6"	N	1.29	66
	CP3	48°27'01.9"/122°57'54.9"	S	1.70	66

*Duration was 69 for 16 individuals at this site because the final photos were not usable.

See Dethier and Williams (2009) for general location descriptions. The Friday Harbor Labs location was at the “old FHL pier”, 290 m west of Pumphouse in Dethier and Williams (2009).

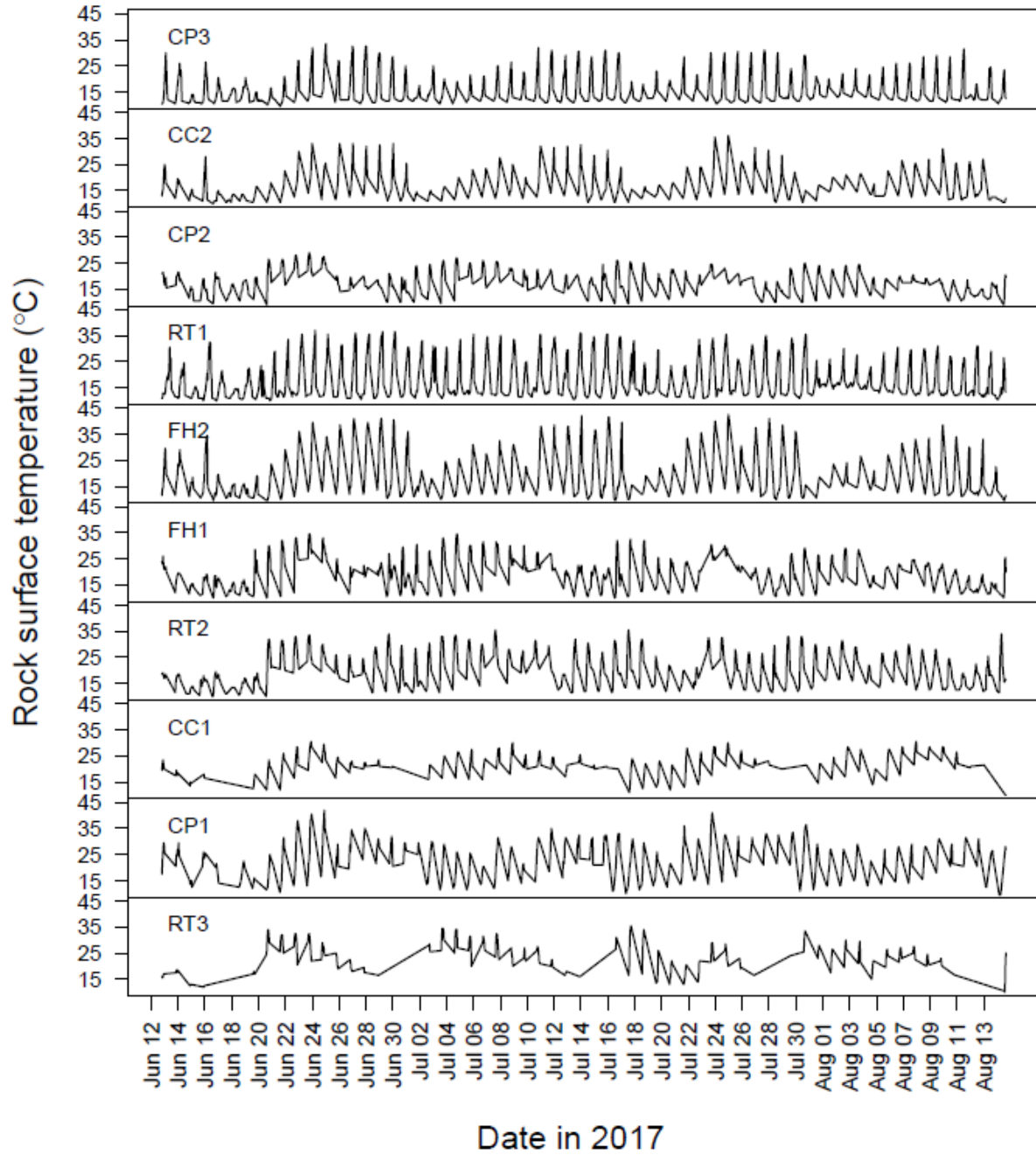
Online Resource 3

Field site low tide temperatures during the study period (June-August 2017) measured hourly by iButtons ($N = 15,360$). Triangles indicate grand mean low tide temperature for each site. Box-and-whisker plots indicate the range (ends of whiskers), median (center horizontal lines in boxes), first and second quartiles (horizontal box edges), and outliers (circles) of all low tide temperature measurements.



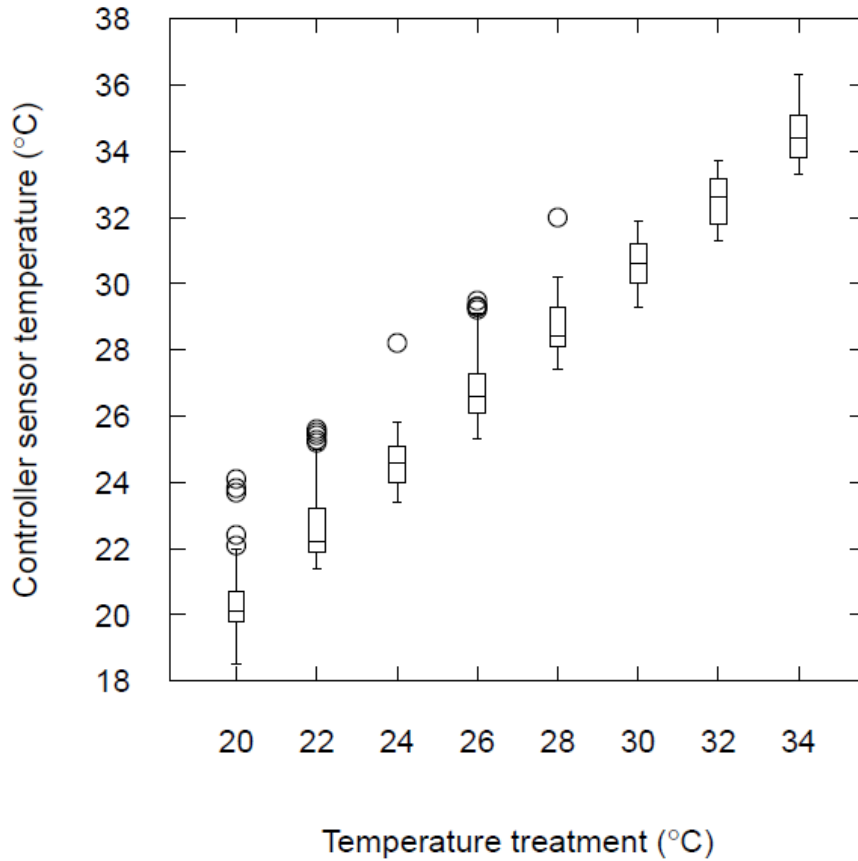
Online Resource 3 continued

Timeseries of field site low tide temperatures during the study period (June-August 2017) measured hourly by iButtons ($N = 15,360$).



Online Resource 4

Mesocosm low tide temperatures during the 42-day experiment based on readings of the temperature controller sensors ($N = 982$). Box-and-whisker plots indicate the range (ends of whiskers), median (center horizontal lines in boxes), first and second quartiles (horizontal box edges), and outliers (circles) of all low tide temperature measurements.



Online Resource 5

Diagram of the mesocosm layout.

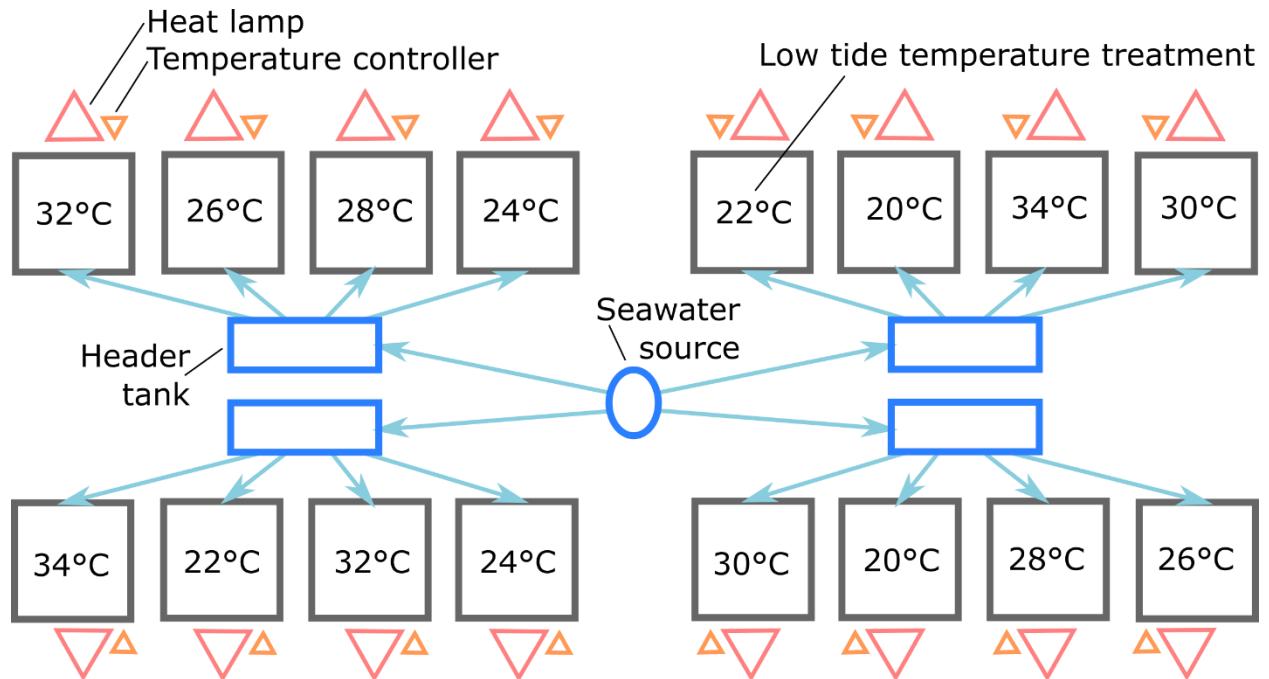
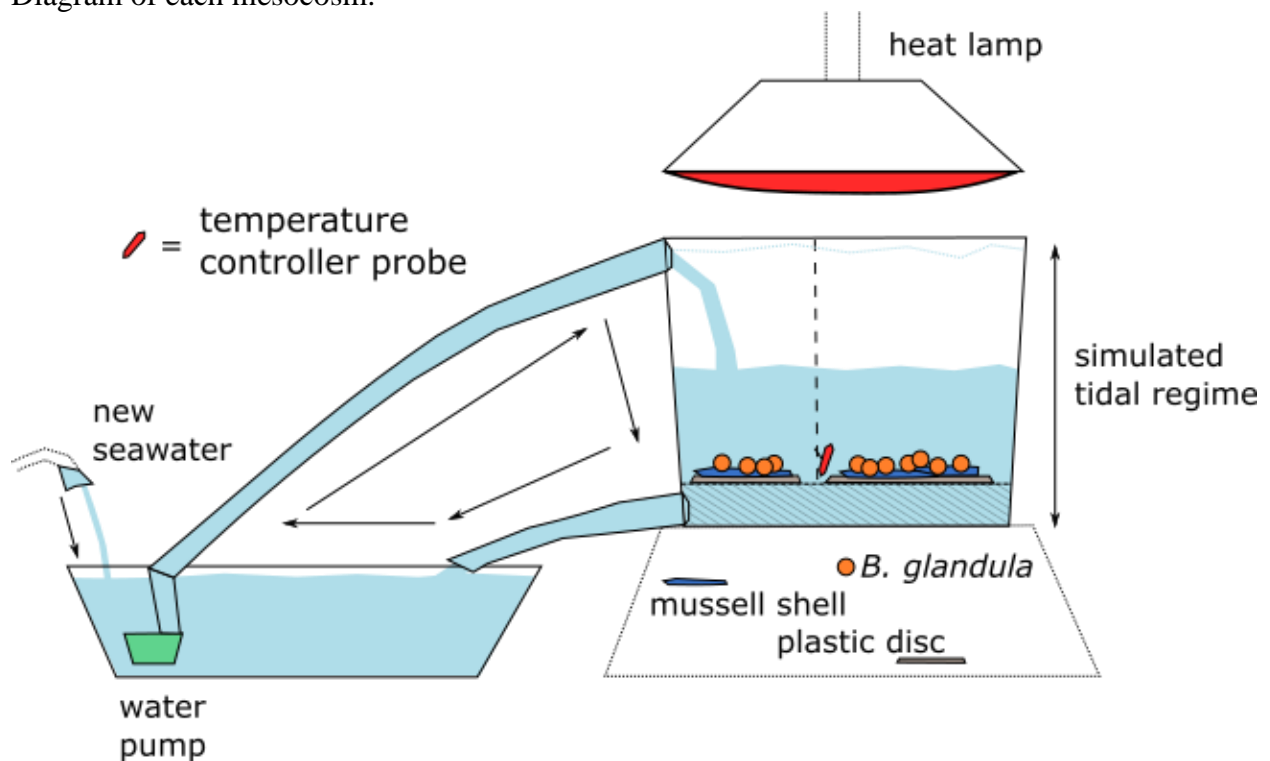


Diagram of each mesocosm.



Online Resource 6

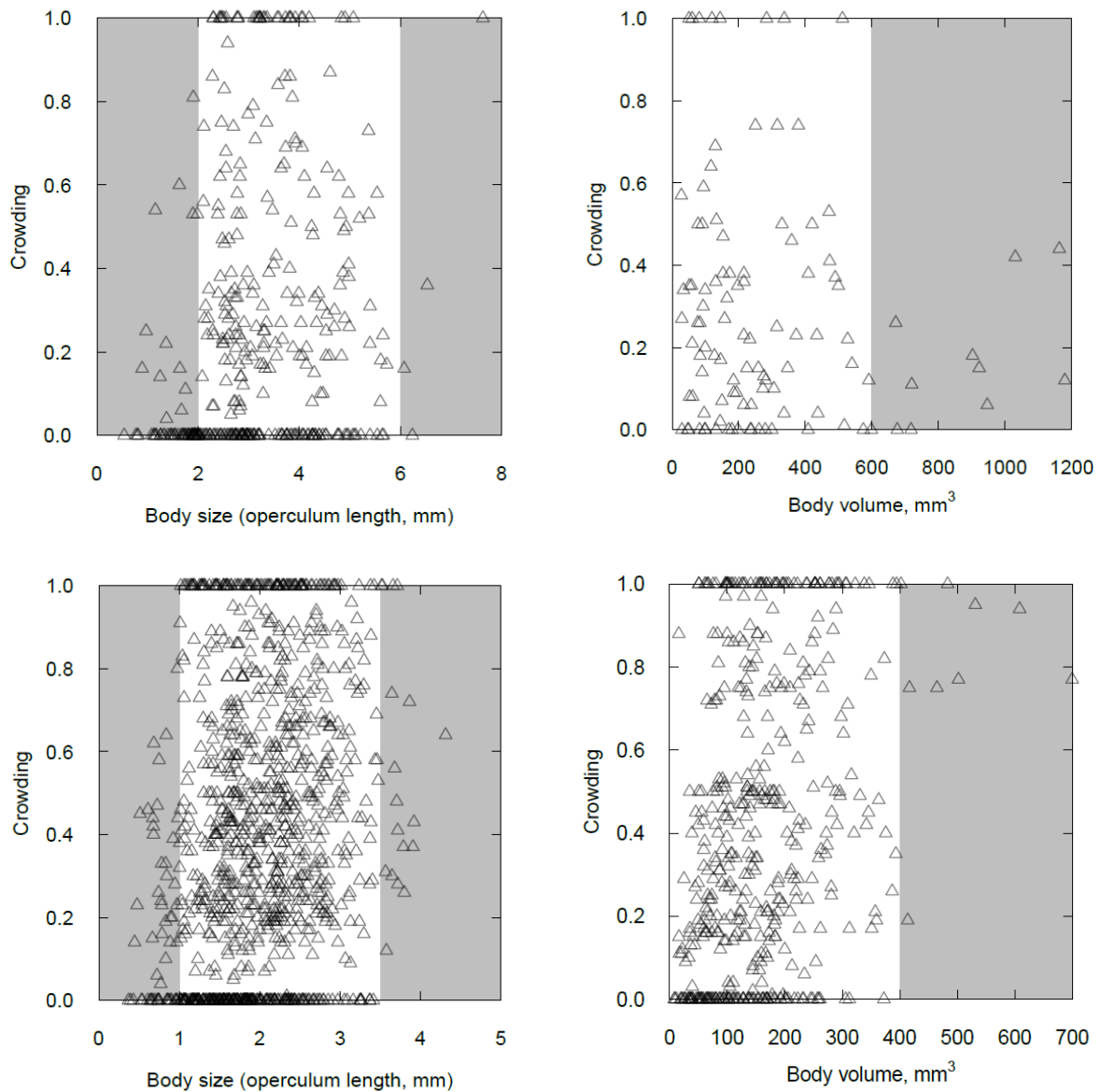
Selection of random effects in models using lowest AIC and BIC values (bold). Location/site indicates site nested within location. Check mark (√) indicates the random effects structure that was selected.

Response	Random effect	AIC	BIC	Choice
Field Survival	None	368.634	397.882	
	Site intercept	368.557	401.461	
	Site intercept and slope for crowding	371.719	411.935	
	Site intercept and slope for body size	367.280	407.496	√*
	Location/site intercept	369.985	406.545	
	Location/site intercept and slope for crowding	376.902	428.086	
	Location/site intercept and slope for body size	373.280	424.464	
Field Growth	None	80.839	107.875	√
	Site intercept	123.785	153.825	
	Site intercept and slope for crowding	125.582	161.630	
	Site intercept and slope for body size	126.490	162.538	
	Location/site intercept	125.722	158.765	
	Location/site intercept and slope for crowding	130.692	175.751	
	Location/site intercept and slope for body size	132.252	177.311	
Field Reproduction	None	67.907	78.122	√
	Site intercept	69.907	82.676	
	Site intercept and slope for crowding	71.913	89.790	
	Site intercept and slope for body size	73.907	91.784	
	Location/site intercept	71.907	87.230	
	Location/site intercept and slope for crowding	77.913	103.452	
	Location/site intercept and slope for body size	79.907	105.446	
Mesocosm Survival	None	808.512	847.563	
	Tank intercept	631.128	675.061	√
Mesocosm Growth	None	880.043	918.549	
	Tank intercept	866.425	909.211	√
Mesocosm Reproduction	None	348.266	381.229	
	Tank intercept	329.344	366.427	√

*In this case where AIC and BIC disagreed, we chose the more conservative model that includes the random effects of intercept and slope for body size. This model gives results qualitatively similar to the model with no random effects.

Online Resource 7

Body size and crowding response surfaces used for analysis of barnacle field survival and growth (top left), field reproduction (top right), mesocosm survival and growth (bottom left), and mesocosm reproduction (bottom right). Triangles indicate individual *B. glandula*, with darker clumps indicating more overlapping points. Data points in the shaded gray regions were excluded from analyses. Note different x-axes.



Online Resource 8

Equations describing models with full fixed effects after random effects have been selected (Appendix S4). An estimated term (α or β) with subscript j indicates that we allowed the term to vary across j (e.g., the random intercept $\alpha_j = \alpha + u_j$, where u is the random effect of j).

Survival

For field data, we modeled probability of survival s for barnacle i in site j following a binomial error distribution with logit link:

$$\text{logit}(s_{ij}) = \alpha_j + \beta_1 \text{Size}_{ij} + \beta_2 \text{Crowding}_{ij} + \beta_3 \text{Tempm}_{ij} + \beta_4 \text{Size}_{ij} \text{Crowding}_{ij} + \beta_5 \text{Size}_{ij} \text{Tempm}_{ij} + \beta_6 \text{Crowding}_{ij} \text{Tempm}_{ij} + \beta_7 \text{Size}_{ij} \text{Crowding}_{ij} \text{Tempm}_{ij}$$

where α is an estimated intercept, β are estimated slopes, Size is initial operculum length, Crowding is individual crowding, and Tempm is site grand mean low tide temperature.

For mesocosm data, we modeled probability of survival s for barnacle i in tank j following a binomial error distribution with logit link:

$$\text{logit}(s_{ij}) = \alpha_j + \beta_1 \text{Size}_{ij} + \beta_2 \text{Crowding}_{ij} + \beta_3 \text{Temptrt}_{ij} + \beta_4 \text{Size}_{ij} \text{Crowding}_{ij} + \beta_5 \text{Size}_{ij} \text{Temptrt}_{ij} + \beta_6 \text{Crowding}_{ij} \text{Temptrt}_{ij} + \beta_7 \text{Size}_{ij} \text{Crowding}_{ij} \text{Temptrt}_{ij}$$

where α is an estimated intercept, β are estimated slopes, Size is initial operculum length, Crowding is individual crowding, and Temptrt is temperature treatment.

Growth

For field data, we modeled growth g for barnacle i in site j following a Gaussian error distribution with identity link:

$$g_{ij} = \alpha + \beta_1 \text{Size}_{ij} + \beta_2 \text{Crowding}_{ij} + \beta_3 \text{Tempm}_{ij} + \beta_4 \text{Size}_{ij} \text{Crowding}_{ij} + \beta_5 \text{Size}_{ij} \text{Tempm}_{ij} + \beta_6 \text{Crowding}_{ij} \text{Tempm}_{ij} + \beta_7 \text{Size}_{ij} \text{Crowding}_{ij} \text{Tempm}_{ij}$$

where α is an estimated intercept, β are estimated slopes, Size is initial operculum length, Crowding is individual crowding, and Tempm is site grand mean low tide temperature.

For mesocosm data, we modeled growth g for barnacle i in tank j following a Gaussian error distribution with identity link:

$$g_{ij} = \alpha_j + \beta_1 \text{Size}_{ij} + \beta_2 \text{Crowding}_{ij} + \beta_3 \text{Temptrt}_{ij} + \beta_4 \text{Size}_{ij} \text{Crowding}_{ij} + \beta_5 \text{Size}_{ij} \text{Temptrt}_{ij} + \beta_6 \text{Crowding}_{ij} \text{Temptrt}_{ij} + \beta_7 \text{Size}_{ij} \text{Crowding}_{ij} \text{Temptrt}_{ij}$$

where α is an estimated intercept, β are estimated slopes, Size is initial operculum length, Crowding is individual crowding, and Temptrt is temperature treatment.

Online Resource 8 continued

Reproduction

For the field observations, we modeled probability of being reproductive r for barnacle i in site j following a binomial error distribution with logit link:

$$\text{logit}(r_{ij}) = \alpha + \beta_1 \text{Size}_{ij} + \beta_2 \text{Crowding}_{ij} + \beta_3 \text{Size}_{ij} \text{Crowding}_{ij}$$

where α is an estimated intercept, β are estimated slopes, Size is final volume, and Crowding is individual crowding.

For the mesocosm experiment, we modeled probability of being reproductive r for barnacle i in tank j following a binomial error distribution with logit link:

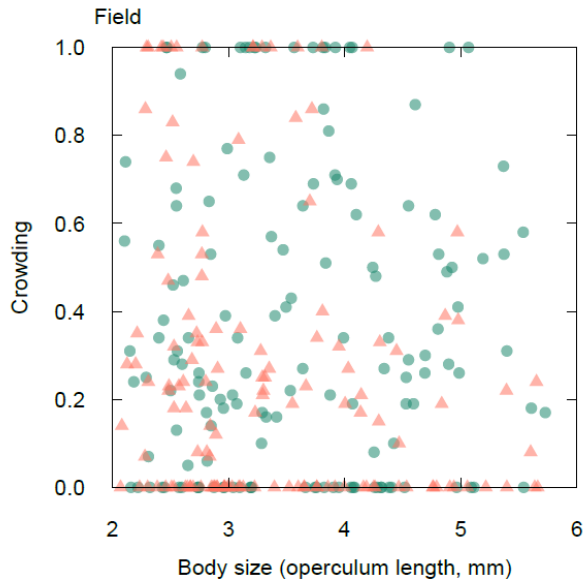
$$\begin{aligned} \text{logit}(r_{ij}) = & \alpha_j + \beta_1 \text{Size}_{ij} + \beta_2 \text{Crowding}_{ij} + \beta_3 \text{Temptrt}_{ij} + \beta_4 \text{Size}_{ij} \text{Crowding}_{ij} \\ & + \beta_5 \text{Size}_{ij} \text{Temptrt}_{ij} + \beta_6 \text{Crowding}_{ij} \text{Temptrt}_{ij} + \beta_7 \text{Size}_{ij} \text{Crowding}_{ij} \text{Temptrt}_{ij} \end{aligned}$$

where α is an estimated intercept, β are estimated slopes, Size is final volume, Crowding is individual crowding, and Temptrt is temperature treatment.

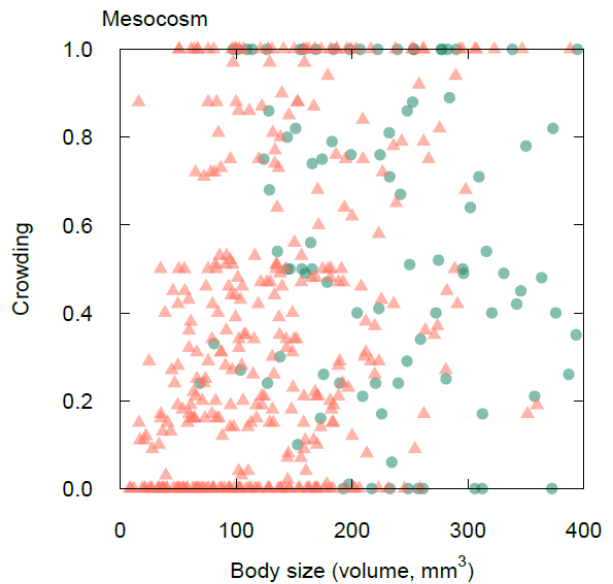
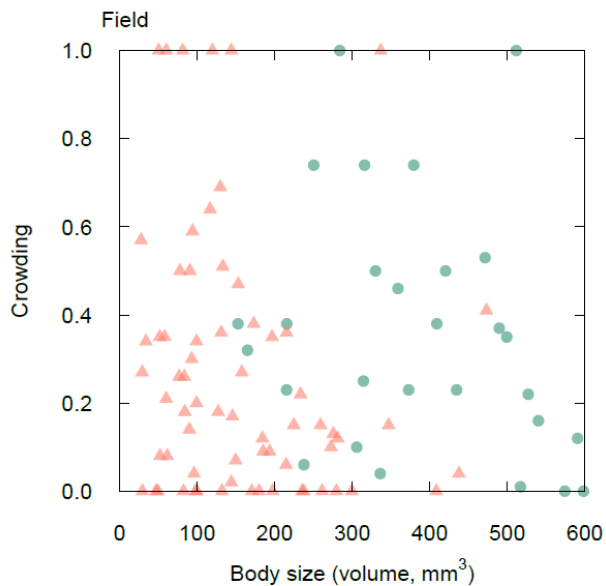
Online Resource 9

Observed survival (top row) and reproductive status (bottom row) of *B. glandula* visualized in body size and crowding response surfaces. Points indicate individual barnacles, with green circles indicating “yes” (survived and were reproductive, respectively) and pink triangles indicating “no” (died and were not reproductive, respectively). Darker clumps indicate more overlapping points. Note different x-axes.

Survival:



Reproductive:



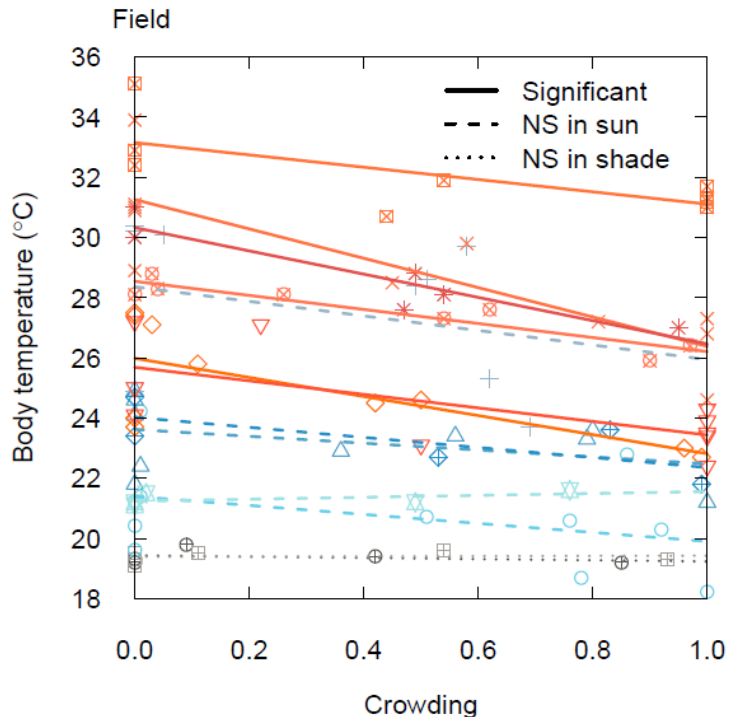
Online Resource 10

Results of models examining the relationship between individual body temperatures and crowding.

Type	Date	Site	N	Slope	SE	P	R ²
Sun	May 16	RT2	11	-1.496	1.208	0.247	0.146
Sun	May 16	CC2	10	-1.141	0.952	0.265	0.152
Sun	May 21	CC2	10	-2.417	2.883	0.426	0.081
Sun	May 22	RT2	10	-4.877	1.135	0.003	0.698
Sun	June 11	FH1	10	-3.168	1.144	0.024	0.489
Sun	June 14	CP3	9	-2.045	0.775	0.033	0.499
Sun	June 14	CP2	10	-2.248	0.899	0.037	0.439
Sun	June 19	RT2	6	-3.864	0.797	0.008	0.855
Sun	June 19	RT2	5	-1.671	0.950	0.177	0.508
Sun	June 25	CC1	5	0.318	0.305	0.373	0.267
Sun	July 5	CC2	8	-2.336	0.375	<0.001	0.866
Shade	May 16	FH1	5	-0.199	0.375	0.633	0.086
Shade	June 15	CC2	5	0.039	0.281	0.899	0.006

All sessions were conducted in year 2018. Type refers to the general low tide weather conditions in which the session was conducted. SE indicates standard error. Bold indicates $P < 0.05$.

Body temperature of *B. glandula* as a function of crowding in the field as measured during 13 low tide sessions. Lines indicate model predictions based on data for each session analyzed separately, with icons distinguishing sessions. Significant and non-significant (NS) refer to whether the regression slopes differ from 0. Colors are only to help visually distinguish sessions.

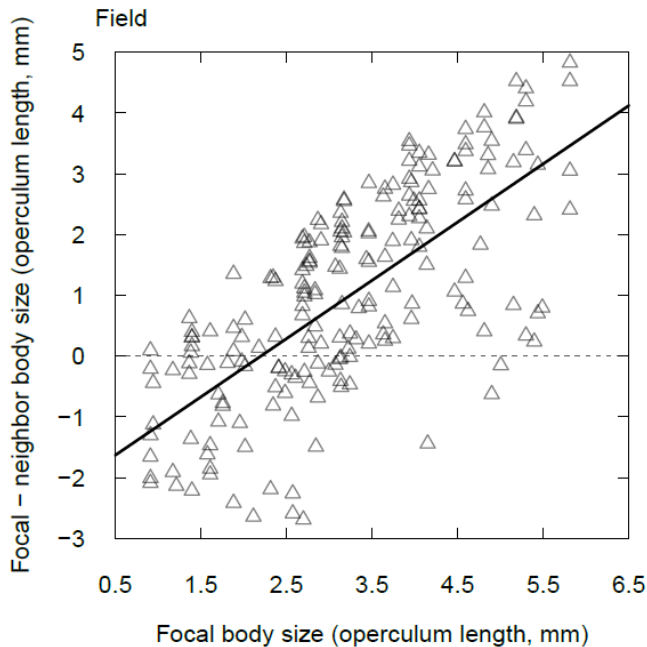


Online Resource 11

A sessile organism exhibits size asymmetry when its body size differs from those of their contiguous neighbors. To determine whether barnacles in the field exhibit size asymmetry, we haphazardly chose and measured the body sizes of 202 pairs of focal individuals and their contiguous neighbors in the initial photos from our main survey of the ten sites. Using data pooled across sites, we conducted a simple linear regression of the difference between neighbor and focal size as a function of focal size.

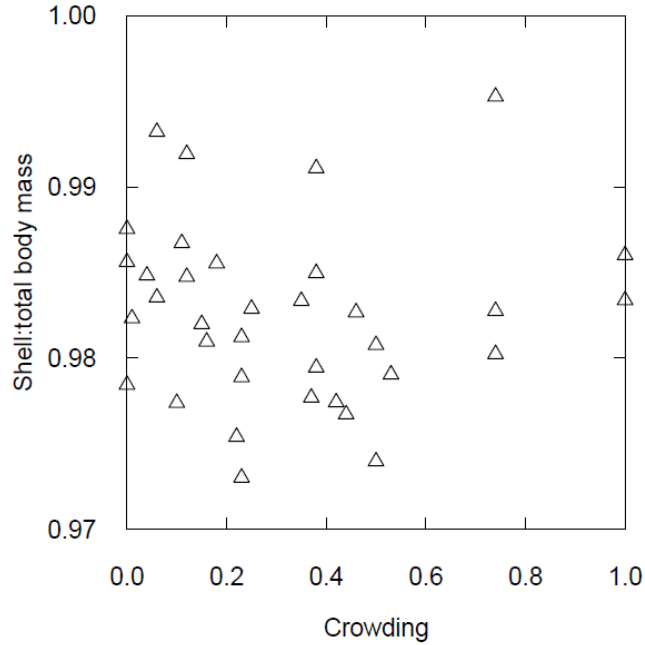
We found that barnacles in the field exhibited size asymmetry (see figure below), with focal individuals of ~3.5 mm operculum length or larger generally being larger than their neighbors (Slope $F_{1, 199} = 176.3$, $P < 0.001$, $R^2 = 0.470$).

Size-asymmetry of *B. glandula* in the field at the start of the study period. Line indicates model predictions based on 202 pairs of focal individuals and their contiguous neighbors from nine sites. Triangles indicate pairs, with darker regions indicating more overlapping points.

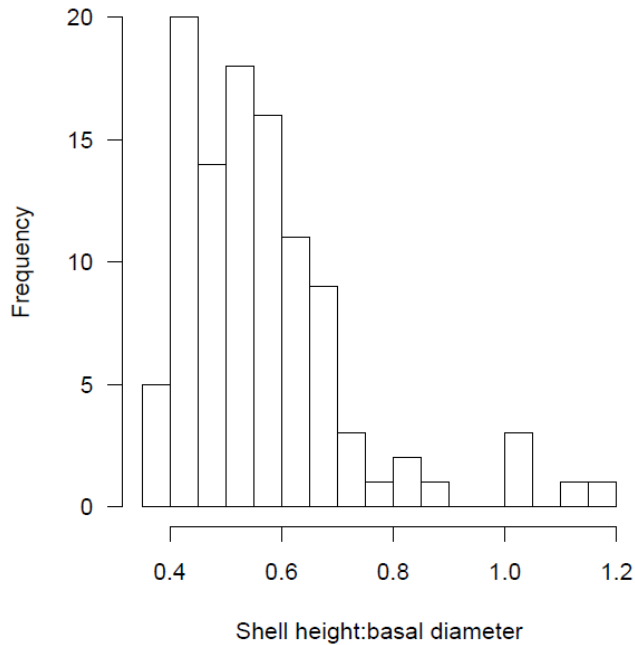


Online Resource 12

Ratio of shell mass to total body mass as a function of crowding based on *B. glandula* collected in the field as part of the reproduction analysis. Barnacles were dissected and the components dried in a 60°C oven for ~48 h before weighing (± 0.0001 g). Each triangle indicates an individual barnacle.



Ratio of shell height to basal diameter based on *B. glandula* collected in the field as part of the reproduction analysis.



Chapter 3

Title

Ontogenetic shifts in intraspecific interactions alter population dynamics in a sessile ectotherm

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Abstract

Ontogenetic shifts in biotic interactions affect the individual vital rates that underly population dynamics. Compared to consumer-interactions, there is a dearth of information on how ontogenetic shifts in interactions within a trophic level affect population dynamics. This is problematic because interactions within a trophic level (e.g., competition and facilitation) are critical determinants of community structure. We investigated the conditions under which ontogenetic shifts in intraspecific interactions affect the population dynamics of acorn barnacles *Balanus glandula*. To do so, we first conducted a year-long survey on barnacle survival and growth in the field on San Juan Island, Washington. Consistent with the literature, we found that body size had the predominant effect on individual vital rates. However, crowding modified the size effect in an important way: the direction of intraspecific interactions on barnacle growth shifted from negative to positive across size. At 1 mm initial size, high crowding decreased barnacle growth by ~50% compared to no crowding. At 6 mm, however, crowding increased barnacle growth slightly. Based on these findings, we then built integral projection models parameterized in part by vital rates observed in the field (survival and growth) to examine barnacle population dynamics under both empirical and theoretical crowding scenarios. The theoretical scenarios varied crowding distributions (uniform, low, and high) for both recruits and established individuals. Populations modeled with theoretical crowding distributions showed differences in population growth rates consistent with the observed ontogenetic shifts. Populations with low crowding in established individuals and high crowding in recruits had the lowest population growth rate (estimate [95% confidence interval]; 0.94 [0.75, 1.15]). Conversely, populations with high crowding in established individuals and low crowding in recruits had the highest population growth rate (1.34 [1.09, 1.61]). This difference in population

growth rate was mediated by changes in the population size distribution. Together, these findings highlight the importance of considering how ontogenetic shifts in competition and facilitation alter population dynamics when predicting the responses of sessile ectotherms to global change.

Key words: Ontogenetic shifts; Intraspecific interactions; Population dynamics; Integral projection models; Acorn barnacles; *Balanus glandula*

Introduction

Modern science is tasked with predicting how ecological systems respond to global change (Sala et al. 2000). Mounting evidence suggests that one of the major outcomes of global change is decreasing body size (Sheridan and Bickford 2011; Ohlberger 2013). Changing body sizes affect the ecosystem functions (Woodward et al. 2005; Petchey and Belgrano 2010) that provide valuable goods and services to humans (Costanza et al. 1997). Changes in body size have important ecological consequences because body size is a fundamental driver of individual vital rates (survival, growth, reproduction; Peters 1983), which in turn drive population dynamics (Ebenman and Persson 2012). In addition to changes at the organismal level, however, evidence suggests that biotic interactions can also change with body size, shifting sign and/or strength across ontogeny (Werner and Gilliam 1984; de Roos et al. 2003; de Roos and Persson 2013). Incorporating these ontogenetic shifts into the general understanding of biotic interactions and population processes remains a challenge in predicting how ecological communities respond to global change (Yang and Rudolf 2010). This study examines how ontogenetic shifts in biotic interactions affect population dynamics in a sessile ectotherm.

Ontogenetic shifts in biotic interactions affect the individual vital rates that underly population dynamics. Mechanisms causing ontogenetic shifts include changes in niche requirements (Werner and Gilliam 1984; de Roos and Persson 2013), ability to exploit resources (Ebenman and Persson 2012), and the timing of interactions with neighbors (Yang and Rudolf 2010). While many studies have examined the causes and consequences of ontogenetic shifts in consumer-resource interactions (e.g., Werner and Hall 1988; Dahlgren and Eggleston 2000; de Roos and Persson 2013; Caie and Shima 2019), the consequences of shifts within a trophic level are less well known (Miller and Rudolf 2011). Much of the variation in interactions within a

trophic level has been attributed to abiotic factors (context dependency and Stress Gradient Hypothesis: Bertness and Callaway 1994). Part of the variation, however, is also due to ontogenetic factors (Miriti 2006; He et al. 2013; de Nesnera 2016). In some cases, the effects of ontogenetic shifts in interactions within a trophic level can outweigh habitat effects (e.g., Schiffers and Tielbörger 2006; le Roux et al. 2013). Ultimately, improved understanding of shifts in biotic interactions will likely require integration of environmental and ontogenetic controls (Callaway and Walker 1997; Miriti 2006; Schiffers and Tielbörger 2006; He et al. 2013). Here, we focus on the latter.

Examples of ontogenetic shifts within a trophic level often involve competition and facilitation among sessile organisms. In plants, studies generally document shifts from positive to negative interspecific interactions across size: nurse plants that provide habitat amelioration to small or intermediate sized plants become competitors throughout development (e.g., Miriti 2006; Schiffers and Tielbörger 2006; Armas and Pugnaire 2009; Álvarez-Yépez et al. 2014). However, shifts from negative to positive interactions also occur. In a marine alga, for example, competition against barnacles at an early life stage becomes facilitation at a later life stage (Kordas and Dudgeon 2009, 2011). Regardless of the direction of change, many studies of ontogenetic shifts within a trophic level have focused on effects at individual (e.g., survival and growth; de Nesnera 2016) or community levels (e.g., species diversity; Lasky et al. 2015). Fewer studies have examined the population consequences (e.g., size distribution and population growth rate) of such shifts (le Roux et al. 2013; but see Kordas and Dudgeon 2009; le Roux et al. 2013). This knowledge gap is important to address because population level processes form the link between the effects of biotic interactions on individuals to community dynamics.

Acorn barnacles in the rocky intertidal zone provide a useful system in which to study how ontogenetic shifts in competition and facilitation affect population dynamics. Sessile organisms in the rocky intertidal zone have proven fruitful for elucidating principles that now pervade ecology (e.g., Connell 1961a, b; Paine 1966; Dayton 1971). Interactions between acorn barnacles can be competitive (Connell 1961a, b; Dayton 1971) or facilitative (Lively and Raimondi 1987; Bertness 1989; Bertness et al. 1999; Leonard et al. 1999; Leslie 2005). In a companion study, we found that the balance of these interactions varied with ontogeny for the barnacle *Balanus glandula* (Darwin 1854): the effect of intraspecific crowding shifted from negative to positive across body size (King and Sebens in prep). These barnacles thus provide a promising system in which to examine the population consequences of ontogenetic shifts.

Two aspects of barnacle biology suggest important factors to account for when studying the population consequences of ontogenetic shifts. First, controls on barnacle population growth can exhibit strong seasonality (Fukaya et al. 2010). Since our companion study occurred in the summer, the ontogenetic shifts we observed may differ at longer time scales. It is worth examining ontogenetic shifts in *B. glandula* at the year-long scale. Second, the population dynamics of barnacles depend on both recruitment and post-recruitment processes (Gaines and Roughgarden 1985; Menge 1991, 2000; Menge et al. 2010). The densities of established individuals can be decoupled from those of the recruits, depending on context. Thus, it may be useful to examine the effects of biotic interactions across both size and stage (recruit vs. established individuals) when considering population dynamics.

This study investigated the conditions under which ontogenetic shifts in biotic interactions affect the population dynamics of acorn barnacles *Balanus glandula*. Using field observations and population modeling, we tested two hypotheses. First, that ontogenetic shifts in

intraspecific interactions between *B. glandula* occur at the year-long scale. Second, that ontogenetic shifts in intraspecific interactions affect the population dynamics of *B. glandula*. Our findings highlight the importance of considering ontogenetic shifts in competition and facilitation when predicting the population responses of sessile ectotherms to global change.

Methods

Field data

Surveys and study sites

We surveyed *B. glandula* in the middle of the barnacle zone on San Juan Island, Washington, USA in June-August 2017 and July-August 2018. We aimed to survey barnacles varying in both body size and crowding. Our metric for body size was initial operculum length (Lohse 1993; Gilman et al. 2013). Our metric for crowding was the initial proportion of an individual's shell perimeter directly touching alive conspecifics, which we measured using careful drawings and a protractor. As examples, crowding = 0 indicated isolation, crowding = 0.5 indicated half of the perimeter contiguous with conspecifics, and crowding = 1 indicated all of the perimeter contiguous with conspecifics.

We surveyed at multiple sites (see below). Each site had three horizontally adjacent (within 0.5 m) quadrats (10 x 10 cm) marked by epoxy dots on vertical boulders and rocky walls. To ensure a range of individual-level crowding, we first created a range of quadrat-level densities (~ 1 , 3, and ≥ 4 individuals cm^{-2}) by haphazardly removing individuals immediately before the first survey. Individuals of all crowding levels were sampled from all quadrats. We photographed the quadrats approximately every two weeks during the summers of 2017 and 2018 and analyzed these and all other photos in this study using ImageJ (Schneider et al. 2012).

To focus on conspecific crowding, our analyses excluded *B. glandula* that were mainly (~50% or more) crowded by heterospecific barnacles (*Chthamalus dalli* and *Semibalanus cariosus*). We removed macroalgae (primarily *Fucus distichus*) throughout each summer to decrease the confounding effects of their interactions with barnacles.

The study sites used in this study were a subset of sites used in a companion study (King and Sebens in prep). We used sites and quadrats for which reasonable numbers of individual barnacles could be identified confidently at the end of the one-year survey (12 quadrats across five sites; Supplement 1). The full set of sites used in the companion study spanned a gradient of summer low-tide temperatures (Supplement 2). The companion study did not find interaction effects between site-level, summer low-tide temperatures and body size or crowding on barnacle vital rates (King and Sebens in prep).

Individual survival and growth

Individual *B. glandula* were categorized as alive or dead at the end of the survey ($N = 351$). A barnacle was considered dead if its opercula were missing or collapsed, or if its shell was missing entirely. If a barnacle was categorized as alive (survived), its final size (operculum length) was measured to determine growth ($N = 94$). Survival and growth analyses were conducted using field photos.

Population growth rate and size distribution

The quadrats surveyed in this study were considered samples of one population. Field population growth rate (λ) was estimated as the ratio between final and initial abundance of barnacles in a particular quadrat: $\lambda = N_{t+1}/N_t$, where N is number of barnacles and t is time in

years. Initial photos were taken for eight quadrats before any density manipulations (see above) and were included as samples for estimating field population growth rate (four quadrats were excluded due to lack of initial photos; Supplement 3). Population size distribution was estimated as the final size frequency of all barnacles across all quadrats.

Estimation of field survival and growth

Analytic approach

We explored how intraspecific interactions affect *B. glandula* survival and growth across ontogeny using a generalized linear mixed model framework. In this section, “models” refer to statistical models, not population models. To examine our first hypothesis, we focused on testing the statistical significance ($\alpha = 0.05$) of the interaction effects between initial body size and crowding (fixed effects) on each vital rate. We initially considered random intercepts for sites both nested and not nested within locations, and in each case random slopes for body size or crowding. We modeled the probability of survival following a binomial error distribution with logit link to accommodate the binary response variable (Supplement 4). We modeled growth (final size) following a Gaussian error distribution with identity link (Supplement 4). To check that slight differences in growth durations (Supplement 1) did not confound our conclusions, we also examined growth rate (Supplement 5).

Model selection followed the top-down strategy described by Zuur et al. (2009). First, we selected random structures for models with all fixed effects using AIC and BIC (Supplement 6). Then, we selected fixed structures using Wald χ^2 test for both survival (Supplement 7) and growth (Bolker et al. 2009). Finally, we determined the most parsimonious models by excluding nonsignificant terms. Results of models with full fixed effects (after selection of random

structures) are reported in the results tables. To avoid confounding our inferences on interaction effects, we limited analyses to the ranges size and crowding where both factors were reasonably well-sampled (Supplement 8). Model residuals were checked visually throughout model selection. Analyses were conducted using R v3.5.1 (R Core Team 2018) and the packages lme4 (Bates et al. 2015), car (Fox and Weisberg 2011), and MuMIn (Bartoń 2017).

Population modeling approach

We used integral projection models (IPMs), which describe the dynamics of a population (in discrete time) in which individual vital rates vary with one or more continuous state variables (Ellner et al. 2016). Other studies have modeled population structure in barnacles using discrete size or age classes (e.g., Hyder et al. 2001; Poloczanska et al. 2008). IPMs have the advantages of avoiding size classes, which can be somewhat arbitrary (Hyder et al. 2001), and accommodating smaller data sets (< 300 individuals) compared to matrix models (Ramula et al. 2009). We built two types of IPMs: one with only body size (z) as a continuous state variable (IPM_{size-only}) and another with both body size and crowding (q) as continuous state variables (Figure 1; Supplement 9). Models of the latter type were adapted from the size-quality model described by Ellner et al. (2016). Subscript notation for the IPMs that included crowding indicate the crowding distributions of the established individuals and recruits. For example, IPM_{eFrF} used field data (F) to parameterize both the established (e) and recruit (r) crowding distributions. Established individuals are defined as individuals in the population at time t which were present at the previous time step, $t-1$ (Fig. 1). Biologically, this includes both adult and juvenile barnacles. Recruits are defined as new individuals arriving into the population at time t (Fig. 1).

Biologically, this corresponds to barnacles that have settled and grown just large enough to be identified in photos as recent recruits.

We examined our second hypothesis by making two types of comparisons. First, we compared the outputs of an IPM with only body size as a continuous variable (IPM_{size-only}) against an IPM with crowding distributions parametrized by field data (IPM_{eFrF}). This comparison allowed us to examine whether incorporating information about field crowding conditions changes predictions of population dynamics. Second, we compared the predictions of IPMs with the same model structures (includes crowding) but different theoretical crowding scenarios. This allowed us to examine how different distributions of crowding across ontogeny can affect barnacle population dynamics. Parameterization of models is detailed below.

IPM_{size-only} predicts body size distribution at year $t+1$ ($n(t+1, z')$) given the body size distribution at year t ($n(t, z)$). The kernel components describing yearly transition probabilities are survival ($s(z)$); growth ($G(z', z)$), which describes the probability density for an individual of size z at year t to obtain size z' at year $t+1$; probability of reproducing ($p_b(z)$); fecundity (number of offspring, $b(z)$); probability of recruitment (p_r); and recruit size distribution ($R(z')$), which describes the probability density of recruit size z' at year $t+1$:

$$n(t+1, z') = \int [s(z)G(z', z) + s(z)p_b(z)b(z)p_r R(z')]n(t, z)dz$$

The IPMs that included crowding predict body size and crowding distributions at year $t+1$ ($n(t+1, z', q')$) given the body size and crowding distribution at year t ($n(t, z, q)$). These models are extensions of IPM_{size-only} and have the same kernel components with modifications for growth ($G(z', z, q)$), which describes the probability density for an individual of size z and crowding q at year t to obtain size z' at year $t+1$; probability of reproducing ($p_b(z, q)$); crowding distribution of established individuals ($C_I(q')$), which describes the probability density of

crowding q' at year $t+1$ for established individuals; and crowding distribution of recruits ($C_0(q')$), which describes the probability density of crowding q' at year $t+1$ for recruits:

$$n(t+1, z', q') = \iint [s(z)G(z', z, q)C_1(q') + s(z)p_b(z, q)b(z)p_r R(z')C_0(q')]n(t, z, q)dzdq$$

For numerical implementation, each IPM was discretized into a four-dimensional matrix (100 x 100 for z and 50 x 50 for q), with z ranging between 0.1 and 10 mm and q ranging between 0.0 and 1.0. In the field, we observed barnacles up to 7.63 mm. In the IPMs, we allowed barnacles to reach up to 10 mm to prevent eviction of large individuals from the model (Williams et al. 2012; Ellner et al. 2016). To avoid unfounded extrapolation of vital rates at large sizes, we enforced a ceiling on vital rates (Ellner et al. 2016): all barnacles > 6 mm had the same survival, growth, probability of reproducing, and fecundity as 6 mm barnacles.

Our IPMs assume that the barnacles in this study come from one closed population. Barnacle populations are typically considered open because barnacles have larval stages with broad dispersal potential (Strathmann 1987), although somewhat restricted dispersal has also been documented (e.g., *B. glandula* in central California: (Sotka et al. 2004). In a companion study, we found that crowding had a positive effect on barnacle probability of reproduction during the summer (Supplement 10; King and Sebens in prep). Assuming a closed population allowed us to examine the potential consequences of this effect on population dynamics.

Population model parameterization using vital rates

Survival

We estimated probability of survival using a linear regression against body size. The intercept and slope coefficients of the regression were parameterized using the respective coefficients from the generalized linear model for field survival data (see above). Probability of

survival was back-transformed from logit to linear scale. Since crowding did not affect survival (see Results), the same survival parameter values were used for all IPMs.

Growth

We estimated the probability density function of growth using a normal distribution described by the expected growth (mean, \hat{g}) and the variation (σ_g) around that mean. For IPM size-only, the mean was estimated using a linear regression against body size where the intercept and slope coefficients were parametrized using the respective coefficients from the linear model for field growth data with crowding terms excluded. For IPMs with crowding included, the same procedure was used but using coefficients from the linear model for field growth data with crowding terms included (main and interaction effects). In both cases, intercept and slope coefficients were for fixed effects only. Variation (σ_g) was estimated as the standard deviation of the residuals of each model. Our approach to modeling growth allowed operculum length to increase or decrease with each time step. In reality, opercula do not shrink. We used this approach because preventing shrinkage resulted in IPMs with extremely high population growth rates ($\lambda \sim 10$) and right-shifted size distributions inconsistent with field observations. To summarize, we estimated probability density functions of growth as $G(z', z) = Normal[z' | \hat{g}(z), \sigma_g]$ and $G(z', z, q) = Normal[z' | \hat{g}(z, q), \sigma_g]$ for IPMs without and with the effects of crowding, respectively.

Probability of reproducing

We estimated the probability of reproducing using a linear regression against body size or against the additive effects of body size and crowding as appropriate for the IPM. The intercept

and slope coefficients of the regressions were parameterized using data from our companion study (Supplement 10; King and Sebens in prep). The companion study built generalized linear models of the probability of being reproductive based on field observations made in summer 2017. Since the metric for size in this field data was shell volume, we first transformed volume to operculum length using a linear regression (Supplement 11). In using this field data, we make two assumptions. First, that a reproductive barnacle (has yolky ovarian tissue) will successfully reproduce. Note that *B. glandula* is hermaphroditic (Strathmann 1987) and thus we considered all individuals rather than just females as is common for dioecious systems. Second, that the probability of reproducing based on summer observations applies to our IPMs for year-long time steps. Probability of reproducing was back-transformed from logit to linear scale.

Fecundity

We estimated fecundity as a power function of body size as determined by Strathmann et al. (1981) for *B. glandula* from San Juan Island and other sites in the region: $b(z) = 0.147z^{2.74}$.

Probability of recruitment

Probability of recruitment in this study includes the processes occurring to an individual barnacle from its release as a larva into the water column to being censused as a recruit in the intertidal benthos. We estimated probability of recruitment as the ratio between the total number of recruits and total larval production (Ellner et al. 2016). Total number of recruits was estimated as the average number of new individuals per quadrat at site RT3 ($N = 3$ quadrats; mean \pm SE, 599 ± 46.9) in the July 10, 2018 photos, when *B. glandula* grew large enough (~1-2 mm) to be identified as such. We used site RT3 because most (~75%) of the previous year's cohort had

been naturally removed over the course of the year, allowing us to reliably identify individuals in these quadrats as new recruits. This site had higher recruitment than other sites (100s vs. 10s of recruits) and thus represents the estimated upper bound of total number of recruits for the entire population. Total larval production was estimated as the sum of the fecundity of all individuals from all sites that survived the year. Our goal was not to find the true value of the probability of recruitment, which is difficult for organisms that broadcast spawn, but to garner reasonable estimates to allow comparisons between the IPMs.

Recruit size distribution

We estimated the probability density function of recruit size using a normal distribution described by the expected size (mean, $\hat{\phi}$) and the variation around that mean (σ_{ϕ}): $R(z') = \text{Normal}[z' | \hat{\phi}(z'), \sigma_{\phi}]$ (Supplement 12). The mean and variation were parameterized with maximum likelihood estimates based on the observed size distribution of all recruits at site RT3 in the July 10, 2018 photos. All fits of distributions to field data in this study were conducted using the R package *fitdistrplus* (Delignette-Muller and Dutang 2015). The body sizes of recruits in our models did not depend on the sizes of established individuals in the population.

Field crowding distributions

We estimated the probability density functions of crowding for IPM_{cFF} using beta distributions described by two shape parameters. Beta distribution was chosen to accommodate the bounds of crowding: $[0, 1]$. The shape parameters were parameterized with maximum likelihood estimates based on field data (Supplement 12). For established individuals, this was

based on the observed crowding distribution of all individuals. For recruits, this was based on individuals observed at site RT3.

Theoretical crowding scenarios

To understand the conditions under which ontogenetic shifts in intraspecific interactions can affect barnacle population dynamics, we examined the effects of theoretical crowding scenarios using our IPMs. Conducting a field experiment to manipulate individual crowding was logistically prohibitive; we used our modeled populations as the ‘experimental system’ and the crowding scenarios, chosen *a priori*, as the ‘treatments’. A full factorial design varying crowding distribution (uniform, low, high) for both established individuals and recruits led to nine theoretical scenarios (Supplement 13). The uniform distribution was chosen as a control: with all levels of crowding equally likely, any effects on vital rates that differ across ontogeny would ‘average out’. The low and high theoretical distributions were chosen to be extreme representations of the low and high distributions that we observed in the field (Supplement 13). The scenarios included cases with different distributions for recruits and established individuals. Biologically, changes in crowding distributions across size can occur in either direction. For example, a large settlement event can result in high crowding among recruits. As the recruits grow, they may undergo self-thinning (Hughes and Griffiths 1988), which results in lower crowding at larger sizes. Conversely, recruits may experience low crowding because of low settlement or mortality soon after settlement (e.g., predation). The survivors may then develop and experience higher crowding at larger sizes as they grow into one another.

We estimated probability density functions of crowding for each theoretical scenario using beta distributions. For a uniform distribution, the shape parameters of the beta distribution

(α and β) were both set to 1, leading to equal relative likelihood (10%) for all levels of crowding. For a low crowding distribution, $\alpha = 2$ and $\beta = 50$, leading to a relative likelihood of 96% that crowding is 0.0-0.1 and 99% for 0.0-0.2. For a high crowding distribution, $\alpha = 50$ and $\beta = 2$, leading to a relative likelihood of 96% that crowding is 0.9-1.0 and 99% for 0.8-1.0.

Analysis of population dynamics

We analyzed IPM population dynamics in two steps. First, we compared the asymptotic population growth rates (λ) of each model. Then, for models with the largest difference in λ , we compared their stable size distributions and conducted perturbation analyses. Asymptotic population growth rates were the dominant eigenvalues of each IPM estimated by iteration (Ellner et al. 2016). We estimated uncertainty in λ using 95% confidence intervals constructed by bootstrapping (Caswell 1989; Ellner et al. 2016). We report normal confidence intervals (normality checked visually); other types of intervals were similar to within 0.01. Each IPM was run 1,000 times. Each run drew a random permutation of the survival and growth dataset with replacement. Since only the survival and growth data were bootstrapped, the confidence intervals exclude uncertainties in the other vital rates. Bootstrapping was conducted using the R package *boot* (Canty and Ripley 2019). The significance of the largest difference in λ was evaluated using a Welch's t-test (two-sided and without assuming equal variance) on the bootstrapped values of λ .

Stable size distributions (right eigenvectors corresponding to dominant eigenvalues) for the two models with the largest difference in λ were calculated by iteration (Ellner et al. 2016). These size distributions were dominated by individuals < 2 mm (see below). The shapes of these

distributions appeared different for individuals > 2 mm. To test this, we used a Kolmogorov-Smirnov statistic.

For the two IPMs with the largest difference in λ , we then conducted perturbation analyses to examine the elasticity of population growth rate to the transitions of individuals between states (Caswell 1989). Individuals in the model occupy some state (a given combination of z and q) which change (transition) to a new state at each time step. The likelihood of transitions depends on individual vital rates. In general, elasticity is “the fractional change in the response relative to the fractional change in the quantity being perturbed” (Ellner et al. 2016). Since matrices in four-dimensions (z to z' and q to q') are difficult to visualize, we visualized the total elasticity of all transitions from a given state to all other states (Ellner et al. 2016). Total elasticity in this study can be interpreted as the proportional sensitivity of the population growth rate to a change in abundance of individuals with a particular state. For example, if the number of barnacles with a given z and q increases by 10%, what is the corresponding percentage change in λ ?

Results

Survival and growth in the field

Body size had a small positive effect on the survival of *B. glandula* (Fig. 2); no crowding or interaction effects were detected (Table 1). Size, however, explained little of the variation in survival ($R^2 = 0.043$). The direction of the crowding effect on barnacle growth (final size) was mediated by initial body size (Table 1; Fig. 2). At 1 mm, crowding had a negative effect: crowding = 0.8 (almost completely surrounded) decreased a barnacle’s average growth by ~50% compared to crowding = 0 (completely isolated). At 6 mm, however, crowding had a slightly

positive effect on barnacle growth. Growth rate showed a similar response to size and crowding (Supplement 5).

IPM parameterization

Based on the year-long field results, the vital rate model for survival in the IPMs included only the effect of size (Table 2). The vital rate model for growth (final size) included the main and interaction effects of both size and crowding. Based on findings in a companion study (King and Sebens in prep), the vital rate model for probability of reproducing included the main effects of size and growth (Table 2; Supplement 10). Parameter values of the other components of the IPMs are available in Supplement 14.

Comparison of population growth rates

Population growth rates estimated by IPMs were comparable to field estimates (Fig. 3), which varied across sites (0.61-3.73; Supplement 3). Incorporating field-parameterized crowding did not change population growth rate; $IPM_{\text{size-only}}$ and IPM_{cFrF} estimated nearly identical values of λ . Theoretical crowding scenarios, however, changed estimates of population growth (Fig. 3; Supplement 3). The effects of crowding were dependent on both the type of crowding distribution and the ontogenetic stage. Compared to a uniform distribution, low crowding in recruits and high crowding in established individuals tended to increase λ . Conversely, high crowding in recruits and low crowding in established individuals tended to decrease λ . Accordingly, the largest difference in population growth rate was between IPM_{cLrH} (estimate [95% confidence interval]; 0.94 [0.75, 1.15] and IPM_{cHrL} (1.34 [1.09, 1.61]). Although the confidence intervals overlapped by 0.06, these estimates can be considered statistically different

(Austin and Hux 2002; Cumming 2009). This is supported by the t-test, which found a significant difference between the two estimates ($t = -76.167$, $DF = 1829.9$, $P < 0.001$).

Comparison of stable size distributions of IPM_{eLrH} and IPM_{eHrL}

The stable states of IPM_{eLrH} and IPM_{eHrL} were both dominated by recruits but had different distributions of larger individuals (Fig. 4). The distributions of recruits were similar between the two IPMs ($D = 0.158$; $P = 0.978$). However, the distributions of established individuals > 2 mm differed ($D = 0.222$; $P = 0.036$) in that the stable population of IPM_{eLrH} had more barnacles ~ 2 -3 mm while the stable population of IPM_{eHrL} had more barnacles ~ 3 -4 mm. The estimates of stable size distributions were comparable to the $t + 1$ distribution observed in the field (Fig. 4).

Perturbation analyses of IPM_{eLrH} and IPM_{eHrL}

The population growth rates of IPM_{eLrH} and IPM_{eHrL} were elastic to the transitions of both recruits and established individuals (Fig. 5). The λ of IPM_{eLrH} was elastic to recruits with high crowding and established individuals with low crowding, and vice versa for IPM_{eHrL} . This simply reflects the crowding scenario of each model. What was not predetermined, however, was how the elasticities of established individuals differed by size in the two models. The population growth rate of IPM_{eHrL} was elastic to larger individuals (3-8 mm) compared to IPM_{eLrH} (2-6 mm).

Discussion

Understanding the consequences of ontogenetic shifts in biotic interactions may be important for improving predictions of how ecological communities respond to global change (Yang and Rudolf 2010). While a variety of ontogenetic shifts in biotic interactions have been documented (Werner and Gilliam 1984; de Roos et al. 2003; Yang and Rudolf 2010; de Roos and Persson 2013), we lack information on the population-level consequences of shifts within a trophic level (Miller and Rudolf 2011; le Roux et al. 2013). In this study, we tested two hypotheses. First, that ontogenetic shifts in intraspecific interactions between *B. glandula* occur at the year-long scale. Second, that ontogenetic shifts in intraspecific interactions affect the population dynamics of *B. glandula*. We found that, consistent with our hypotheses, the direction of intraspecific interactions on barnacle growth shift from negative to positive across ontogeny in the field at the year-long scale. This shift affected population dynamics. Populations modeled with theoretical crowding distributions showed differences in population growth rates consistent with the observed ontogenetic shifts. The differences were mediated by changes in the population size distribution. This study highlights the importance of considering how the effects of ontogenetic shifts in biotic interactions propagate up to population dynamics and presents a framework in which to examine this process.

Sign shifts in interactions across ontogeny

Interactions between sessile organisms often depend on the tension between competition and facilitation (Callaway and Walker 1997; Miriti 2006; Schiffrers and Tielbörger 2006; Álvarez-Yépez et al. 2014). Acorn barnacles are a classic example of space competition (Connell 1961a, b; Dayton 1971); however, they also exhibit facilitation through habitat amelioration (Lively and Raimondi 1987; Bertness 1989; Bertness et al. 1999; Leonard et al. 1999). One

framework for predicting the balance of these interactions is the Stress Gradient Hypothesis, which posits that the sign and/or strength of biotic interactions depend on abiotic conditions; positive interactions are predicted to increase with environmental stress (Bertness and Callaway 1994). However, abiotic conditions do not account for all of the variation in biotic interactions; some of the unexplained variation is attributable to ontogenetic controls (Miriti 2006; He et al. 2013; de Nesnera 2016). In this study, we found that the balance between competition and facilitation in *B. glandula* also varies along an ontogenetic axis at the year-long scale (Fig. 2). Based on our companion study, the observed transition in intraspecific interactions between barnacles from negative to positive across ontogeny likely involves thermal stress (King and Sebens in prep). At smaller sizes, crowding has overall negative effects due to size-asymmetric competition against larger neighbors (Wetthey 1983; King and Sebens in prep). At larger sizes, crowding has overall positive effects due to the habitat ameliorating effects of neighbors under stressful warm conditions (King and Sebens in prep). We are aware of only a few other studies that explicitly examine such shifts in sessile marine organisms (barnacles, furoid algae, and mussels: Kordas and Dudgeon 2009, 2011; de Nesnera 2016; King and Sebens in prep). Possibly, the low representation in the marine literature (at least compared to terrestrial plants) does not indicate lack of generality but lack of attention. For example, one study on the interaction between eelgrass adults and seedlings found a shift from negative to positive interactions with increasing stress (Yang et al. 2016), which leads to the question of how this shift may also change across ontogeny, e.g., do adults under high stress have net positive interactions on each other?. Given the importance of understanding interactions among sessile marine organisms such as foundation species (Angelini et al. 2011), adding the additional axis of

ontogeny may be a worthwhile direction for future studies of the stress gradient hypothesis (Callaway and Walker 1997; Miriti 2006; Schiffers and Tielbörger 2006; He et al. 2013).

The results of this study differed from our companion study. In this study, we observed an ontogenetic shift for growth rate and no effect of crowding for survival (Fig. 2). In a companion study, we observed a flipped pattern: there was an ontogenetic shift for survival and no effect of crowding on growth (King and Sebens in prep). These results can be reconciled by considering the differences in the time frames of each study. This study measured survival and growth over one year while the companion study measured over one summer. For barnacles at our study sites, the potential for thermal stress is strongest during the summer, when afternoon low tides coincide with warm temperatures (Helmuth et al. 2002). It follows that the effects of habitat amelioration may be stronger during the summer and weaker during other parts of the year (Stress Gradient Hypothesis: Bertness and Callaway 1994). If so, it is possible that the signal of the sign shift in barnacle survival observed during the summer was lost because barnacle survival was less sensitive to crowding during the rest of the year. The weak effect of body size on survival was likely because our initial sampling occurred after the initial high-mortality phase of recent settlers (Gosselin and Qian 1997). For growth, competition and facilitation were probably acting during the summer, but their effects were only detected after a full year of growth by the surviving individuals.

Population consequences of sign shifts in interactions across ontogeny

Our results support the hypothesis that ontogenetic shifts in intraspecific interactions affect the population dynamics of *B. glandula*. Under theoretical crowding distributions, estimated population growth rates tended to increase with low crowding in recruits and high

crowding in established individuals (Fig. 2). This pattern is consistent with the ontogenetic sign change in the effect of crowding on barnacle growth (Fig. 2). Recruits in the IPMs were generally < 2 mm (Fig. 3; Supplement 12). At these smaller sizes, the field data indicated that growth decreases with crowding. Accordingly, IPMs in which recruits experienced high crowding had slightly lower population growth rates (e.g., IPM_{eUrL} vs. IPM_{eUrH}). Established individuals in the IPMs were generally > 2 mm (Fig. 3). At larger sizes, the field data indicated that growth increases with crowding. Accordingly, IPMs in which established individuals experienced high crowding had slightly higher population growth rates (e.g., IPM_{eLrU} vs. IPM_{eHrU}). Shifts in population growth matched the ontogenetic shifts in individual growth.

The mechanism by which the ontogenetic shift propagated up to population dynamics is a change in the population size distribution. This is clearest by contrasting the stable size distributions of IPM_{eLrH} and IPM_{eHrL} (Fig. 4), which exhibited the lowest and highest population growth rates, respectively. The stable states of the two models differed in the size distribution of larger individuals (>2 mm): IPM_{eLrH} had more individuals 2.0-3.0 mm whereas IPM_{eHrL} had more individuals ~ 3.0 -4.5 mm. This pattern is consistent with the ontogenetic shift observed in the field (Fig. 2). In IPM_{eLrH} , recruits experienced high crowding, which negatively affected growth. These recruits only grew to 2.0-3.0 mm. In contrast, the growth of recruits in IPM_{eHrL} was increased by low crowding, allowing them to reach larger sizes. Since larger barnacles had higher reproductive values (Supplement 15), higher numbers of larger individuals led to more offspring, which in turn increased population growth. It is possible that higher survival at larger sizes (Fig. 2) also contributed to increases in population growth rates.

Given their relatively low abundance in the stable populations, it may be surprising that larger individuals impacted population dynamics. Perturbation analysis supports their impact

(Fig. 5). The total elasticities of both IPM_{eLrH} and IPM_{eHrL} indicated high elasticity of population growth rate to smaller individuals, which simply reflects the high abundance of recruits in the populations. More edifying is that larger individuals had comparable elasticities; despite relatively low abundance, the fates of larger individuals had appreciable influence over the population growth rates of both models. The difference to note between the models is the size ranges at which larger individuals had high elasticities. Whereas the population growth rate of IPM_{eLrH} was elastic to individuals of 2-6 mm, population growth rate of IPM_{eHrL} was elastic to individuals of 3-8 mm. This is consistent with the stable size distributions of the models, supporting the idea that a change in the distribution of larger established individuals driven by differential growth of recruits under different crowding scenarios impacted population growth rate.

Crowding modifies the predominant effect of size

Body size is one of the fundamental drivers of variation in vital rates and population dynamics (Peters 1983; Ebenman and Persson 2012). Our population models found a predominant effect of size on the population dynamics of barnacles, with a smaller but important effect of crowding: $IPM_{size-only}$ and IPM_{eFrF} predicted nearly identical population growth rates (Fig. 3). That the model predictions were similar to each other makes sense when considering the crowding distributions that parameterized IPM_{eFrF} . Crowding distributions observed in the field combined across all sites were right skewed, tending towards low levels of crowding for both established individuals and recruits (Supplement 12). Since low crowding had opposite effects on growth in established individuals and recruits (Fig. 2), it is possible that those effects ‘canceled out’ at the population level, resulting in zero net effect on population dynamics. In this

case, including crowding in the population model did not improve our ability to predict field population growth rates. Nevertheless, our models parameterized by theoretical crowding scenarios suggest that shifts in the effect of crowding across ontogeny can have appreciable impact on the population dynamics of barnacles.

Three limitations of this study provide avenues for future research. First, our population models were spatially implicit. We assumed that barnacles always had free space available for recruitment and growth, which does not apply under conditions of high density (Roughgarden et al. 1985; Raimondi 1990; Hyder et al. 2001). Incorporating space availability can reveal how the effects of local crowding on population dynamics observed in this study are modulated by population density. Second, barnacle populations in this study were modeled as closed. In some cases, recruit supply can overshadow post-recruitment controls on population dynamics (Gaines and Roughgarden 1985; Menge 1991, 2000; Connolly and Roughgarden 1999). It would be useful to how annual variation in barnacle recruit supply (Caffey 1985; Raimondi 1990) affects how ontogenetic shifts propagate up to population dynamics. Third, future studies should extend our models to explicitly examine the effects of temperature. The effects of ontogenetic shifts in biotic interactions can depend on environmental context (e.g., Schiffers and Tielbörger 2006; le Roux et al. 2013). Our companion study indicated that environmental temperature affected barnacle survival and growth in the field during the summer (King and Sebens in prep). Examining how the complex interplay between the effects of body size, crowding, and temperature on barnacle vital rates scale up to population dynamics could provide useful information on how populations of sessile ectotherms respond to global temperature change.

Conclusions

Extrapolating the behavior of natural systems from lower to higher levels is one of the challenges of ecology (Levin 1992). Addressing this challenge is especially important in the context of predicting the consequences of global change, which often acts on the individual but has consequences of interest (e.g., ecosystem services) at higher levels of organization (Levin 1992). Evidence suggests that body sizes are decreasing with global change (Sheridan and Bickford 2011). Understanding the causes and consequences of changes in body size is a research priority (Sheridan and Bickford 2011; Ohlberger 2013). Our results suggest that, for barnacles, decreased size will affect vital rates through not only direct size-dependent effects but also indirect effects mediated by crowding. These indirect effects may alter the population size distribution, which in turn impacts population growth rate. We have demonstrated a framework that links individual trait and crowding effects to population consequences. This framework can be applied to other sessile, ectotherm systems of interest (e.g., mussels or plants) to investigate where, when, and how ontogenetic shifts in biotic interactions scale up to population dynamics.

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Tables

Table 1. Results of statistical models testing how body size and crowding affect *Balanus glandula* survival and growth

Effect	Probability of survival <i>N</i> = 351 from 5 sites $R^2 = 0.043$			Growth (final size) <i>N</i> = 94 from 5 sites $R^2_m = 0.579$		
	DF	χ^2	<i>P</i>	DF	χ^2	<i>P</i>
Size (initial)	1	5.297	0.021	1	122.914	<0.001
Crowding	1	3.119	0.077	1	2.468	0.116
Size × Crowding	1	0.151	0.698	1	17.161	<0.001

Sample size (*N*) refers to number of individuals. R^2_m refers to marginal R^2 , which indicates the variance explained by fixed effects. Bold indicates $P < 0.05$.

Table 2. Regression coefficients of survival, growth, and probability of reproducing used in *Balanus glandula* population models

Model	Survival		Growth				Probability of Reproducing		
	β_0	β_z	β_0	β_z	β_q	β_{zq}	β_0	β_v	β_q
IPM _{size-only}	-1.73	0.30	2.21	0.73	n/a	n/a	-4.55	0.01	n/a
IPMs with crowding	-1.73	0.30	2.98	0.48	-2.43	0.71	-5.38	0.01	2.24

IPM stands for integral projection model. IPM_{size-only} does not include a crowding term, hence parameters for modeling crowding are not applicable (n/a). Subscripts of β indicate the type of coefficient: intercept (0), slope for body size measured as operculum length (z), slope for crowding (q), interaction effect between size and crowding (zq), and slope for body size measured as shell volume (v). Values for growth are for fixed effects. Values of other population model parameters are available in Supplement 10.

Figure captions

Fig. 1 Summary of the life cycle of *Balanus glandula* modeled by the integral projection models that included both body size (z) and crowding (q) as state variables. The models began with a field-observed distribution of established individuals each of a certain size and crowding state, $n(t, z, q)$, and proceeded in one-year time steps. In each time step, each established individual (large blue circle) had a probability of survival $s(z)$; the survivors then grew with probability density $G(z', z, q)$ and reproduced. The population was modeled as closed: each individual had a probability of reproducing $P_b(z, q)$; those who reproduced generated offspring based on their fecundity $b(z)$. The offspring (small blue circles) recruited with probability P_r , size distribution $R(z')$, and crowding distribution $C_0(q')$, joining the established individuals with crowding distribution $C_I(q')$ to form the distribution of established individuals at the next time step, $n(t+1, z', q')$. Individuals in the models were separated into established individuals and recruits, but the vital rates of all individuals were size structured.

Fig. 2 *Balanus glandula* a) probability of survival as a function of body size and b) growth (final size) as a function of initial body size and crowding in the field after 327-340 days. Lines indicate model predictions based on observations of a) 351 individuals from five sites and b) 94 individuals from five sites. Shaded areas indicate 95% confidence intervals, with darker regions indicating overlap. Points indicate observations, with darker colors indicating higher crowding. Crowding is a continuous variable and we visualize predictions for two levels: 0 = isolated and 0.8 = 80% surrounded. Thin gray line indicates a 1:1 line of zero growth.

Fig. 3 Population growth rates estimated using field photos and integral projection models (IPMs). Field estimates are based on the ratio of abundances in photos after one year, with white points indicating means across all sites and quadrats and bars indicating standard errors ($N = 8$). IPM estimates are asymptotic population growth rates, with black points indicating estimates and bars indicating bootstrapped 95% confidence intervals. State variables in IPMs included only size (size-only) or both size and crowding (others). Models including crowding had different parameterizations for the distribution of crowding in established individuals (e) and recruits (r): field (F), uniform (U), low (L), or high (H). Asterisks indicate $P < 0.001$ for the comparison between IPM_{eLrH} and IPM_{eHrL} . Thin gray line indicates zero growth.

Fig. 4 Stable size distributions of IPM_{eLrH} (thin line) and IPM_{eHrL} (thick line). The P -value is for a comparison of the size distributions estimated by the two models for barnacles 2 mm and greater (indicated by dashed lines). Gray bars indicate the size distribution observed in the field (all sites combined) at the end of the study.

Fig. 5 Total elasticities of IPM_{eLrH} and IPM_{eHrL} . Total elasticity refers to the summed elasticity of all transitions by individuals in the model from a given state (combination of size and crowding) to all other states. Shading and contour lines indicate magnitude of elasticity, with lighter colors and higher numbers indicating higher elasticities. Note break in y-axis: areas not shown have very low elasticities equal to the darkest gray color shown in these plots.

Fig. 1

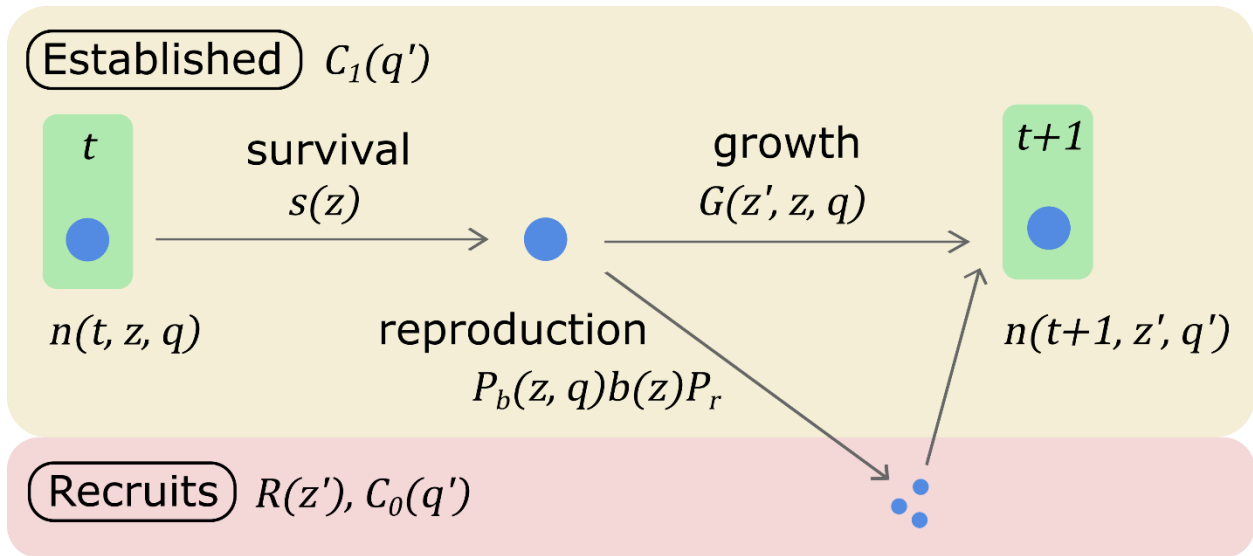


Fig. 2

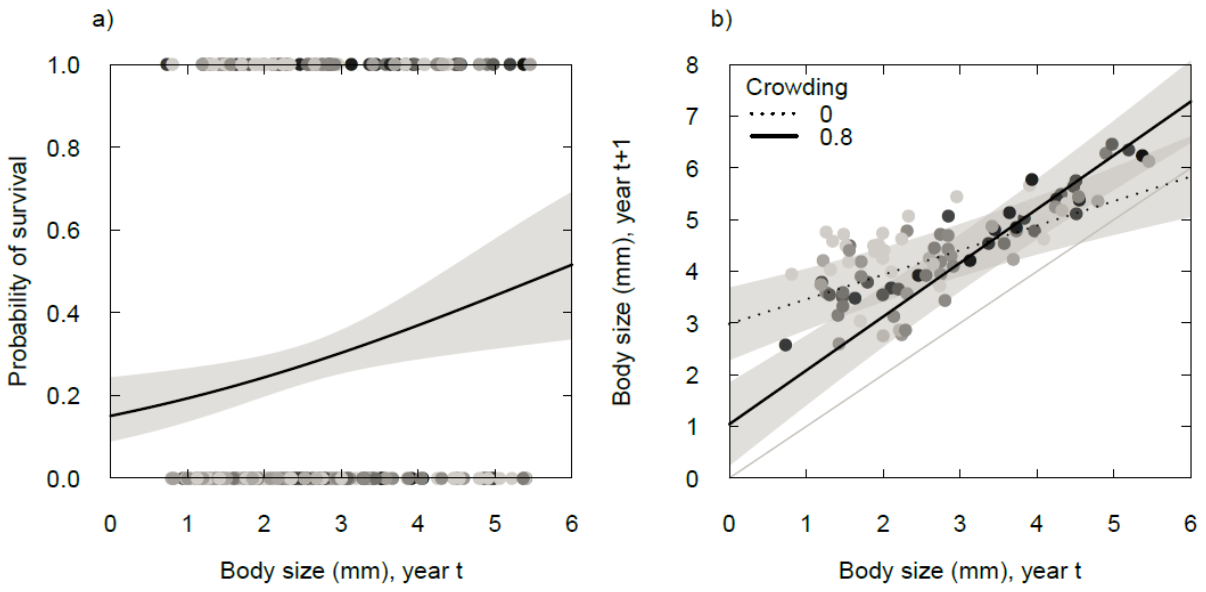


Fig. 3

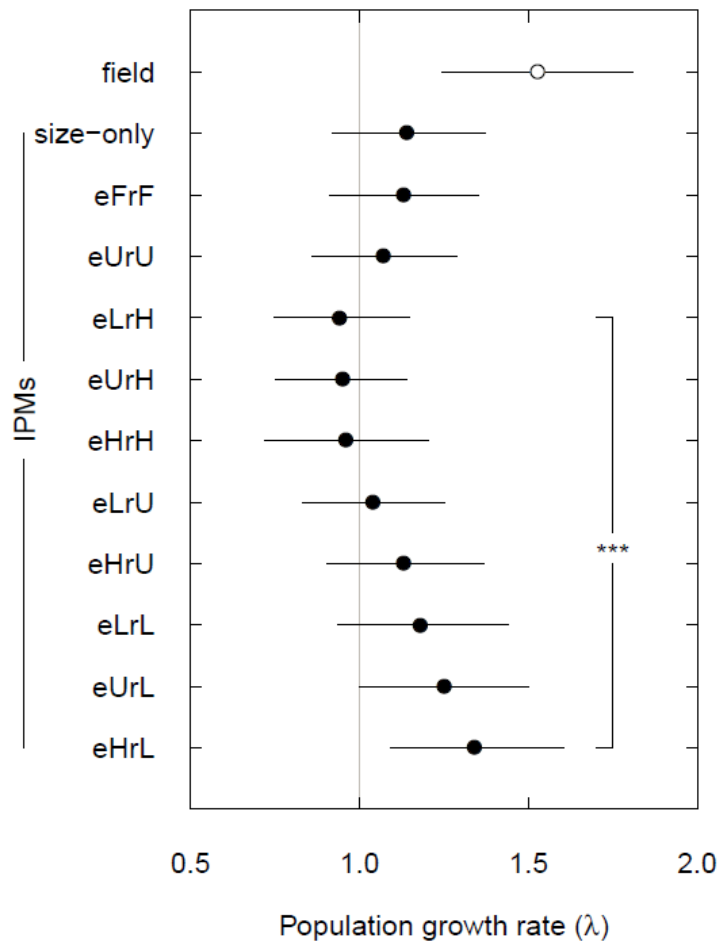


Fig. 4

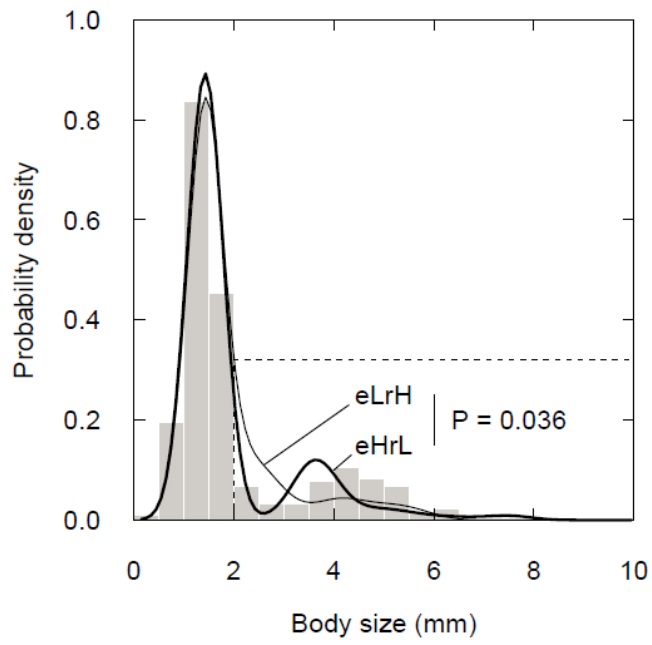
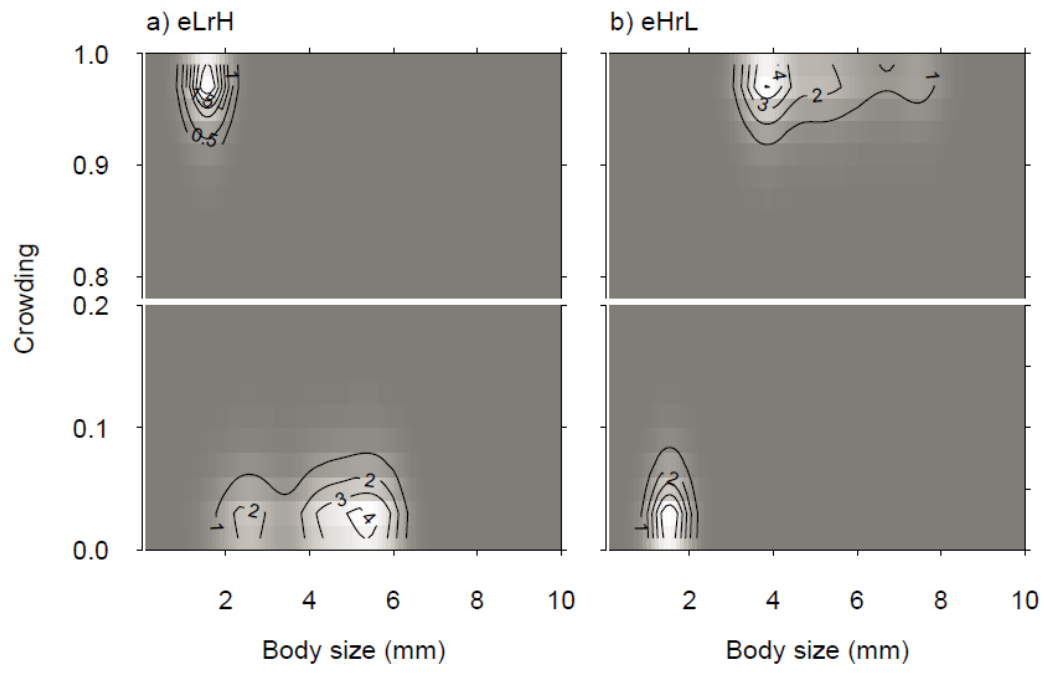


Fig. 5



Supplement

Title:

Ontogenetic shifts in intraspecific interactions alter population dynamics in a sessile ectotherm

Author names and affiliations:

William King^{a,b} and Kenneth P. Sebens^{a,b,c}

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Supplement 1

Study locations and sites on San Juan Island, WA, USA. Duration refers to the number of days between the first and final photos used for analyses of survival and growth.

Location	Site	Coordinates N/W	Aspect	Tidal elevation (m above MLLW)	Duration
Reuben Tarte	RT2	48°36'45.0"/123°05'51.9"	SW	1.52	327
	RT3	48°36'42.1"/123°05'55.0"	NE	0.94	327
Colin's Cove	CC2	48°32'53.6"/123°00'24.1"	SW	1.12	339
Friday	FH1	48°32'45.4"/123°00'42.1"	NE	1.31	340
Harbor Labs	FH2	48°32'45.4"/123°00'42.1"	SW	1.31	340

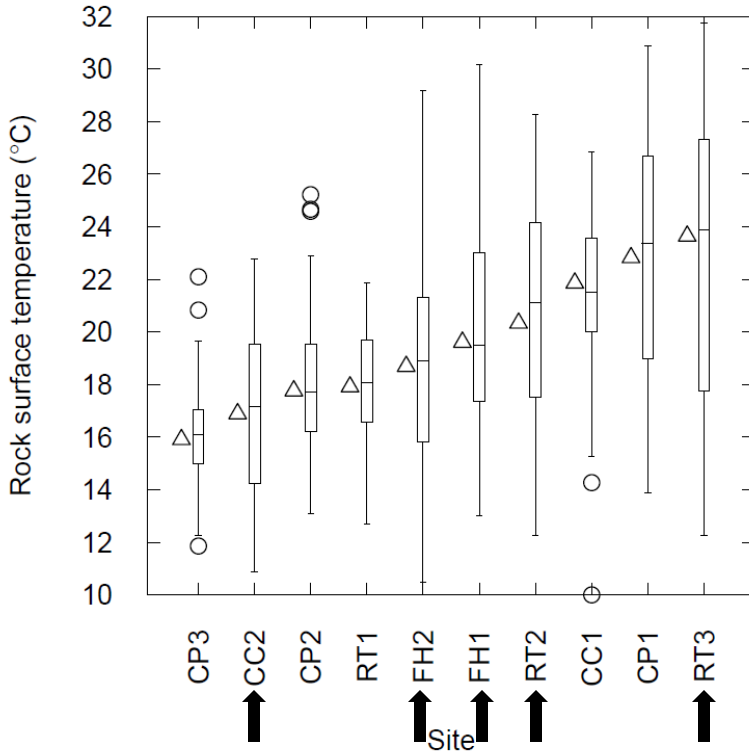
See Dethier and Williams (2009) for general location descriptions. The Friday Harbor Labs location was at the “old FHL pier”, 290 m west of Pumphouse described in Dethier and Williams (2009).

References:

Dethier MN, Williams SL. (2009). Seasonal stresses shift optimal intertidal algal habitats. *Mar Biol* 156:555–567. doi: 10.1007/s00227-008-1107-8

Supplement 2

Information in this supplement is taken from a companion study (King and Sebens in prep); sites relevant to this study are indicated by the arrows below the x-axis. Field site low tide temperatures during June-August 2017 measured hourly by iButtons ($N = 15,360$). Triangles indicate grand mean low tide temperature for each site. Box-and-whisker plots indicate the range (ends of whiskers), median (center horizontal lines in boxes), first and second quartiles (horizontal box edges), and outliers (circles) of all low tide temperature measurements.



Supplement 3

Population growth rates estimated using field photos and IPMs. Duration indicates number of days between initial and final photos. Quadrats for which initial photos were not available are marked as “n/a”.

Type	Site	Quadrat	Name	λ	95% CI	Duration
Field	CC2	H		1.57		341
	FH1	H		3.73		340
	FH1	L		1.76		340
	FH1	M		1.27		340
	FH2	H		1.53		340
	FH2	M		0.61		340
	RT2	H		0.89		327
	RT2	L		n/a		n/a
	RT2	M		n/a		n/a
	RT3	H		0.86		396*
	RT3	L		n/a		n/a
	RT3	M		n/a		n/a
	IPM			Size-only	1.14	[0.92, 1.37]
			eFrF	1.13	[0.91, 1.35]	
			eUrU	1.07	[0.86, 1.29]	
			eLrH	0.94	[0.75, 1.15]	
			eUrH	0.95	[0.75, 1.14]	
			eHrH	0.96	[0.72, 1.20]	
			eLrU	1.04	[0.83, 1.25]	
			eHrU	1.13	[0.91, 1.37]	
			eLrL	1.18	[0.94, 1.44]	
			eUrL	1.25	[1.00, 1.50]	
		eHrL	1.34	[1.09, 1.61]		

*Used later photos to be able to identify *B. glandula* recruits (extremely small individuals are indistinguishable in photos from other species).

Supplement 4

Equations describing statistical models with full fixed effects after random effects have been selected (Supplement 6). An estimated term (α or β) with subscript j indicates that we allowed the term to vary across j (e.g., the random intercept $\alpha_j = \alpha + u_j$, where u is the random effect of j).

We modeled probability of survival s for barnacle i in site j following a binomial error distribution with logit link:

$$\text{logit}(s_{ij}) = \beta_{0j} + \beta_z \text{Size}_{ij} + \beta_q \text{Crowding}_{ij} + \beta_{zq} \text{Size}_{ij} \text{Crowding}_{ij}$$

and we modeled final size g for barnacle i in site j following a Gaussian error distribution with identity link:

$$g_{ij} = \beta_{0j} + \beta_z \text{Size}_{ij} + \beta_q \text{Crowding}_{ij} + \beta_{zq} \text{Size}_{ij} \text{Crowding}_{ij}$$

where, for both models, β_0 is an estimated intercept, β_z , β_q , and β_{zq} are estimated slopes, Size is initial operculum length, and Crowding is individual crowding.

Supplement 5

To check that slight differences in growth durations (Supplement 1) did not confound our conclusions of how final size responded to the interaction effect between initial size and crowding, we also examined growth rate (change in size per day) as a response variable. We used the same statistical framework as for final size, modeling growth rate following a Gaussian error distribution with identity link and a random effect of site.

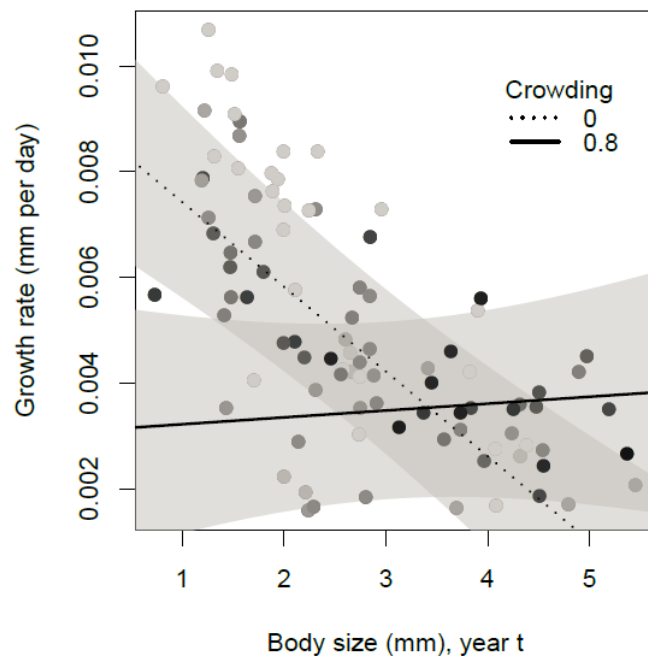
We found results that lead to similar conclusions as the analysis for final size. Crowding and body size had an interaction effect on growth rate, with a negative effect of crowding at smaller sizes shifting to a positive effect at larger sizes.

Results of statistical model testing how body size and crowding affect *Balanus glandula* growth rate (mm per day)

Effect	DF	χ^2	<i>P</i>
Size (initial)	1	15.447	<0.001
Crowding	1	2.438	0.118
Size \times Crowding	1	17.470	<0.001

Sample size is 94 individuals from 5 sites. $R^2 = 0.538$. Bold indicates $P < 0.05$.

Balanus glandula growth rate as a function of body size and crowding in the field after 327-340 days. Lines indicate model predictions based on observations of 94 individuals from five sites. Shaded areas indicate 95% confidence intervals, with darker regions indicating overlap. Points indicate observations, with darker colors indicating higher crowding. Crowding is a continuous variable and we visualize predictions for two levels: 0 = isolated and 0.8 = 80% surrounded.



Supplement 6

Selection of random effects in statistical models for field survival and growth using lowest AIC and BIC values (bold). Location/site indicates site nested within location. Check mark (√) indicates the random effects structure that was selected.

Response	Random effect	AIC	BIC	Choice
Survival	None	411.388	426.842	√
	Site intercept	412.012	431.330	
	Site intercept and slope for crowding	415.727	442.772	
	Site intercept and slope for body size	415.894	422.939	
	Location/site intercept	414.012	437.193	
	Location/site intercept and slope for crowding	421.729	460.366	
	Location/site intercept and slope for body size	429.894	460.530	
Growth (final size)	None	150.192	162.962	
	Site intercept	133.215	148.538	√
	Site intercept and slope for crowding	135.583	156.014	
	Site intercept and slope for body size	133.877	154.308	
	Location/site intercept	133.472	151.349	
	Location/site intercept and slope for crowding	140.205	168.298	
	Location/site intercept and slope for body size	138.652	166.745	

Supplement 7

We modeled the probability of survival following a binomial error distribution with logit link (no random effects; Supplement 4 and 6). Based on Bolker et al. (2009), both Wald χ^2 and Z tests are appropriate tests for this situation. The Wald χ^2 indicated a weak but significant effect of body size on survival (see Results). In contrast, the Z test indicated no effect of body size (nor crowding, nor their interaction effect; $P > 0.05$ for all). Given these conflicting results, we used AIC and BIC to compare a null model (intercept only) against an alternative model (intercept and size effect only). Both AIC and BIC supported the alternative model. Thus, we proceeded with the alternative model and used the Wald χ^2 test.

Selection of models using lowest AIC and BIC values (bold)

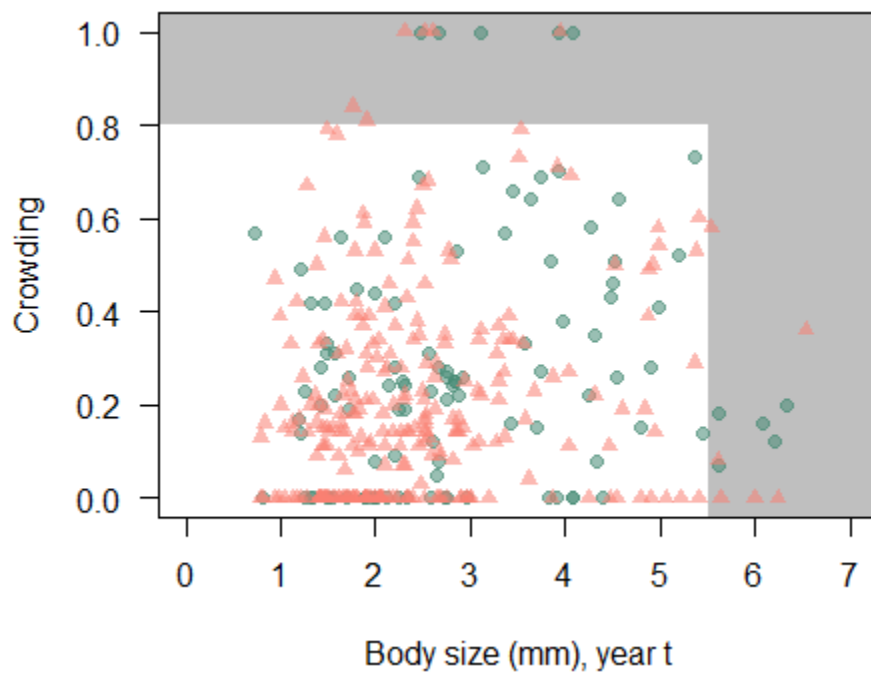
Model	Supported by Wald χ^2 test	Supported by Z test	AIC	BIC	Choice
Null (Survival ~ 1)		√	416.458	420.322	
Alternative (Survival ~ Size)	√		410.658	418.386	√

References:

Bolker BM, Brooks ME, Clark CJ, et al. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol Evol* 24:127–135.
doi: 10.1016/j.tree.2008.10.008

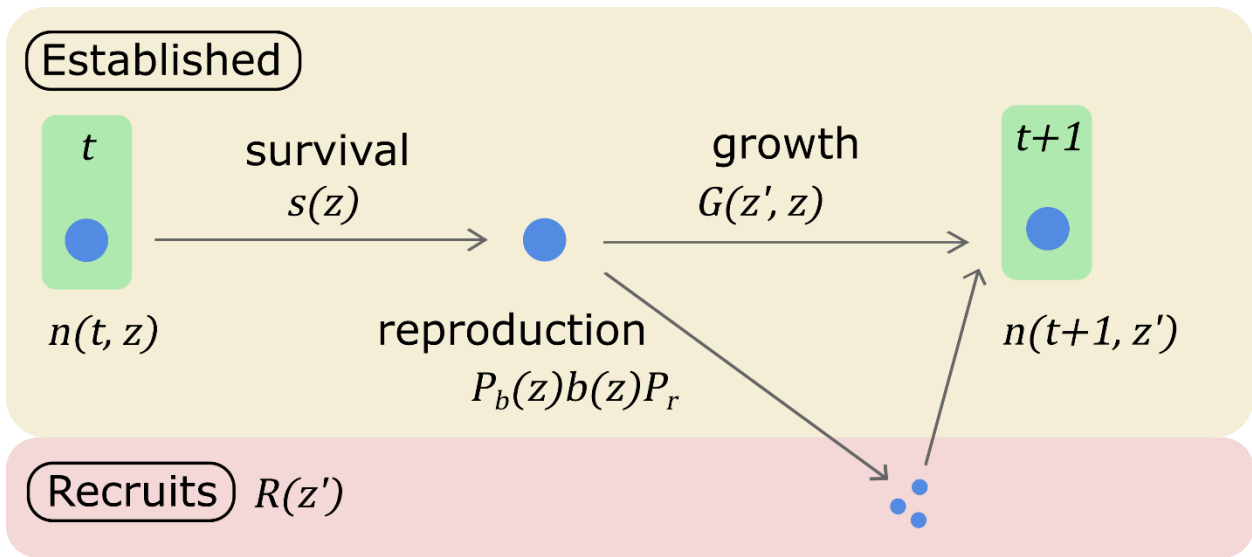
Supplement 8

Data used for analysis of barnacle field survival and growth. Data points in the shaded gray regions were excluded from analyses. Points indicate individual barnacles, with green circles indicating alive (survived) and pink triangles indicating dead (did not survive) at the year t+1 (summer 2018) survey. Final sizes of surviving individuals were measured for growth analysis. Darker clumps indicate more overlapping points.



Supplement 9

Summary of the life cycle of *Balanus glandula* modeled by the integral projection models that included only body size (z) as a state variable. The model began with a field-observed distribution of established individuals of a given size, $n(t, z)$, and proceeded in one-year time steps. In each time step, each established individual (large blue circle) had a probability of survival $s(z)$; the survivors then grew with probability density $G(z', z)$ and reproduced. The population was modeled as closed: each individual had a probability of reproducing $P_b(z)$; those who reproduced generated offspring based on their fecundity $b(z)$. The offspring (small blue circles) recruited with probability P_r and size distribution $R(z')$, joining the established individuals to form the distribution of established individuals at the next time step, $n(t+1, z')$. Individuals in the models were separated into established individuals and recruits, but the vital rates of all individuals were size, not stage, structured.



Supplement 10

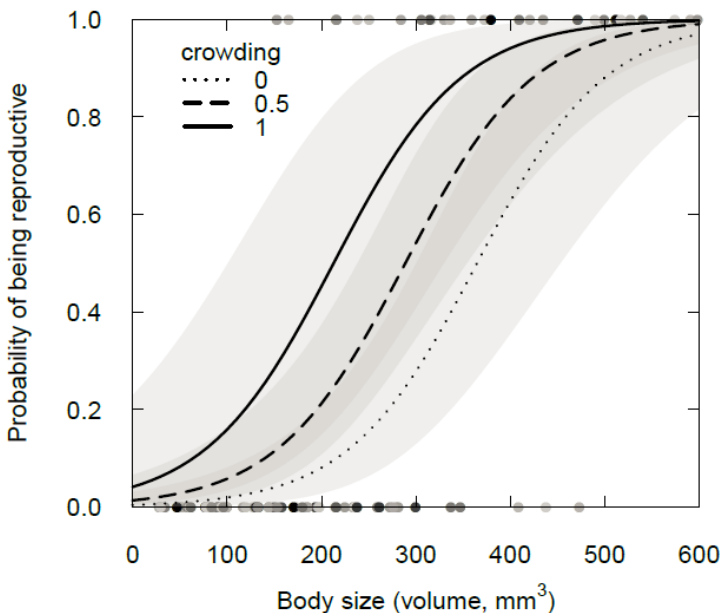
Results from a companion study (King and Sebens in prep) supporting an interaction effect between body size and crowding on the probability of reproducing of *Balanus glandula*. This data comes from field sites around San Juan Island (including those used in this study). We determined barnacle probability of being reproductive (based on presence of yolky ovarian tissue) during the summer of 2017.

Results of model testing how body size, crowding, and temperature affect *Balanus glandula* probability of being reproductive

Effect	DF	χ^2	<i>P</i>
Size	1	43.819	<0.001
Crowding	1	4.260	0.042
Temperature			
Size × Crowding	1	0.363	0.548
Model residuals ~ Temperature	1	1.215	0.273

Size refers to body size as measured by final shell volume (reproduction). Temperature refers to site grand mean temperatures. Sample size is 95 individuals from 10 sites. R^2 is 0.619. Bold indicates $P < 0.05$. Due to small sample size, the model only included Size and Crowding as fixed effects; the model residuals were tested against temperature to check for temperature effects.

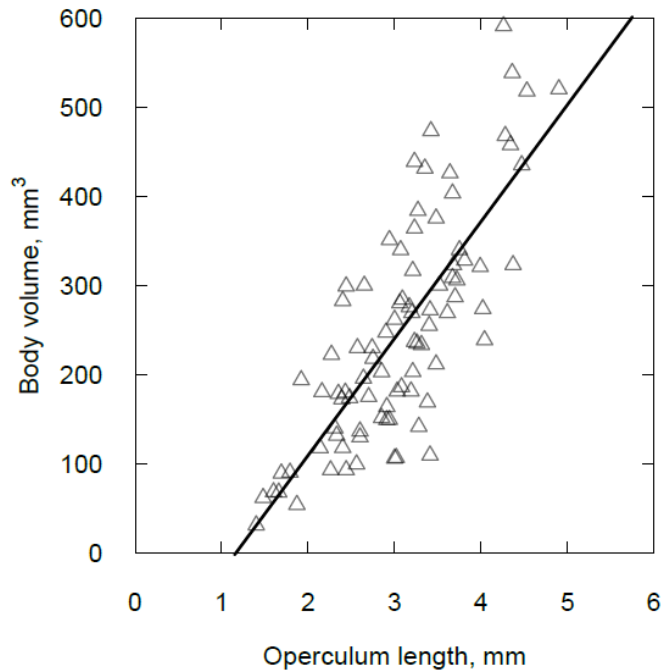
Probability of being reproductive of *B. glandula* as a function of body size and crowding in the field. Crowding is a continuous variable and we visualize predictions for three levels: 0 = isolated, 0.5 = half of perimeter contiguous with conspecifics, 1 = completely surrounded. Lines indicate model predictions based on observations of 95 individuals from 10 sites. Shaded areas indicate 95% confidence intervals, with darker regions indicating overlap. Points indicate observations, with darker colors indicating higher crowding.



Supplement 11

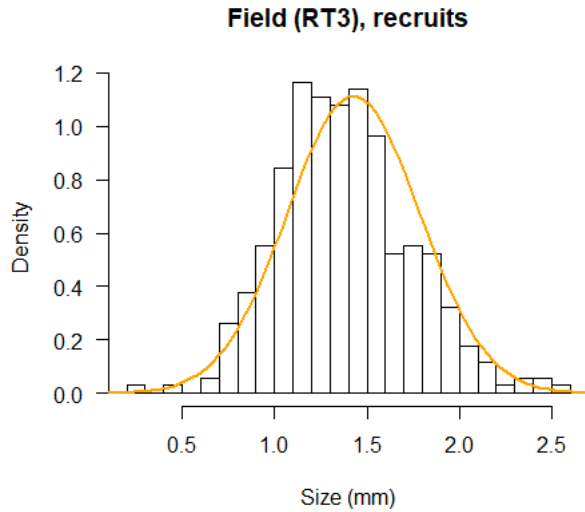
Linear regression estimating barnacle body volume based on operculum length. This was necessary to predict probability of reproduction based on shell volume while aligning with the state variable (body size based on operculum length) used in the IPMs. The regression equation is $Body\ volume = 131.2(Operculum\ length) - 152.5$, with $N = 85$, $P < 0.05$ for the effect of operculum length on body volume, and $R^2 = 0.619$.

These data were collected as part of a companion study (King and Sebens in prep) during summer 2017. The data is composed of 100 individuals collected from field sites around San Juan Island, including those used in this study. We only used data in the range of the operculum lengths (0-6 mm) consistent with the range used in the probability of being reproductive regression (Supplement 10; King and Sebens in prep), making sample size 85.

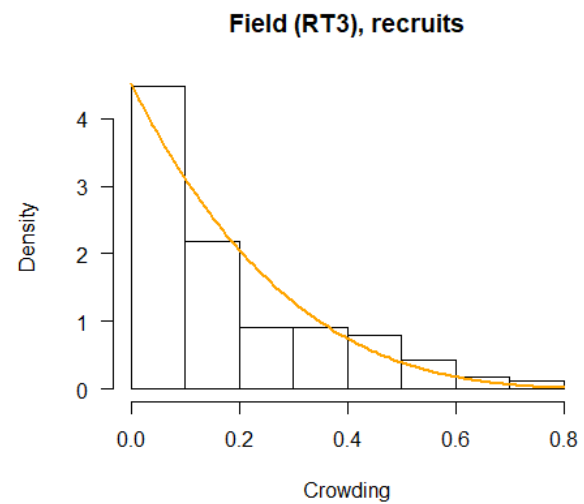
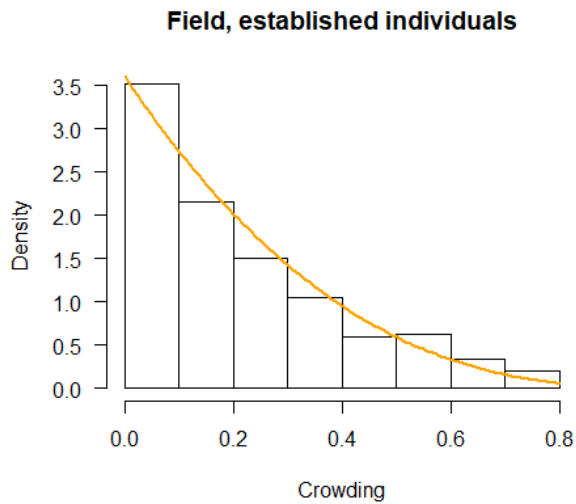


Supplement 12

Size distribution of recruits observed in the field in this study. The distribution was a fitted normal distribution. The parameter values are available in Supplement 14.

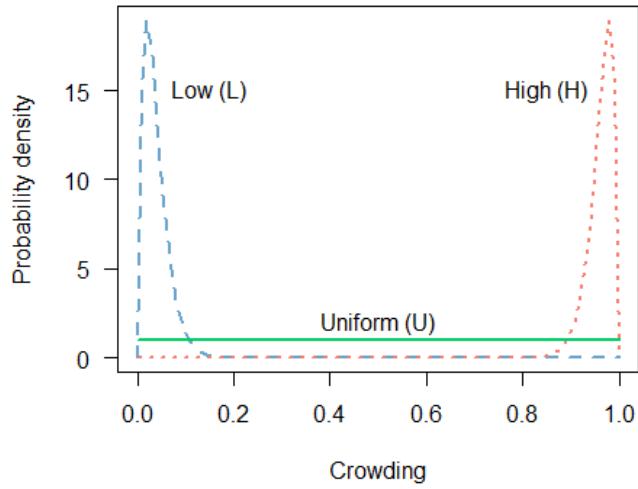


Crowding distributions of established individuals and recruits observed in the field in this study. Distributions were fitted beta distributions. Shape parameter values are available in Supplement 14.



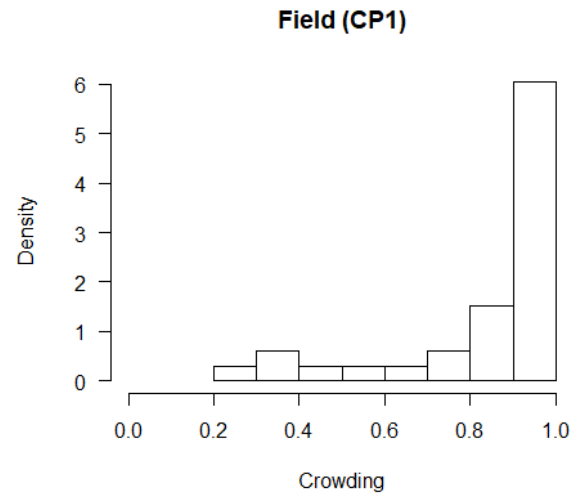
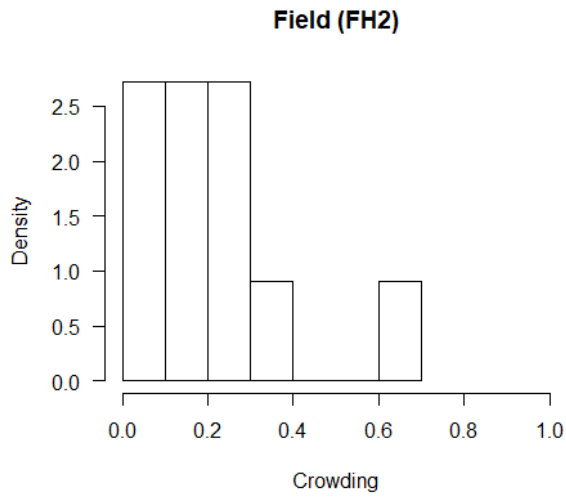
Supplement 13

Theoretical crowding distributions (left) and scenarios (right) for IPMs.



Distribution of established individuals	Distribution of recruits		
	U	L	H
U	eUrU	eUrL	eUrH
L	eLrU	eLrL	eLrH
H	eHrU	eHrL	eHrH

Examples of crowding distributions observed in the field that support the theoretical Low and High crowding distributions. CP1 is a site on San Juan Island that was not otherwise part of this study.



Supplement 14

Values used to parameterize *Balanus glandula* population models.

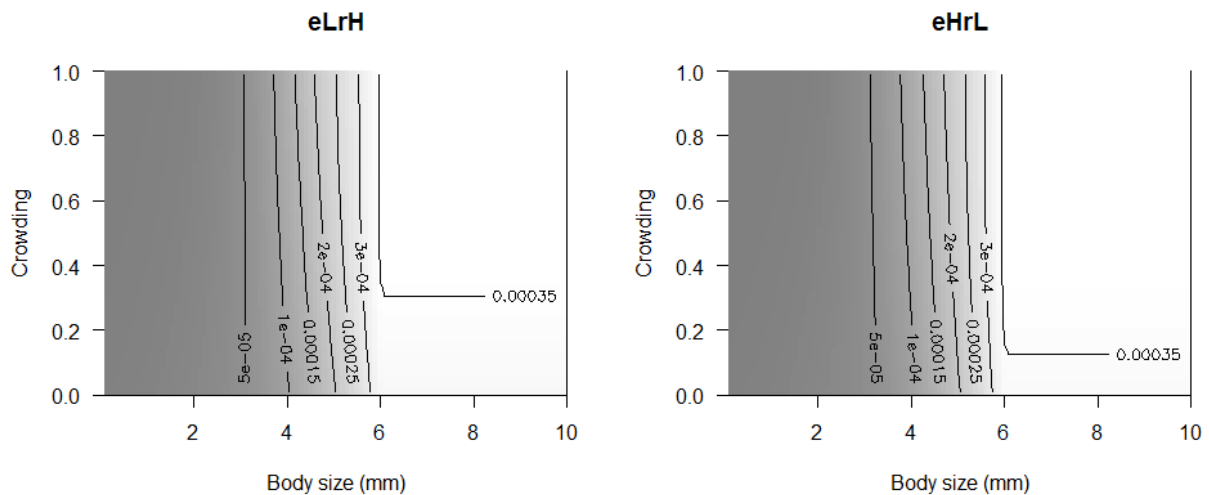
IPM	Survival		Growth					P_b			$C_1(q')$		$C_0(q')$											
	β_0	β_z	β_0	β_z	β_q	β_{zq}	σ_g	β_0	β_v	β_q	α	β	α	β										
Size-only	-1.73	0.30	2.21	0.73	n/a	n/a	0.45	-4.55	0.01	n/a	n/a	n/a	n/a	n/a										
eFrF											1	3.61	1	4.52										
eUrU											300	300	300	300										
eLrH											2	50	50	2										
eUrH											300	300	50	2										
eHrH											50	2	50	2										
eLrU											-1.73	0.30	2.98	0.48	-2.43	0.71	0.41	-5.38	0.01	2.24	2	50	300	300
eHrU											50	2	300	300										
eLrL											2	50	2	50										
eUrL											300	300	2	50										
eHrL											50	2	2	50										

IPM stands for integral projection model. Size-only is an IPM without a crowding term, hence parameters for modeling crowding are not applicable (n/a). The names of the other IPMs indicate the crowding scenario (F: field, U: uniform, L: low, H: high, with U, L, and H being theoretical distributions) for barnacles of different types (e: established individuals, r: recruits). P_b , $C_1(q')$, and $C_0(q')$ refer to probability of reproducing, established individuals crowding distribution, and recruit crowding distribution respectively. β 's with subscripts indicate regression model coefficients (subscript 0: intercept, z: slope for body size (operculum length), q: slope for crowding, zq: interaction effect between size and crowding, v: slope for body size (shell volume)). α 's and β 's without subscripts indicate shape parameters for beta distributions. σ_g refers to the variation (standard deviation of residuals) of each regression model for growth. Not shown in the table are the parameters for fecundity ($b(z) = 0.147z^{2.74}$), probability of recruitment ($P_r = 0.0033$), and recruit size distribution ($R(z') = Normal[z'|1.43, 0.36]$); these parameters are the same for all models. The box indicates that the values are the same for all of the models that include crowding.

Supplement 15

Reproductive value of individuals for a given state (size and crowding) in IPM_{eLrH} and IPM_{eHrL} . Reproductive value is the relative reproductive potential of an individual with a given state, based on state-specific vital rates (Lanciani 1998). It is calculated as left eigenvector corresponding to the dominant eigenvalue, λ (Caswell 1989). Lighter colors in the plots indicate higher reproductive values (delineated by contour lines).

Barnacles of a given state had similar reproductive values in the two IPMs: reproductive value tended to increase with body size after ~ 3 mm operculum length until 6 mm, after which the ceilings in the models enforced the same vital rates and therefore the same reproductive values. Crowding did not have a strong effect on reproductive value compared to size.



References:

- Caswell, H. (1989). Matrix population models. Sinauer, Sunderland, Massachusetts, USA.
Lanciani, C. A. (1998). A simple equation for presenting reproductive value to introductory biology and ecology classes. *Bulletin of the Ecological Society of America*, 79, 192–193.