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Carry-Over Effects in Complex Life Cycles: Linking Larval Food Supply with Juvenile Recruitment Success in Sea Stars

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ABSTRACT

The supply of new individuals into a population is one of the most important factors impacting species distributions and ecological interactions within a community. For marine invertebrates with complex life cycles, the supply of new individuals into a population can be influenced by factors experienced throughout their life history—before, during, or after metamorphosis. In recent years, scientists have begun to take a more holistic approach to understanding marine population assemblages by considering links between early life stages. When experiences in the pre-metamorphic life stages impact post-metamorphic life stages, this is known as carry-over effects. Because carry-over effects impact fitness of individuals, they could determine which individuals are recruited into the population and ultimately influence adult population structure. Using the keystone sea star *Asterias forbesi*, I tested how carry-over effects of larval food environment influence post-metamorphic performance in juveniles. I also tested whether carry-over effects could be compensated for if juvenile sea stars are fed juvenile mussels. Larvae were reared to metamorphosis under high larval food concentration and low larval food concentration. To test for carry-over effects of larval food concentration, my response variables at metamorphosis were survival, age, juvenile area, and juvenile spine number. To test if carry-over effects could be compensated for, each juvenile sea star was reared for 2-3 weeks on a juvenile feeding treatment of unfed, 1 juvenile mussel week^{-1}, 3 juvenile mussels week^{-1}, or 6 juvenile mussels week^{-1}. My main response variables for the juvenile feeding experiment were mussel mass consumed and juvenile growth rate. I predicted that juveniles that settled early would experience the most severe carry-over effects, so I conducted the juvenile feeding experiment on the first settlers (“early”) and settlers that delayed their metamorphosis relative to the first settlers (“late”). Overall, I found that *A. forbesi* larvae reared under low food concentration took longer to reach metamorphosis and settled as smaller juveniles with fewer spines compared to those juveniles reared on high larval food concentration. For early settlers, juveniles from low larval food background metamorphosed at smaller sizes, so they reduced feeding and had lower mean growth rates compared to juveniles from high larval food background. Therefore, carry-over effects significantly impacted early settler performance, and this could not be overcome through juvenile feeding. However for late settlers, there was no significant difference in area at settlement between juveniles reared from high versus low larval food background. Therefore, carry-over effects of larval food environment were not present among late settlers, and thus there were no differences observed in juvenile performance. The differences observed between early and late settlers suggest that there may be a trade-off between larval duration time (i.e. delaying metamorphosis) and post-metamorphic performance.

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Introduction

The supply of new individuals into a population is one of the most important factors impacting species distributions and ecological interactions within a community (Underwood & Fairweather 1989; Zimmer et al. 2009). Supply-side ecology emphasizes the recruitment of offspring, as well as processes such as competition, predation, and physical disturbance, in models that predict species assemblages (Underwood & Fairweather 1989). The supply-side perspective is commonly applied to organisms with complex life cycles—those with multiple, distinct life history stages that either require metamorphosis to transition between them (e.g. amphibians, insects, etc.) or those that alternate between gametic generations (e.g. plants) (Underwood & Fairweather 1989; Wilbur 1980; Willson 1981). Supply-side ecology is important for species with complex life cycles because many of these species have dispersive early-life stages, so population dynamics are ultimately determined by processes affecting the supply of individuals away from the parental habitat (Underwood & Fairweather 1989; Gosselin & Qian 1997; Hunt & Scheibling 1997; Zimmer et al. 2009).

While supply-side ecology is broadly accepted as essential to understanding population and community structure, there has traditionally been an emphasis on the quantity of offspring in a cohort, rather than the quality of offspring (reviewed by Marshall & Morgan 2011). For example, current models that aim to predict biogeographic distribution and population density of plants focus on how the supply of seeds, the availability of habitat, and dispersal agents

(e.g. wind, animal disperser) affect recruitment (Willson 1981; Levin et al. 2003; Zimmer et al. 2009; Duncan et al. 2009). However, there is mounting evidence that the number of offspring in a cohort may not determine recruitment and that offspring phenotype may be more important (Pechenik 2006; Marshall & Morgan 2011). Offspring phenotype is determined by the interaction of genetic and environmental components. For organisms with complex life cycles this becomes more complicated, because environment in pre-metamorphic stages can affect phenotype in post-metamorphic stages (Pechenik 1999). Specifically, it is called a carry-over effect when abiotic (e.g. temperature, salinity, delayed metamorphosis) or biotic (e.g. food availability, predators, competitors) environmental factors occur in the pre-metamorphic stages but affect post-metamorphic phenotype, and ultimately, fitness (Pechenik 2006). For example, in the plant *Brassica rapa*, when seeds were placed in nutrient deficient soil, the resulting adult plants had normal growth rates, but they produced fewer seeds (Steinbrenner et al. 2012). Similarly, when tadpoles (*Rana* spp.) were exposed to predators, they had reduced growth rates as juvenile frogs and were smaller at maturity compared to individuals that were not exposed to predators as tadpoles (Altwegg & Reyer 2003).

Carry-over effects have also been shown in a number of marine invertebrate taxa including annelids, molluscs, arthropods, echinoderms, and chordates (Pechenik 2006). Many of these taxa develop via microscopic planktonic larvae and transition to the benthic adult habitat through a metamorphosis that requires significant morphological, physiological, and

ecological changes (Thorson 1950). It has long been understood that larval supply to the benthos is impacted by both abiotic and biotic factors, including ocean currents (Roughgarden et al. 1988), availability of settlement habitat (Balch & Sheibling 2000), food supply (Pechenik 1999), larval predation (Pechenik 1999), larval behavior (Roy et al. 2012), and early post-settlement processes (Gosselin & Qian 1997; Hunt & Scheibling 1997; Jennings & Hunt 2010). More recently, however, studies have demonstrated that carry-over effects link the larval environment with juvenile phenotype, performance, and ultimately, recruitment (reviewed by Pechenik 2006). For example, laboratory experiments showed that when larvae of a colonial ascidian (*Diplosoma listerianum*) were forced to delay metamorphosis, there was no significant effect on larval survival to settlement, but delaying metamorphosis did significantly reduce colony growth during the juvenile stage (Marshall et al. 2003). Similarly, when competent gastropod larvae (*Crepidula fornicata*) were reared under food-limiting conditions, the resulting juveniles had reduced growth rates (Pechenik et al. 1996).

Traditionally, models that predict recruitment of marine invertebrate larvae into adult populations include parameters such as fecundity, egg size, larval duration time, and survival to metamorphosis (Vance 1973a; Vance 1973b; Havenhand 1993). However, recruitment can be defined as the entrance of reproductively immature individuals into the population that are large enough to have surpassed exponential post-settlement mortality experienced by juveniles (Metaxas 2013). By this definition of recruitment, current models that are only

parameterized with information about the embryonic and larval environments are oversimplified and unlikely to predict recruitment into the juvenile and adult stages, because they do not include any parameters affecting post-metamorphic survival and fitness. A more comprehensive approach to predict recruitment of marine invertebrates is to include carry-over effects that affect offspring supply and phenotype at settlement, as well as the post-metamorphic processes that influence survival of offspring.

There are already numerous studies showing how ecological processes affect survival during the larval and juvenile stages. Mortality during the larval and juvenile stages is high (>90% in each) and most commonly impacted by ecological processes such as physiological stress, competition, and predation (Rodriguez et al. 1993; Gosselin & Qian 1997; Hunt & Scheibling 1997; Pechenik 1999). There is evidence that both pre-metamorphic and post-metamorphic processes can regulate marine populations and communities. One example of a pre-metamorphic process controlling population structure is in barnacles (*Balanus* spp.) along the West Coast of the U.S. (Shanks et al. 2017). Barnacle larval supply was higher at sites with wide surf zones in comparison to sites with narrow surf zones, because at sites with wide surf zones, barnacle larvae could be delivered to settlement habitat (Shanks et al. 2017). Sites with wide surf zones therefore had higher recruitment rates and larger adult population densities (Shanks et al. 2017). Post-metamorphic processes can regulate populations as well; Prichard et al. (2016) found that at some sites in Oregon, settlement of oyster larvae (*Ostrea lurida*) was high, but there were no juveniles

or adults present several months later. They concluded that the reason there was no juvenile recruitment at those sites with high larval supply was that post-metamorphic processes controlled the population structure (Pritchard et al. 2016). Post-metamorphic processes can also have significant effects on community structure (Gosselin & Qian 1997; Hunt & Scheibling 1997). For example, recruitment of the mussel *Mytilus edulis* in the Gulf of Maine was temporally and spatially variable in consecutive years, and recruitment patterns had a significant bottom-up effect on the population structure of subtidal predators such as sea stars and crabs (Witman et al. 2003).

While these examples demonstrate how pre-metamorphic and post-metamorphic processes affect population and community assemblages, there is a need to further investigate links between the larval and juvenile stages to determine whether these links influence the regulation of populations. There is already evidence that phenotype can regulate populations. Burgess & Marshall (2011) found that in the marine bryozoan *Bugula neritina*, parent colonies that released few offspring yielded larger colonizer populations than parent colonies that released more offspring, and this could be attributed to the offspring phenotype (Burgess & Marshall 2011; Marshall & Morgan 2011). This study demonstrates that the phenotype of offspring, rather than the quantity of offspring, can determine population size and fitness of adults. A limitation to this study is that the phenotype was inherited from the parent, so a next step in understanding how marine invertebrate populations are regulated by phenotype

is to determine if larval environment determines juvenile phenotype and whether this impacts performance.

Additionally, there are several limitations to current studies of carry-over effects in marine invertebrates. Most studies use species with lecithotrophic, or non-feeding, larvae and short generation times (Qian & Pechenik 1998; Maldonado & Young 1999; Pechenik 2006; Hartmann et al. 2013; Hettinger et al. 2013). However, most marine invertebrates develop via planktotrophic, or feeding larvae, that remain in the water column for weeks to months (Thorson 1950; Pechenik 1999), which means that our understanding of carry-over effects is weak for most species. A second limit to studies of carry-over effects is that they fail to investigate possible mitigation of negative effects through compensatory growth (Pechenik & Eyster 1989; Pechenik et al. 1996; Marshall et al. 2003; Hettinger et al. 2013). Compensatory growth is a strategy used by offspring that experience a “poor start”; by increasing their growth rate early in life they can mitigate effects of poor body condition or nutritional reserves (Metcalfe & Monaghan 2001). Compensatory growth may be particularly important for organisms that need to reach a minimum size quickly (Arendt 1997), as is the case for marine invertebrates that only recruit once they are large enough to have surpassed exponential post-settlement mortality (Metaxas 2013). Compensatory growth has been shown to affect juveniles in a number of vertebrate systems (Metcalfe & Monaghan 2001). For example, a laboratory study that kept juvenile Atlantic salmon (*Salmo salar*) in cold water for several months resulted in low body weights for those fish, but once they were

transferred to warm water, they experienced compensatory growth (Mortensen & Damsgård 1993; Metcalfe & Monaghan 2001). However, compensatory growth does not always occur; Altwegg and Reyer (2003) found no evidence for compensatory growth in frogs that experienced carry-over effects of predator exposure during the tadpole phase. For marine invertebrates, compensatory growth in response to carry-over effects is less well known. A few studies have suggested that if larvae are well fed, this can prevent carry-over effects in the juvenile stage (Pechenik & Eyster 1989; Thiyagarajan & Qian 2003). For example, when the gastropod *Crepidula fornicata* were forced to delay metamorphosis in the laboratory, this had no significant effects on juvenile fitness as long as larvae were well fed throughout development (Pechenik & Eyster 1989). However, there is no evidence of compensatory growth during the juvenile stage in marine invertebrates. Hettinger et al. (2013) found that when oyster larvae (*Ostrea lurida*) were reared in acidic conditions, they did not exhibit compensatory growth as juveniles when placed in normal pH conditions for several months. The presence of compensatory growth in certain animal systems but not others suggests that further investigation of compensatory growth is needed to understand the role it plays in mitigating poor offspring condition. In the framework of organisms with complex life cycles, whether an organism exhibits compensatory growth after negative carry-over effects ultimately indicates whether pre-metamorphic (the carry-over effect) or post-metamorphic processes (juvenile growth) are more important for determining recruitment.

In this study I used the keystone predator *Asterias forbesi* (Menge 1983) to investigate carry-over effects of larval food concentration and whether any negative consequences can be mitigated through juvenile feeding and growth. I chose to focus on larval food as a pre-metamorphic process, because many echinoderm larvae, including asteroids, exhibit plasticity in response to low food concentrations by increasing their body size and elongating their feeding structures (George 1994; George 1999; Podolsky & Alister 2005; Miner 2007; Wolfe, Graba-landry, et al. 2015). These examples of larval feeding plasticity indicate that there has been strong selection on responses to larval food in this phylum (McAlister & Miner 2018). Additionally, a study in *A. forbesi* that investigated how intra-clutch egg size variation and larval food concentration affect larval development found that egg size had no significant consequences, but larvae reared on low larval food concentration had reduced survival, took longer to reach settlement, and were smaller with fewer spines at metamorphosis (Trackenberg et al. unpublished manuscript). This result indicates that endogenous energy reserves supplied in the egg are not as important for larval development as exogenous energy collected in the plankton, so investigating the effects of larval food further is essential to understanding the ecology of this species. Furthermore, carry-over effects of low larval food environment reduced size and spine number in *A. forbesi* juveniles at settlement (Trackenberg et al. unpublished manuscript), but it is unknown whether these effects persist during the juvenile stage or whether they can be overcome through juvenile feeding. Here I further investigated these carry-over effects of larval food in *A. forbesi* to

determine whether they affect early post-metamorphic survival, growth, and performance, so that my results can ultimately determine what factors determine recruitment in an ecologically-relevant species.

Methods

Larval Feeding Experiment

In June 2017, adult *Asterias forbesi* were hand collected from the subtidal habitat at Rockland Breakwater, Rockland, Maine (44°6'14.55"N, 69°4'39.16"W). Individuals were transported to the Bowdoin College Schiller Coastal Studies Center, Orrs Island, Maine (43°47'22.13"N, 69°57'26.92"W) and kept in flow-through sea tables at ambient salinity (~33 ppt), pH (~8.1), and temperature (~18°C) for one day.

Spawning was induced by intracoelomic injection of 3 mL of 100 μM 1-methyladenine (Strathmann 1987). To generate a population of larvae, 1000 eggs from each of six female *A. forbesi* were combined in 1000 mL 0.45-μm filtered seawater (FSW). Ten mL dilute sperm from each of 10 males were combined in a beaker and mixed well, and eggs were fertilized with 1 mL dilute sperm from the combined sperm beaker. To confirm high fertilization success in the population, and the viability of each female's eggs, 50 eggs from each female were fertilized separately from the other females and scored for the presence of a fertilization envelope. All 6 females had fertilization scores greater than 90%.

Developing embryos reached the early gastrula stage after 24 hours and were transferred to 45 glass beakers filled with 200 mL FSW at a density of 1

larva 10 mL^{-1}. Beakers were placed under a stirring rack in a flow-through sea table and stirred at a rate of 10 strokes min^{-1} (Strathmann 1987). Every other day beakers were cleaned and 50% of the water from each beaker was reverse filtered through 35 μm Nitex mesh. New FSW was then added to the beaker to return the volume to 200 mL. After water changes, larvae were fed equal amounts of three phytoplankton species: *Dunaliella tertiolecta* (UTEX Culture Collection of Algae, Austin TX, Catalog #LB999), *Isochrysis galbana* (National Center for Marine Algae and Microbiota, West Boothbay Harbor, ME, Catalog #CCMP1323), and *Rhodomonas lens* (National Center for Marine Algae and Microbiota, West Boothbay Harbor, ME, Catalog #CCMP739). Larvae in 25 beakers were fed a high food concentration of 7,500 algal cells $species^{-1}$ ml^{-1} and larvae in 20 beakers were fed a low food concentration of 2,500 algal cells $species^{-1}$ ml^{-1}. Water pH was checked throughout larval rearing using a Metrohm Primatrode with NTC pH electrode to ensure conditions between the larval food treatments were not significantly different.

When the first larvae developed brachiolar arms and the beginnings of a juvenile rudiment, beakers were no longer cleaned to allow biofilm growth (Cameron & Hinegardner 1974) and a blue mussel shell (*Mytilus edulis*) was placed in each beaker to encourage larval settlement (Trackenberg 2016). Shells and beakers were checked for settlement once per day. When a settler was found, age at settlement was recorded and the location of the juvenile sea star was noted. However, juveniles were not removed from the shell or beaker until two days after they were first observed in order to ensure that juveniles had

completed metamorphosis and to prevent damaging them upon removal. In a pilot study, we found that two-day old juveniles were much more robust to handling than newly metamorphosed individuals. Once removed, the number of spines on each juvenile was counted under a compound microscope. Juveniles were then photographed at 40x magnification, and the greatest two-dimensional area in the plane of view was later measured using ImageJ64 (Schneider et al. 2012). Each juvenile was then isolated in 2 mL of FSW in a single well of a 24-well plate that was placed in a sea table at ambient temperature.

Larval Plasticity Experiment

During larval rearing, 10 beakers from the high food treatment and 10 beakers from the low food treatment were randomly selected for measurements of larval plasticity. Measurements were conducted 10 and 17 days post-fertilization. Five larvae from each replicate beaker were removed and placed on a microscope slide in a droplet of FSW. A photograph was taken of each larva at 100x magnification (10 days post-fertilization) or 40x magnification (17 days post-fertilization) on an Olympus CX41 compound microscope. Larvae were immediately returned to their designated beaker after the photograph was taken to minimize the amount of time spent on a microscope slide.

Body length, body width, posterior body width, two-dimensional gut surface area, and ciliated band length (as in Wolfe et al. 2015) were measured from each photograph in ImageJ64. Ciliated band length was calculated by summing the lengths of the oral hood, gut hood, and larval sides.

Juvenile Feeding Experiment

I conducted an experiment to evaluate the relative importance of larval food environment and juvenile food environment in determining post-metamorphic survival, growth, and performance. Juvenile sea stars from the high larval food background and juvenile sea stars from the low larval food background were randomly assigned to a juvenile feeding treatment. Juvenile *A. forbesi* were fed juvenile *M. edulis* that were removed from filamentous algae collected in the field at Giant's Stairs and McIntosh Lot Preserve, Bailey Island, Maine (43°43'36.09"N, 69°59'33.15"W). I predicted that the first settlers would experience the most severe carry-over effects. Therefore, I conducted this experiment on the first settlers ("early settlers") as well as settlers that delayed their metamorphosis relative to the first settlers ("late settlers") to evaluate differences in carry-over effects of larval food environment.

For early settlers, the two larval food treatments were fully crossed with three juvenile feeding treatments, yielding six total treatments, each with 25 juvenile sea stars. The first 75 juveniles that settled in each larval food treatment were randomly assigned to one of three juvenile feeding treatments: unfed, fed 1 juvenile *M. edulis* week^{-1}, or fed 3 juvenile *M. edulis* week^{-1}. The average age at settlement for individuals in this experiment was 24.0 days (figure S1*a*). Juvenile *M. edulis* that were fed to juvenile *A. forbesi* ranged from 300-1000 μm in length. Juvenile sea stars were reared for 18 to 24 days, depending on when they completed metamorphosis. For each juvenile, checks were conducted each week to record the number of mussels eaten by each individual. In the first week, three

checks were conducted, and one check was conducted each week thereafter. If a juvenile sea star had consumed a juvenile mussel, the empty shell was removed and the shell width was measured at 40x magnification on a compound microscope. Consumed mussels and, on rare occasions, dying mussels (determined by observation of decaying tissue), were replaced during each check. Survival of *A. forbesi* juveniles was recorded throughout the experiment. Photographs were taken of all juveniles at 10 days and 20 days post-metamorphosis, so that two-dimensional area could be measured in ImageJ64. Using those area measurements, I calculated total juvenile growth rate (2 to 20 days post-metamorphosis), early juvenile growth rate (2 to 10 days post-metamorphosis) and late juvenile growth rate (10 to 20 days post-metamorphosis) for each juvenile sea star.

For the late settlers, the experiment was designed in the same way as for early settlers with an additional juvenile feeding experiment, yielding eight total treatments, each with 20 or 21 juvenile sea stars. *A. forbesi* juveniles reared on either low larval food concentration or high larval food concentration were randomly assigned to one of four juvenile feeding treatments: unfed, fed 1 juvenile *M. edulis* week^{-1}, fed 3 juvenile *M. edulis* week^{-1} or fed 6 juvenile *M. edulis* week^{-1}. The average age at settlement for individuals in this experiment was 29.3 days (figure S1*b*). Juvenile sea stars were reared for 13 to 15 days, and one feeding check was conducted each week during the checks for the early settlers. Survival of *A. forbesi* juveniles was recorded throughout the two weeks,

and photographs for area analysis in ImageJ64 were taken at the conclusion of the experiment, so growth rate could be calculated.

Because we were interested in correlating the amount of food juvenile sea stars eat with their growth and performance, we measured the shell widths and masses of 38 live juvenile *M. edulis* to see if shell width was a predictor of mussel mass. We found that juvenile mussel shell width is a significant predictor of juvenile mussel mass (quadratic regression: $F_{2,35} = 421.400$, $p < 0.001$, $R^2 = 0.958$) (figure S2, table S1). These results align with existing literature in juvenile freshwater mussels (Larson et al. 2014) and adult bivalves (Mirzaei et al. 2015), including *M. edulis* (Mckinney et al. 2004). All consumed juvenile mussel shell widths recorded in the Juvenile Feeding Experiment were converted to mussel mass for analysis using the regression equation $y = 0.0003x^2 – 0.1307x + 26.684$ derived from the above experiment.

Juvenile Performance Experiment

In order to assess juvenile performance, I used juvenile walking speed as a proxy for fitness, because I predicted that speed is directly correlated with juvenile size as well as a juvenile sea star's ability to feed, grow, and ultimately reach recruitment. The early settlers from the Juvenile Feeding Experiment were used to assess performance. A Canon Vixia HFM52 video camera was mounted on a dissecting microscope at 20x magnification. A piece of paper with a 6 mm line was taped onto the stage plate as a scale. On days 2, 10, and 20 following metamorphosis, each juvenile sea star was placed in the center of a 5 cm

diameter Petri dish filled with ~5 mL FSW, and the dish was then placed on the stage with the scale in view underneath. Juvenile sea stars were given a maximum time of five minutes to walk any direction in the Petri dish. Filming was ended if the juvenile sea star walked out of the frame of the video or when five minutes elapsed. On days 10 and 21, each juvenile sea star's area was re-measured so that speed could later be correlated with body size.

The time period of the juvenile sea star's fastest minute was determined visually by watching each film. Using Kinovea computer software (Kinovea 0.8.15) each juvenile sea star's path was tracked during the fastest minute, and a screenshot of the walking path was taken. The length of this path was measured in ImageJ64 using the 6 mm line in each frame as a scale, and juvenile speed was later calculated from the length of this path.

Statistical Analyses

In the program R (Version 1.0.153), a one-way ANOVA was used to analyze the effects of larval food treatment on percent survival to settlement in each culture beaker. A linear mixed model was used to evaluate the following the response variables: age at settlement, juvenile area, and juvenile spine number. Larval feeding treatment was modeled as a fixed factor and beaker was modeled as a random factor. A two-way ANOVA was used to evaluate the response variables in the larval plasticity experiment with larval food treatment and day of measurement as fixed factors. Mans for each response variable (body length,

body width, posterior body width, gut surface area, and ciliated band length) were calculated from each replicate beaker and used for the statistical analyses.

For the Juvenile Feeding Experiment, the data collected for early settlers was analyzed separately from the data collected for late settlers. A logistic mixed model was run to assess juvenile sea star survival in each treatment. Larval food and juvenile food were modeled as fixed factors and beaker was modeled as a random factor. I statistically analyzed area at settlement between all treatments, because growth rates are often affected by initial size (Arendt 1997). Area at settlement was analyzed using a linear mixed model with larval feeding treatment and juvenile feeding treatment modeled as fixed factors and beaker modeled as a random factor. And

I analyzed total mussel mass consumption for early settlers (2 to 20 days post-metamorphosis) and late settlers (2 to 15 days post-metamorphosis) using a linear mixed model with larval food treatment and juvenile food treatment as fixed factors and larval beaker as a random factor. I also analyzed total mussel mass consumption using larval food treatment and area at settlement as fixed factors, and larval beaker as a random factor to see if size influences performance. For this model, only individuals in the “fed” juvenile feeding treatments were used. As with mussel mass consumption, I analyzed total juvenile growth rate for early settlers (2 to 20 days post-metamorphosis) and late settlers (2 to 15 days post-metamorphosis) using a linear mixed model with larval food treatment and juvenile food treatment as fixed factors and larval beaker as a random factor. I also used a linear mixed model to analyze how area and larval food treatment

affected each juvenile growth rate. Finally, I used a linear mixed model to test the effects of larval food treatment and mussel mass consumption on total juvenile growth rate.

For only early settlers, I also analyzed early mussel mass consumption (2 to 10 days post-metamorphosis) and late mussel mass consumption (10 to 20 days post-metamorphosis) because I predicted that carry-over effects would be present early after metamorphosis but may be overcome later in the juvenile period. For both early and late mussel mass consumption, I used a linear mixed model with larval food treatment and juvenile food treatment as fixed factors and larval beaker as a random factor for analysis. I also analyzed each mussel mass consumption variable using larval food treatment and area at settlement as fixed factors, and larval beaker as a random factor to see if size influences performance. Again, for this model, only individuals in the “fed” juvenile feeding treatments were used. As with mussel mass consumption, I analyzed early juvenile growth rate (2 to 10 days post-metamorphosis) and late juvenile growth rate (10 to 20 days post-metamorphosis), using a linear mixed model with larval food treatment and juvenile food treatment as fixed factors and larval beaker as a random factor. I also used a linear mixed model to analyze how area and larval food treatment affected each juvenile growth rate. For the late juvenile growth rate analysis, area 10 days post-metamorphosis was used. Finally, I used a linear mixed model to test the effects of larval food treatment and mussel mass consumption on each juvenile growth rate.

For the Juvenile Performance Experiment, a linear mixed model was used to evaluate walking speed with larval feeding experiment, juvenile feeding treatment, and age at filming as fixed factors and larval beaker modeled as a random factor. I also used a linear mixed model to test the effects of larval food treatment and juvenile area on walking speed 2, 10, and 20 days after metamorphosis. Larval beaker was modeled as a random factor.

For all analyses the residuals for each response variable were tested for normality using a Shapiro-Wilk test. For gut surface area and ciliated band length, data were square-root transformed to meet the assumptions for normality. For age at settlement, juvenile area, juvenile spine number in the Larval Feeding Experiment and for juvenile areas and juvenile growth rates in the Juvenile Feeding Experiment, data could not successfully be transformed to yield residuals with a normal distribution. In such cases in which data could not be successfully transformed, data were aligned-rank transformed and an ANOVA was conducted on those data (Wobbrock et al. 2011). All models were run as full models including an interaction term and reduced to include only main factors if the interaction term yielded a p-value > 0.250. In such cases, I reported both the full model and the reduced model.

Results

Larval Feeding Experiment

Across all beakers, 65.7% of larvae survived to settlement, with 65% survival among larvae reared in the low larval food treatment and 66.4% survival

among larvae reared in the high larval food treatment (figure 1*a*). There was no effect of larval diet on the percent of larvae surviving to settlement (one-way ANOVA: $F_{1,43} = 0.098$, $p = 0.755$; table 1*a*). There was, however, a significant effect of larval diet on age at settlement (linear mixed model: $F_{1,43} = 6.067$, $p = 0.018$) such that larvae reared in the low food treatment took 1.8 days longer to reach settlement (5.9% increase) than those reared in the high food treatment (figure 1*b*, table 1*b*). Juveniles from the low food treatment also had a significantly smaller area (13.5% decrease) (linear mixed model: $F_{1,43} = 16.137$, $p < 0.001$) and significantly fewer spines (11.3% decrease) (linear mixed model: $F_{1,43} = 7.118$, $p = 0.011$) than did larvae in the high food treatment (figure 1*c*-*d*, table 1*c*-*d*).

Larval Plasticity Experiment

There was a significant effect of larval diet on larval body length (two-way ANOVA: $F_{1,36} = 5.759$, $p = 0.022$) such that larvae reared in the low food treatment were longer compared to those in the high food treatment (figure 2, table 2*a*). A significant effect of larval diet was also observed for the other larval morphological features; larvae in the low food treatment had greater body widths (two-way ANOVA: $F_{1,36} = 5.554$, $p = 0.024$; table 2*b*), posterior body widths (two-way ANOVA: $F_{1,36} = 15.819$, $p < 0.001$; table 2*c*), gut surface areas (two-way ANOVA: $F_{1,36} = 4.367$, $p = 0.044$; table 2*d*), and ciliated band lengths (two-way ANOVA: $F_{1,36} = 10.291$, $p = 0.003$; table 2*e*) than those in the high food treatment (figure 2). There was also a significant effect of age at measurement on all larval

morphological features (table 2). Larvae had greater body lengths (two-way ANOVA: $F_{1,36}$ =754.599, $p < 0.001$), body widths (two-way ANOVA: $F_{1,36}$ = 855.372, $p < 0.001$), posterior body widths (two-way ANOVA: $F_{1,36}$ = 657.549, $p < 0.001$), gut surface areas (two-way ANOVA: $F_{1,36}$ = 534.459, $p < 0.001$), and ciliated band lengths (two-way ANOVA: $F_{1,36}$ = 861.579, $p < 0.001$) 17 days post-fertilization than 10 days post-fertilization (figure 2, table 2). There was a significant interaction between larval diet and age at measurement on larval body widths (two-way ANOVA: $F_{1,36}$ = 7.968, $p = 0.008$), but all other interactions were insignificant (table 2).

Juvenile Feeding Experiment

Among early settlers (figure S1*a*), juveniles from the low larval food background had lower survival (logistic mixed model: $\chi^2 = 5.009$, $p = 0.025$) than juveniles from the high larval food background, but juvenile food treatment had no effect on juvenile survival (logistic mixed model: $\chi^2 = 1.564$, $p = 0.457$; figure S3*a*, table S2*a*). Among late settlers (S1*b*) neither larval food treatment (logistic mixed model: $\chi^2 = 0.278$, $p = 0.598$) nor juvenile food treatment (logistic mixed model: $\chi^2 < 0.001$, $p = 0.993$) had a significant effect on juvenile survival (figure S3*b*, table S2*b*).

For early settlers, juveniles reared on low food as larvae were significantly smaller in area at settlement (linear mixed model: $F_{1,32}$ = 24.699, $p < 0.001$), but mean area at settlement did not differ between juvenile food treatments (linear mixed model: $F_{1,159}$ = 0.089, $p = 0.915$; figure 3*a*, table 3*a*). The interaction

between larval food treatment and juvenile food treatment did not have a significant effect on area at settlement (linear mixed model: $F_{1,159} = 2.523$, $p = 0.083$; table 3*a*). However, for late settlers, there were no differences in mean area at settlement between juveniles from high larval food background and low larval food background (linear mixed model: $F_{1,76} = 1.360$, $p = 0.247$), and mean area at settlement did not differ between juvenile food treatments (linear mixed model: $F_{1,151} = 1.460$, $p = 0.229$; figure 3*b*, table 4*a*).

I statistically assessed total mussel mass consumption for both early settlers (2 to 20 days post-metamorphosis), and late settlers (2 to 15 days post-metamorphosis). For early settlers, larval diet (linear mixed model: $F_{1,30} = 6.101$, $p = 0.020$), juvenile diet (linear mixed model: $F_{2,117} = 36.664$, $p < 0.001$), and their interaction (linear mixed model: $F_{2,117} = 6.872$, $p = 0.002$) each had a significant effect on total mussel mass consumption by juvenile sea stars (table 3*b*). Early settlers from low larval food background ate less than those from high larval food background, and, intuitively, juveniles that were fed more mussels, ate more mussels (figure 4*a*). There was also a significant effect of area at settlement (linear mixed model: $F_{1,79} = 6.801$, $p = 0.002$) on total mussel mass consumption by early settlers, but larval food treatment (linear mixed model: $F_{1,79} = 1.340$, $p = 0.251$) and the interaction between the two factors (linear mixed model: $F_{1,79} = 1.874$, $p = 0.175$) were not significant in this model (table S3*a*). This model indicated that early settlers that were large in size at settlement, consumed more mussel mass throughout the experiment (figure S4*a*). For late settlers, total mussel mass consumed was affected by juvenile food treatment (linear mixed

model: $F_{1,140}$ = 198.850, p < 0.001), but larval food treatment (linear mixed model: $F_{1,62}$ = 0.366, p = 0.548) and the interaction between larval food and juvenile food (linear mixed model: $F_{1,140}$ = 0.259, p = 0.612) were insignificant (table 4*b*). This model indicated that late settlers that were fed more consumed more mussel mass (figure 4*b*). There was no significant effect of larval food treatment (linear mixed model: $F_{1,98}$ = 0.026, p = 0.874), area at settlement (linear mixed model: $F_{1,100}$ = 0.852, p = 0.430), or their interaction (linear mixed model: $F_{1,100}$ = 0.021, p = 0.886) on total mussel mass consumption among late settlers (figure S4*b*, table S4*a*).

I also statistically assessed total growth rate for both early settlers (2 to 20 days post-metamorphosis) and late settlers (2 to15 days post-metamorphosis). For early settlers, there was a significant effect of both larval diet (linear mixed model: $F_{1,32}$ = 18.523, p < 0.001) and juvenile diet (linear mixed model: $F_{1,112}$ = 7.591 p < 0.001) on total juvenile growth rate, but their interaction was not significant (linear mixed model: $F_{1,112}$ = 2.107, p = 0.127; table 3*c*). Juveniles from low larval food background had reduced growth rates compared to those from high larval food background, and juveniles fed more mussels had higher growth rates (figure 5*a*). There was also a significant effect of both larval diet (linear mixed model: $F_{1,46}$ = 12.940, p < 0.001) and total mussel mass consumed (linear mixed model: $F_{1,113}$ = 71.024, p < 0.001) on total juvenile growth rate of early settlers, but again, the interaction was not significant (linear mixed model: $F_{1,113}$ = 0.350, p = 0.555; table 3*d*). This model showed that juveniles from low larval food background had lower mean growth rates than those from a high

larval food background, and juveniles that consumed more mussel mass grew more (figure 6).

Additionally, in model containing only main effects, both larval diet (linear mixed model: $F_{1,37} = 9.974$, $p = 0.003$) and area at settlement (linear mixed model: $F_{1,120} = 9.051$, $p = 0.003$) had a significant effect on total juvenile growth rate among early settlers (table S3*c*). This model showed that juveniles from low larval food background had lower growth rates, and overall, juveniles that settled at smaller sizes had lower growth rates (figure S5*a*). Finally, both larval diet (linear mixed model: $F_{1,46} = 12.940$, $p < 0.001$) and total mussel mass consumed (linear mixed model: $F_{1,113} = 71.024$, $p < 0.001$) had significant effects on total juvenile growth rate of early settlers, however, the interaction was insignificant (linear mixed model: $F_{1,113} = 0.350$, $p = 0.555$; table S3*d*). Again, this model showed that juveniles from low larval food background had lower growth rates than juveniles from high larval food background, and the more mussel mass juvenile sea stars consumed, the more they grew (figure S6*a*).

For late settlers, juvenile food treatment significantly impacted total growth rate (linear mixed model: $F_{1,150} = 84.892$, $p < 0.001$), but larval food treatment (linear mixed model: $F_{1,74} = 0.234$, $p = 0.630$) and the interaction between larval food treatment and juvenile food treatment (linear mixed model: $F_{1,150} = 0.021$, $p = 0.885$) were insignificant (table 4*c*). This model indicates that late settlers that were fed more had a greater total juvenile growth rate on average (figure 5*b*). Similarly in a different model, larval food treatment had no effect on total juvenile growth rate (linear mixed model: $F_{1,56} = 1.647$, $p = 0.205$), but total mussel mass

consumed did have a significant effect (linear mixed model: $F_{1,149} = 319.019$, $p < 0.001$; table S4*b*). This model indicates that late settlers that ate more, grew more, and larval food background had no effect on growth (figure S6*b*). Finally, larval food treatment (linear mixed model: $F_{1,134} = 0.300$, $p = 0.585$) and area at settlement (linear mixed model: $F_{1,139} = 0.792$, $p = 0.455$) had no significant effect on total juvenile growth rate of late settlers (figure S5*b*, table S4*c*).

For early settlers, I statistically assessed early mussel mass consumption (2 to 10 days post-metamorphosis) and late mussel mass consumption (10 to 20 days post-metamorphosis). For early mussel mass consumption, there was a significant effect of area at settlement (linear mixed model: $F_{1,81} = 8.381$, $p < 0.001$) but not of larval food treatment (linear mixed model: $F_{1,81} = 2.956$, $p = 0.089$) or the interaction (linear mixed model: $F_{1,81} = 2.829$, $p = 0.096$; table S3*e*). Late mussel mass consumption was significantly affected by area ten days post-metamorphosis (linear mixed model: $F_{1,123} = 6.104$, $p = 0.003$), but not by larval food treatment (linear mixed model: $F_{1,123} = 1.603$, $p = 0.208$) or their interaction (linear mixed model: $F_{1,123} = 2.366$, $p = 0.127$; table S3*f*). These two models demonstrate that larger juveniles consumed more mussel mass during the experiment (figures S7-S8).

For early settlers, I also statistically assessed early growth rate (2 to 10 days post-metamorphosis) and late growth rate (10 to 20 days post-metamorphosis). For early juvenile growth rate, there was no significant effect of juvenile food treatment (linear mixed model: $F_{1,120} = 2.091$, $p = 0.128$), and there was a marginally insignificant effect of larval food treatment (linear mixed model:

$F_{1,32}$ = 3.843, p = 0.059) in that there is a trend indicating that juveniles from low food background had reduced early growth rates (figure 7, table 3*e*). However, early juvenile growth rate was significantly affected by area at settlement (linear mixed model: $F_{1,129}$ = 10.757, p < 0.001), with larger juveniles at settlement having a greater growth rate (figure 8, table 3*f*). In this model, larval diet (linear mixed model: $F_{1,124}$ = 0.034, p = 0.854) had no impact on early juvenile growth rate (figure 8, table 3*f*). Additionally, there was a significant effect of both larval food treatment (linear mixed model: $F_{1,42}$ = 6.133, p = 0.017) and early mussel mass consumption (linear mixed model: $F_{1,130}$ = 68.693, p < 0.001) on early juvenile growth rate (table S3*g*). As in previous models, this model showed that juveniles from the low larval food background had reduced growth rates compared to juveniles from high larval food background, and that juveniles that ate more, grew more (figure S9).

Mean late juvenile growth rates were lower than mean early growth rates in all juvenile feeding treatments, and all mean late growth rates for juveniles from low larval food background were negative (figure 9). There was a significant effect of both larval food treatment (linear mixed model: $F_{1,27}$ = 17.386, p < 0.001) and juvenile food treatment (linear mixed model: $F_{1,122}$ = 4.097, p = 0.019) on mean late juvenile growth rate (table 3*g*). Juveniles from low larval food background had lower late growth rates compared to those from high larval food background, but juveniles that were fed more mussels, grew more (figure 9). Additionally, area ten days post-metamorphosis was a significant predictor of late juvenile growth rate (linear mixed model: $F_{1,109}$ = 3.084, p = 0.049; table S3*h*)

indicating smaller juveniles did not digress in size as much as larger juveniles (figure S10). However, neither larval food treatment (linear mixed model: $F_{1,101}$ = 0.077, p = 0.781) nor the interaction (linear mixed model: $F_{1,109}$ = 1.753, p = 0.188) were significant in this model (table S3*h*). Late growth rate was also significantly affected by larval food treatment (linear mixed model: $F_{1,35}$ = 6.403, p = 0.016) and late mussel mass consumption (linear mixed model: $F_{1,124}$ = 9.620, p = 0.002), but not their interaction (linear mixed model: $F_{1,124}$ = 0.478, p = 0.491; table S3*i*). Again, juveniles that consumed more mussel mass, grew more, and juveniles in from the low food background had lower growth rates (figure S11).

Juvenile Performance Experiment

For early settlers from the Juvenile Feeding Experiment that were subjected to walking speed trials, the age at filming was a significant predictor of speed (linear mixed model: $F_{2,370}$ = 150.322, p < 0.001), with speed being slowest 2 days post-metamorphosis and fastest 10 days post-metamorphosis (figure 10, table 5). However, larval food treatment (linear mixed model: $F_{1,31}$ = 0.034, p = 0.855) and juvenile food treatment (linear mixed model: $F_{2,378}$ = 0.283, p = 0.754) had no effect on speed (figure 10, table 5).

Area at filming was a significant predictor of juvenile walking speed on day 10 (linear mixed model: $F_{1,111}$ = 5.641, p = 0.005; figure S13) and day 20 (linear mixed model: $F_{1,92}$ = 5.577, p = 0.005; figure S14), but not on day 2 (linear mixed model: $F_{1,110}$ = 0.181, p = 0.835; figure S12). In all of three of these models,

larval food treatment was not statistically significant, nor was the interaction between area at filming and larval food treatment (table S5).

Discussion

I found that carry-over effects of a low larval food environment negatively affect juvenile traits of the keystone predator *Asterias forbesi*. Larvae exhibited plasticity in response to low food environment by increasing size of all morphological traits. However, this plastic response did not fully compensate for a low larval food environment, because while overall survival to settlement was not affected, larvae reared on low food took longer to settle and settled as smaller juveniles with fewer spines. I found that among early settlers, juveniles from low larval food background had smaller mean area at settlement compared to juveniles from high larval food background. This reduction in size at settlement reduced feeding and growth rates of juveniles from low larval food background, even when among juveniles that were not fed. However, juveniles from high larval food background did not have faster walking speeds, so the mechanism as to why juveniles from high larval food background ate more is unknown. It is possible that juveniles from the high larval food background were better able to detect, catch, and feed on mussels. Regardless of the mechanism, my study demonstrates that there were significant carry-over effects of low larval food environment impacting early settler performance, and these effects could not be mitigated through juvenile feeding. However, among late settlers, there was no significant difference in mean area at settlement between juveniles from low

larval food background and those from high larval food background. Therefore there were no carry-over effects observed in late settlers and post-metamorphic performance was not impacted. The differences observed between early and late settlers suggest that there may be a trade-off between larval duration time (i.e. delaying metamorphosis) and post-metamorphic performance. Overall, my data demonstrate that links in life history stages of marine invertebrates can have significant effects on offspring phenotype, which can ultimately impact recruitment dynamics and adult population structure (Gosselin & Qian 1997; Hunt & Scheibling 1997; Witman et al. 2003).

Larval plasticity is one mechanism through which organisms compensate for poor food environment. Increasing larval morphological traits in response to food has been shown in a number of taxa including bivalves (Strathmann et al. 1993), polychaetes (Pawlik & Mense 1994), bryozoans (Strathmann et al. 2008), and echinoderms (Miner 2007; Miner & McAlister 2018). My results are similar to other plasticity studies in asteroid species (George 1994; George 1999; Wolfe et al. 2015), but contrast with another (Poorbagher et al. 2010) (figure 11). One unexpected result of the larval plasticity experiment was the increase of gut surface areas among larvae in the low food treatment. At 10 days post-fertilization, the mean gut surface area of larvae in the low food treatment was 28.3% greater than that of larvae in high food treatment. A study in urchins found that there is indeed a trade-off between arm length and stomach size, but in the opposite direction: larvae reared in low food conditions increase their arm lengths and in turn have small stomachs (Miner 2005). The trade-off between arm length

and stomach size in urchins was confirmed in the sea star *Acanthaster planci* (Wolfe et al. 2015). One possible explanation for my contrasting result is that larvae reared under low food must increase their capacity to digest and assimilate food, so increasing gut surface area is one mechanism to achieve that.

The general pattern of larval plasticity in response to low food environment among asteroid species and many other marine invertebrate taxa (McAlister &Miner 2018) suggests that plasticity has likely been selected for. My results suggest that plasticity mitigates consequences of poor larval food environment, but not fully. Survival to settlement among larvae reared on low food was the same as those reared on high food. However, larvae reared on low food were still smaller with fewer spines at metamorphosis. Size at settlement has been shown to predict post-metamorphic performance in organisms with complex life cycles (Moran 1999; Altwegg & Reyer 2003; Torres et al. 2016), and spine number is likely reflective of the individual's ability to evade predation. Therefore despite the plastic response, juveniles reared on low food as larvae are still at risk for poor post-metamorphic performance.

I found that early settlers experienced carry-over effects of low larval food environment during the juvenile stage, even in the unfed juvenile feeding treatment. Because they were not fed as juveniles, differences in growth rates observed between early settlers from low larval food background and those from high larval food background can only be attributed to pre-metamorphic environment. The reason for the lower growth rates among early settlers from

low larval food background is area at settlement—early growth rate (2-10 days post-metamorphosis) was best explained by area at settlement. Early settlers from low larval food background maintained lower growth rates throughout the experiment in all treatments. The maintenance of low growth rates throughout the experiment demonstrates that juvenile sea stars did not exhibit compensatory growth, and thus could not overcome carry-over effects through juvenile feeding.

My results for early settlers contrast with my results among late settlers in that I found no evidence of carry-over effects among late settlers. Carry-over effects in early settlers were driven by differences in size at settlement, however among late settlers, there were no differences in area at settlement between juveniles of different larval food backgrounds. This explains why late settlers from low larval food background did not have reduced growth rates—there was no difference in size at settlement, a trait that correlates with growth rate soon after metamorphosis.

The fact that carry-over effects were observed in early settlers but not in late settlers (those that settled on average five days later than early settlers), suggests that there may be a trade-off between larval duration time and post-metamorphic performance. It is known that food accumulation in the plankton is critical in determining larval duration time and size at metamorphosis (Basch & Pearse 1995; Byrne et al. 2008). Well-fed larvae typically have shorter development times to metamorphosis and settle as larger juveniles (Pechenik & Eyster 1989; Trackenberg et al. unpublished manuscript). Traditionally, delaying metamorphosis is considered a negative consequence for larvae, because the

longer they are on the plankton, the longer they are exposed to larval mortality factors such as predation and physiological stress (Pechenik 1999). However, delaying metamorphosis has been shown to improve juvenile phenotype and fitness (Pechenik & Eyster), suggesting a trade-off. Models created by Werner & Gilliam (1984) take into account this tradeoff, and suggest that switching from the pre-metamorphic habitat to the post-metamorphic habitat is driven by size. That is, an organism will begin metamorphosis once it has reached a size at which growth rate relative to mortality rate is no longer optimal in the pre-metamorphic habitat (Werner & Gilliam 1984). More specifically, when a larva is developing in the plankton, it will eventually reach a size at which it experiences scaling constraints, so energy assimilation is no longer greater than energy expenditure (Werner & Gilliam 1984). Therefore, time to metamorphosis is determined by a trade-off between foraging rates and mortality risk in the pre-metamorphic and post-metamorphic stages (Werner & Gilliam 1984). My data support these models—early settlers reduce the risk of mortality in the plankton by going through metamorphosis first. However, early settlers reared on low food as larvae increase their risk of mortality in the juvenile stage because carry-over effects result in poor juvenile phenotype. In contrast, larvae that delay their metamorphosis relative to early settlers, increase their risk of mortality in the plankton by increasing their exposure to environmental factors and predation. However, by delaying metamorphosis, late settlers reduced the risk of mortality in the juvenile stage, because they do not experience carry-over effects of larval food environment.

When considering only early settlers (those that experienced carry-over effects of larval food environment), juveniles from low larval food background that were reared in the highest juvenile feeding treatment consumed significantly less mussel mass than those from high larval food background. This means that juveniles from low larval food background had a reduced capacity to feed. The mechanism for which this occurred is unknown, because juvenile walking speed did not differ between juveniles with different larval food backgrounds and only weakly correlated with area. A limit to the juvenile walking speed experiment is that juveniles were allowed to roam freely, so it is unknown whether top speeds were recorded. Therefore, much of the variation in speed observed in my study could be explained by factors not controlled in the experiment.

However, speed did change significantly over time and means were fastest 10 days after metamorphosis. Ten days after metamorphosis coincides with the time at which my data showed a decline in growth rate among all treatments. That is, mean late growth rates (10 to 20 days post-metamorphosis) of early settlers were lower than mean early growth rates (2 to 10 days post-metamorphosis) for all treatments. Additionally, mean late growth rates were negative for juvenile treatments from low larval food background. The fact that early growth rates were high, coupled with the fact that speeds two days post-metamorphosis were low, suggests that juvenile sea stars are spending much of their first 10 days after metamorphosis growing from larval energy reserves. Then, at around 10 days post-metamorphosis, juveniles become more active and start looking for food. This would explain why walking speed was fastest 10 days

post-metamorphosis, and why late growth rates were low—juveniles ran out of larval energy reserves.

However, my juvenile walking speed results do not explain why juveniles from low larval food background had a reduced capacity to feed. Other research suggests that performance, like the ability to feed, is driven by offspring size (Pettersen et al. 2015; Malerba et al. 2018), so I predicted that larger juveniles would be faster and feed more. In my study juvenile size only weakly correlated with walking speed and mussel mass consumed which contrasts with a laboratory experiment of juvenile sea stars (*Acanthaster planci*) (Yamaguchi 1974). It is possible that frequency of feeding, rather than speed, is affected by juvenile size. Additionally, we did not control for the exact size of mussel given to each juvenile, so it is possible that juveniles from low larval food background are only able to consume the smallest mussels and therefore if they were fed mussels in the upper size range, their feeding abilities could have been compromised during the experiment. Finally, I may not have fed my juveniles enough mussels to encourage feeding. Yamaguchi (1974) found that juvenile *A. planci* mass predicted feeding rate, so one would predict that larger juveniles should feed more. However, *A. planci* feeds on corals, and therefore feeding does not require catching prey. In my study, juvenile sea stars were in individual wells of a 24 well plate and fed live juvenile mussels. Both mussels and sea stars were free to crawl around, so at low mussel densities, the probability of encountering and feeding on a mussel was most likely lower. Low encounter

rates likely confounded my results correlating juvenile sea star size and mussel mass consumption.

Carry-over effects of low larval food environment are present in early settlers, and this is ultimately driven by a reduction in size at settlement. My study found that carry-over effects of low larval food environment cannot be mitigated through juvenile feeding. I therefore conclude that links in life history stages can have significant effects on later recruitment. However, individuals that delay their metamorphosis do not experience carry-over effects, suggesting a trade-off between larval stage duration and post-metamorphic performance. When it comes to determining whether pre-metamorphic or post-metamorphic processes determine recruitment, my data show this depends on whether individuals experience carry-over effects. For early settlers, I would predict that pre-metamorphic processes determine recruitment success in sea stars. However for settlers that delayed their metamorphosis, I would predict post-metamorphic processes determine recruitment success. Therefore, I would predict that that under natural conditions in the field, in good years when larval food is abundant, post-metamorphic processes control the population structure but in poor years when larval food is patchy or of poor quality, pre-metamorphic processes determine recruitment success and population dynamics.

My results and conclusions about the importance of pre-metamorphic versus post-metamorphic processes in recruitment can be applied to other keystone predator systems, including in asteroids. Currently, scientists involved in conservation efforts are interested in gaining basic ecological knowledge about

recruitment of two sea stars species with feeding larvae. On the West Coast of the U.S., a sea star wasting disease recently wiped out much of the population of the keystone predator *Pisaster ochraceus*. There is immense interest in what factors drive recruitment of this species, so that scientists can work to bring *P. ochraceus* back and conserve the rocky intertidal community. Additionally, on the Great Barrier Reef in Australia, massive recruitment events of the coral-eating crown-of-thorns sea star (COTS; *A. Planci*) are having detrimental effects in the ecosystem (reviewed by Pratchett et al. 2017). Population outbreaks result in hundreds of thousands of adult COTS on the reef, and they can consume and kill upwards of 96% of coral (Pratchett et al. 2017). A leading hypothesis as to why COTS are recruiting so heavily is that larval food is abundant because of agricultural run-off that is causing eutrophication in the waters on the reef (reviewed by Pratchett et al. 2017). My data support this hypothesis that larval food environment is pivotal in determining recruitment of sea stars into the adult population and will hopefully aid in conservation efforts both in rocky intertidal and coral reef ecosystems.

The most important future direction for studies of carry-over effects is to determine whether these effects exist and persist in the field, because this will ultimately test whether carry-over effects truly impact recruitment. Hettinger et al. (2013) found that acidic conditions during the larval stage significantly reduces performance in juvenile oysters in the field. However, additional studies are needed because results in studies of carry-over effects have been shown to be highly variable interspecifically (reviewed by Pechenik 2006). Studies such as

this must be conducted to fully understand the ecological importance of links in life history stages and whether carry-over effects can ultimately control population and community structure in marine systems.

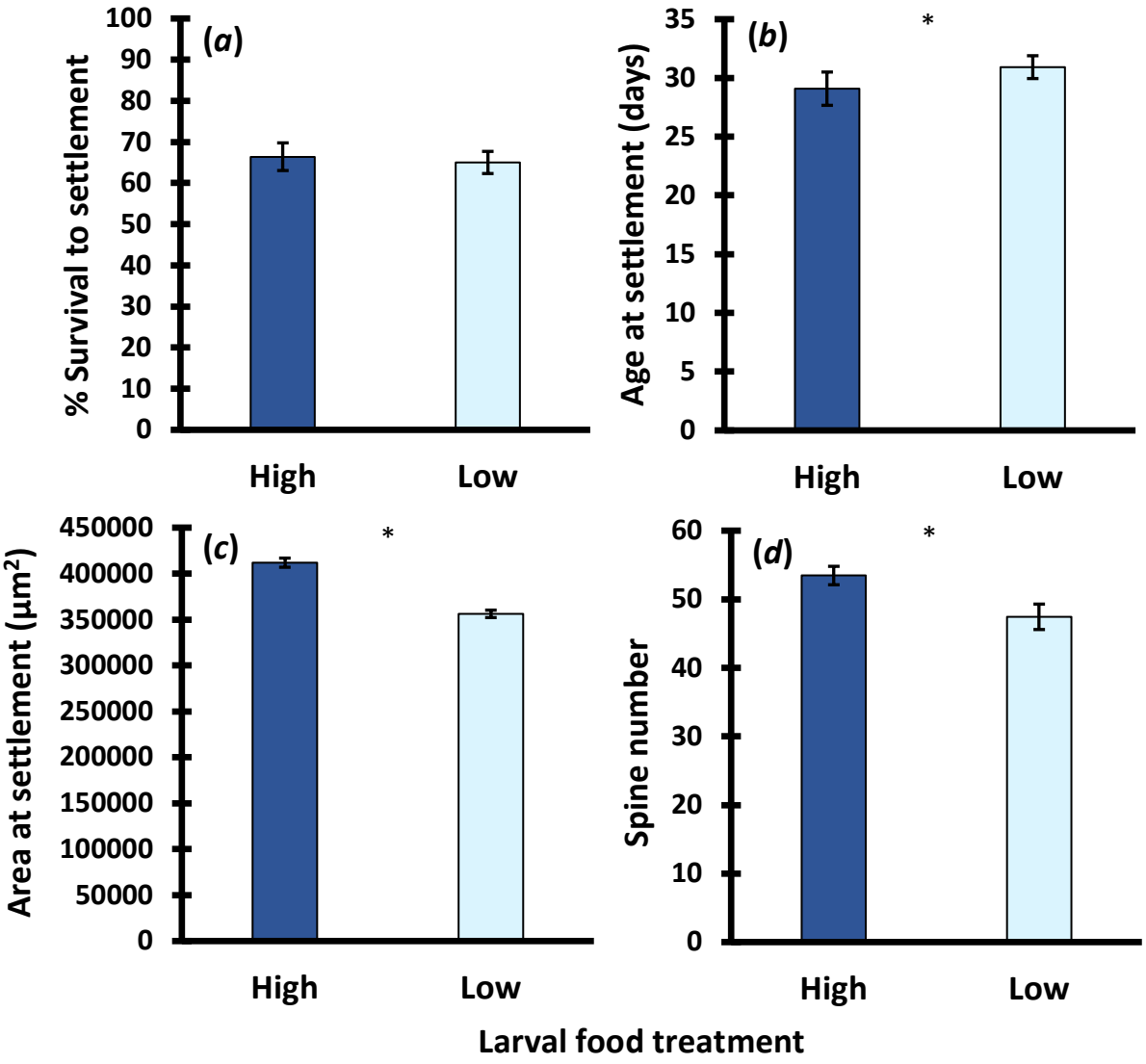

Figure 1. Mean (±SE) (*a*) percent survival, (*b*) age, (*c*) juvenile area, and (*d*) juvenile spine number at settlement for *Asterias forbesi* larvae reared with high food concentration (n = 25 beakers, 20 larvae beaker^{-1}) and with low food concentration (n = 20 beakers, 20 larvae beaker^{-1}). Percent survival to settlement in each beaker was analyzed using a one-way ANOVA. Age, area, and spine number were each analyzed using a linear mixed model. Asterisks over bars indicate a significant effect ($p < 0.05$) of larval food treatment on the response variable.

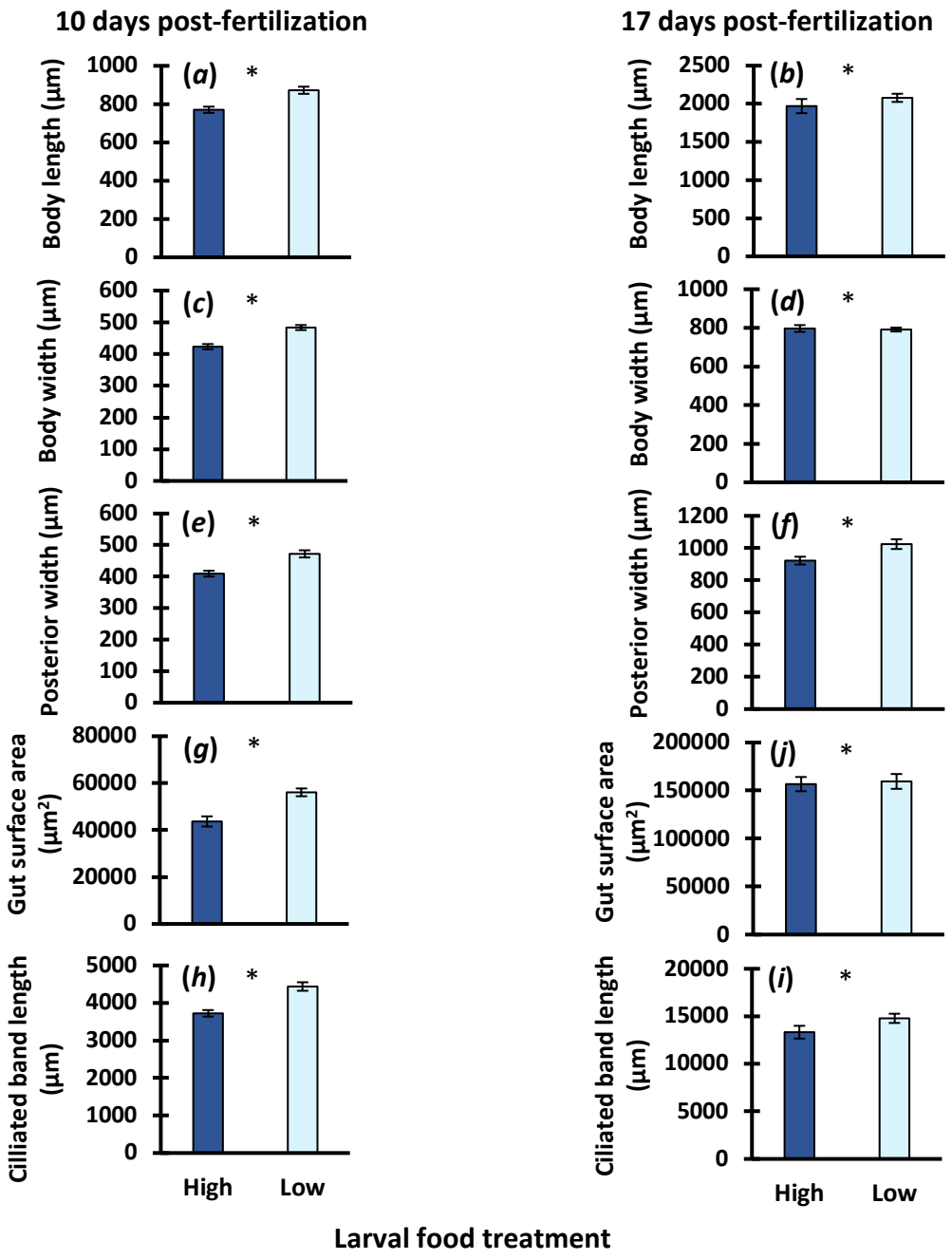

Figure 2. Mean (±SE) (*a*-*b*) body lengths, (*c*-*d*) body widths, (*e*-*f*) posterior body widths, (*g*-*j*) gut surface areas, and (*h*-*i*) ciliated band lengths of *Asterias forbesi* larvae reared under high food concentration and low food concentration (n = 10 replicate beakers larval food treatment^{-1}, 5 larvae beaker^{-1}). Measurements were

taken 10 days (left column) and 17 days (right column) post-fertilization. A two-way ANOVA with larval food treatment and age at measurement as fixed effects was conducted for each larval morphological trait. Asterisks over bars indicate a significant effect ($p < 0.05$) of larval food treatment on the larval morphological trait; there was also a significant effect of age at measurement for each larval morphological trait.

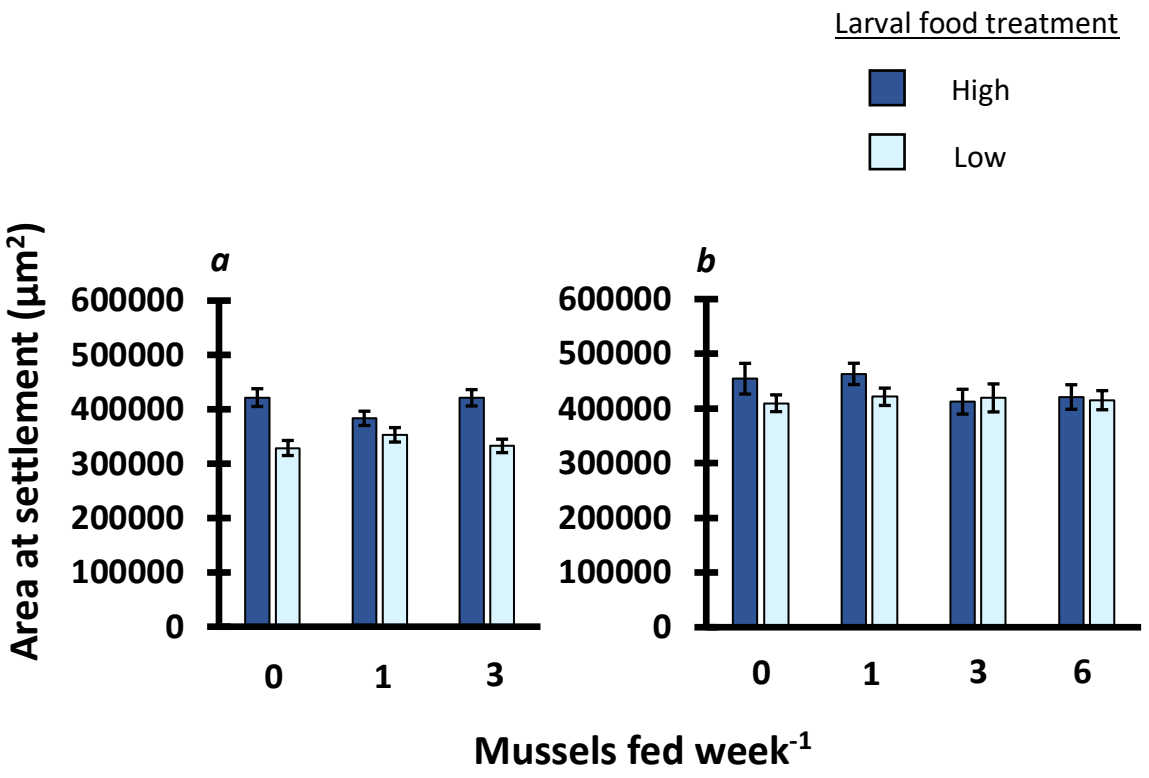

Figure 3. Mean (±SE) area at settlement for *Asterias forbesi* (*a*) early settlers (*n* = 25 treatment^{-1}) and (*b*) late settlers (*n* = 20 or 21 treatment^{-1}) in the Juvenile Feeding Experiment. Among early settlers, juveniles from low larval food background had significantly smaller area at settlement (linear mixed model: $p < 0.001$), but mean area at settlement did not differ between juvenile food treatments (linear mixed model: $p = 0.915$). Among late settlers, there was no significant effect of larval food treatment (linear mixed model: $p = 0.247$) or juvenile food treatment (linear mixed model: $p = 0.229$) on juvenile area at settlement.

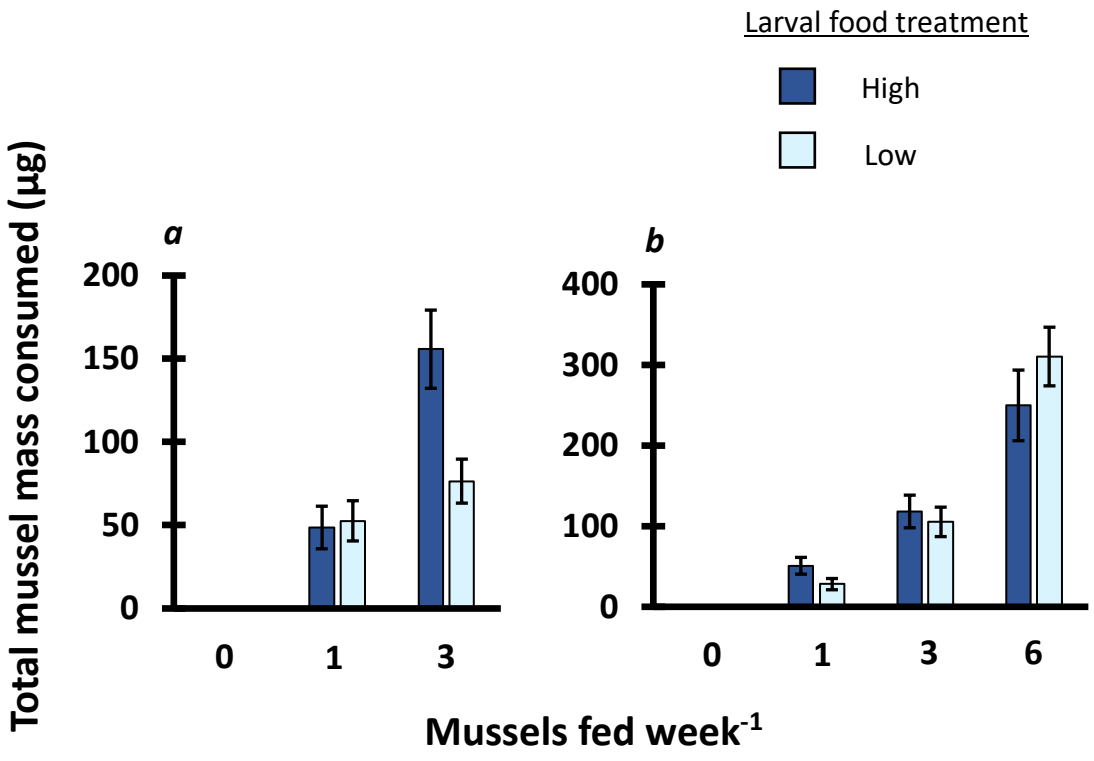

Figure 4. Mean (±SE) mussel mass consumed (mean ±SE) for *Asterias forbesi* (*a*) early settlers (n = 25 treatment^{-1}) and (*b*) late settlers (n = 20 or 21 treatment^{-1}) in the Juvenile Feeding Experiment. For early settlers, both larval food treatment (linear mixed model: p = 0.020) and juvenile food treatment (linear mixed model: p < 0.001) had significant effects on total mussel mass consumed. For late settlers, there was no significant effect of larval food treatment (linear mixed model: p = 0.548) on total mussel mass consumed but there was a significant effect of juvenile food treatment (linear mixed model: p < 0.001).

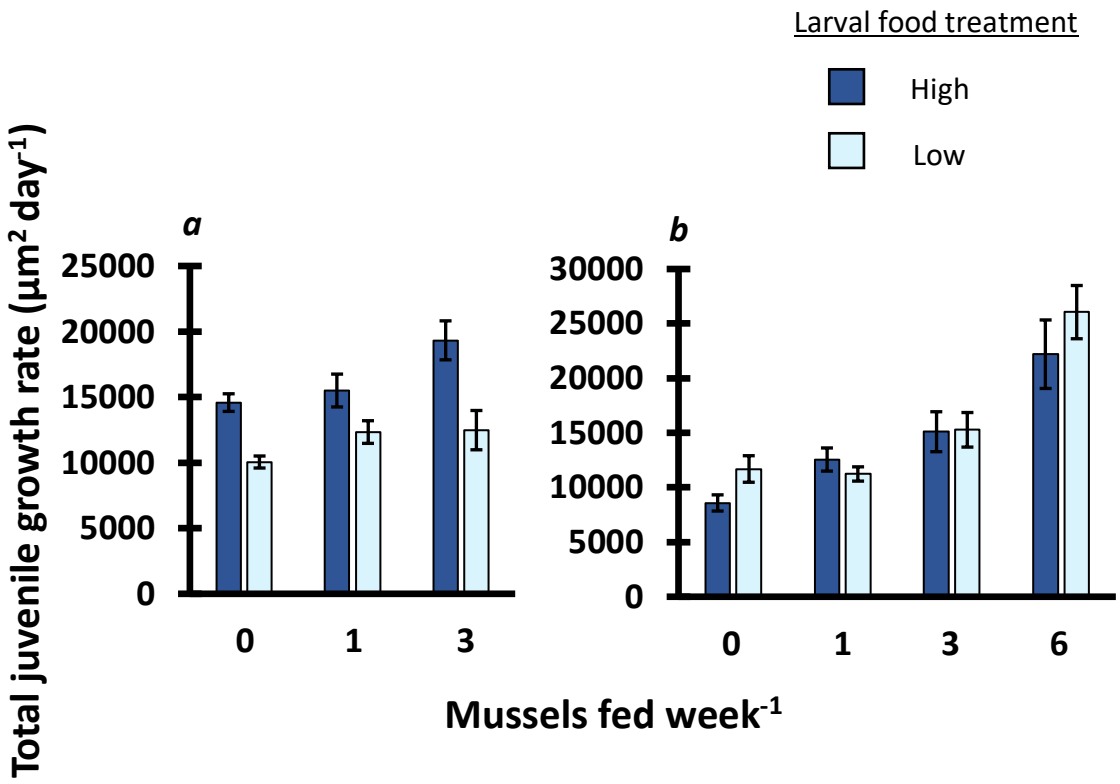

Figure 5. Mean (±SE) total juvenile growth rate (mean ±SE) for *Asterias forbesi* (*a*) early settlers (n = 25 treatment^{-1}) and (*b*) late settlers (n = 20 or 21 treatment^{-1}) in the Juvenile Feeding Experiment. For early settlers, both larval food treatment (linear mixed model: $p < 0.001$) and juvenile food treatment (linear mixed model: $p < 0.001$) had significant effects on total juvenile growth rate. For late settlers, juvenile food treatment had a significant effect on total growth rate (linear mixed model: $p < 0.001$) but larval food treatment had no significant effect ($p = 0.630$).

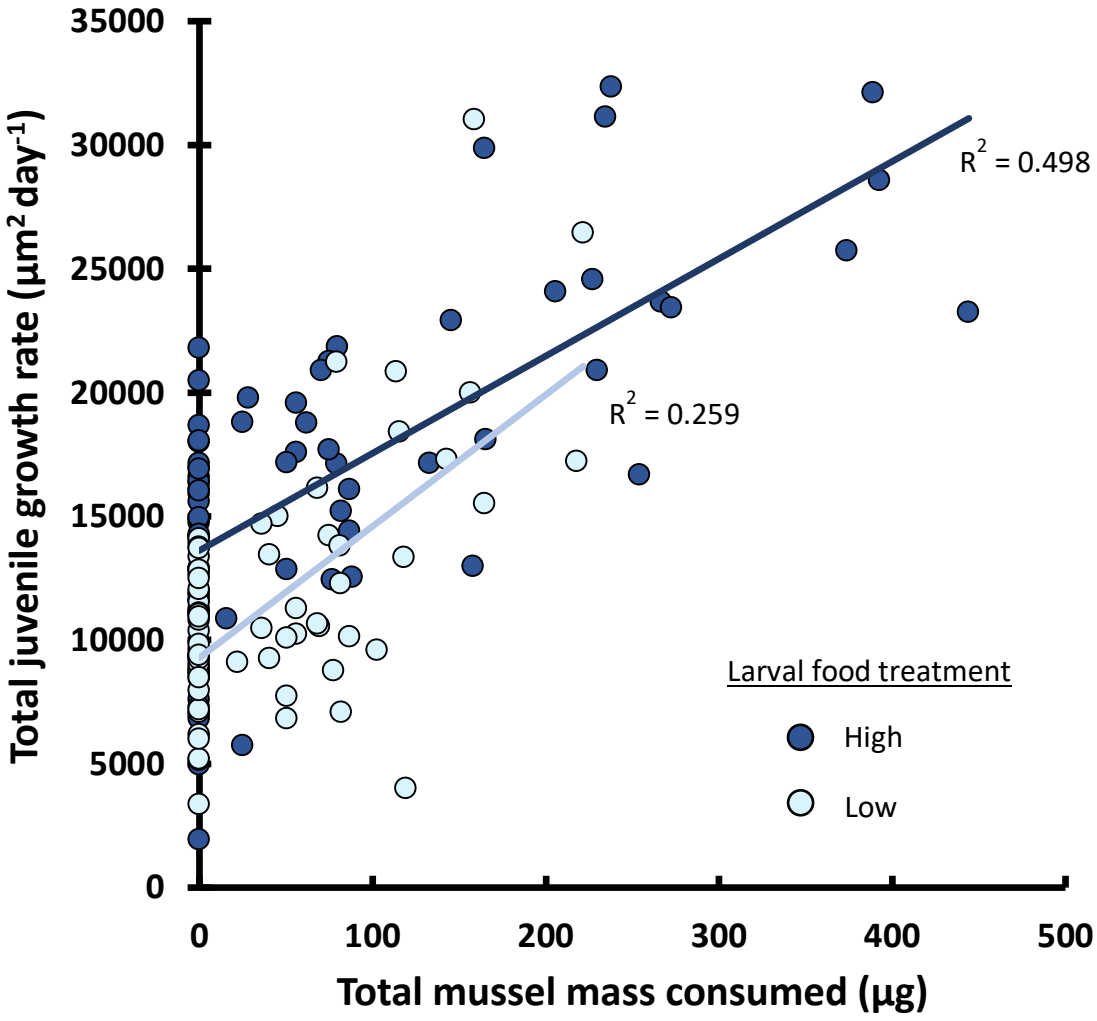

Figure 6. Total juvenile growth rate as a function of the total mussel mass consumed during for early settlers in the Juvenile Feeding Experiment (n = 75 treatment^{-1}). Larval food treatment (linear mixed model: p = 0.001) and juvenile food treatment (linear mixed model: p < 0.001) each had a significant effect on total juvenile growth rate.

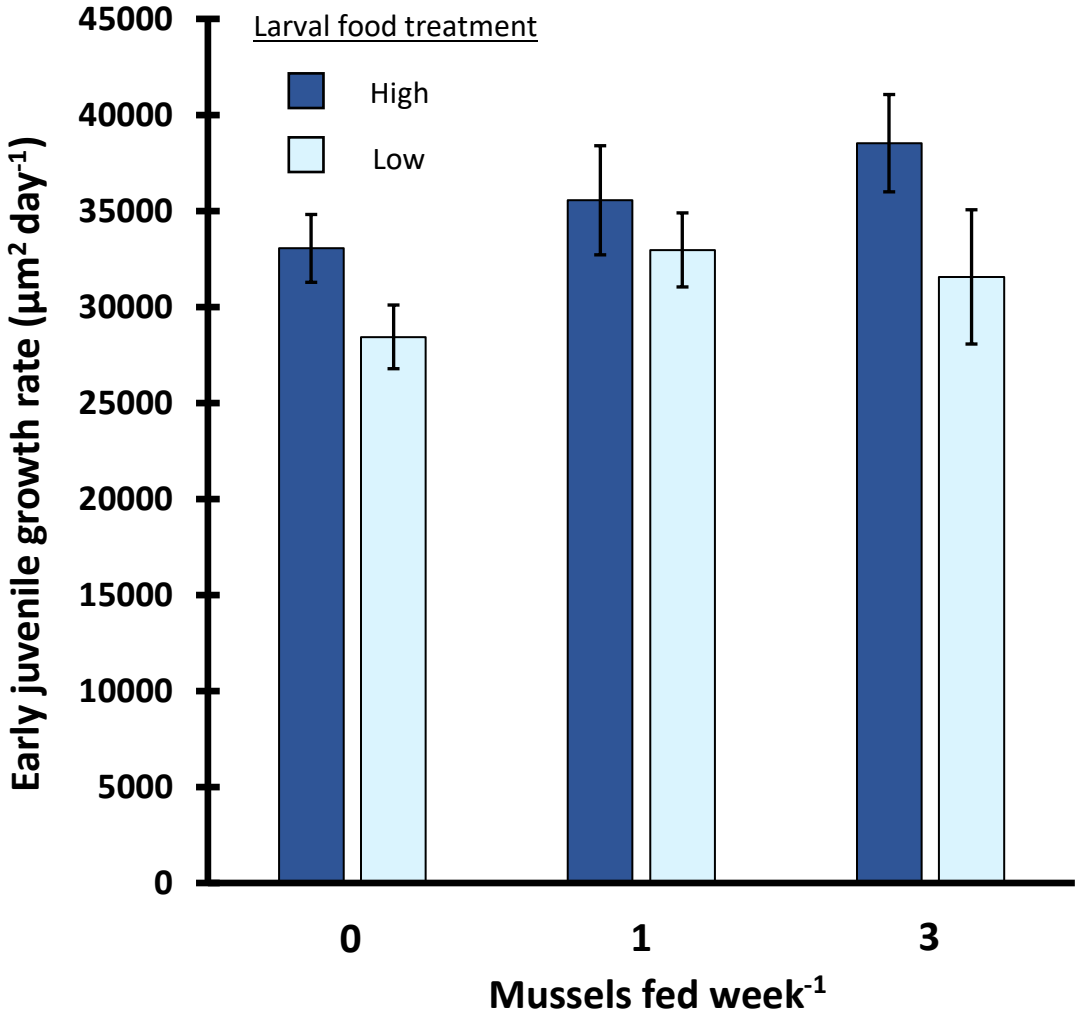

Figure 7. Early juvenile growth rate (mean ±SE) for *Asterias forbesi* early settlers in Juvenile Feeding Experiment (n = 25 treatment^{-1}). Larval food treatment was marginally insignificant (linear mixed model: p = 0.059), and juvenile food treatment had no significant effect (linear mixed model: p = 0.128) on early juvenile growth rate.

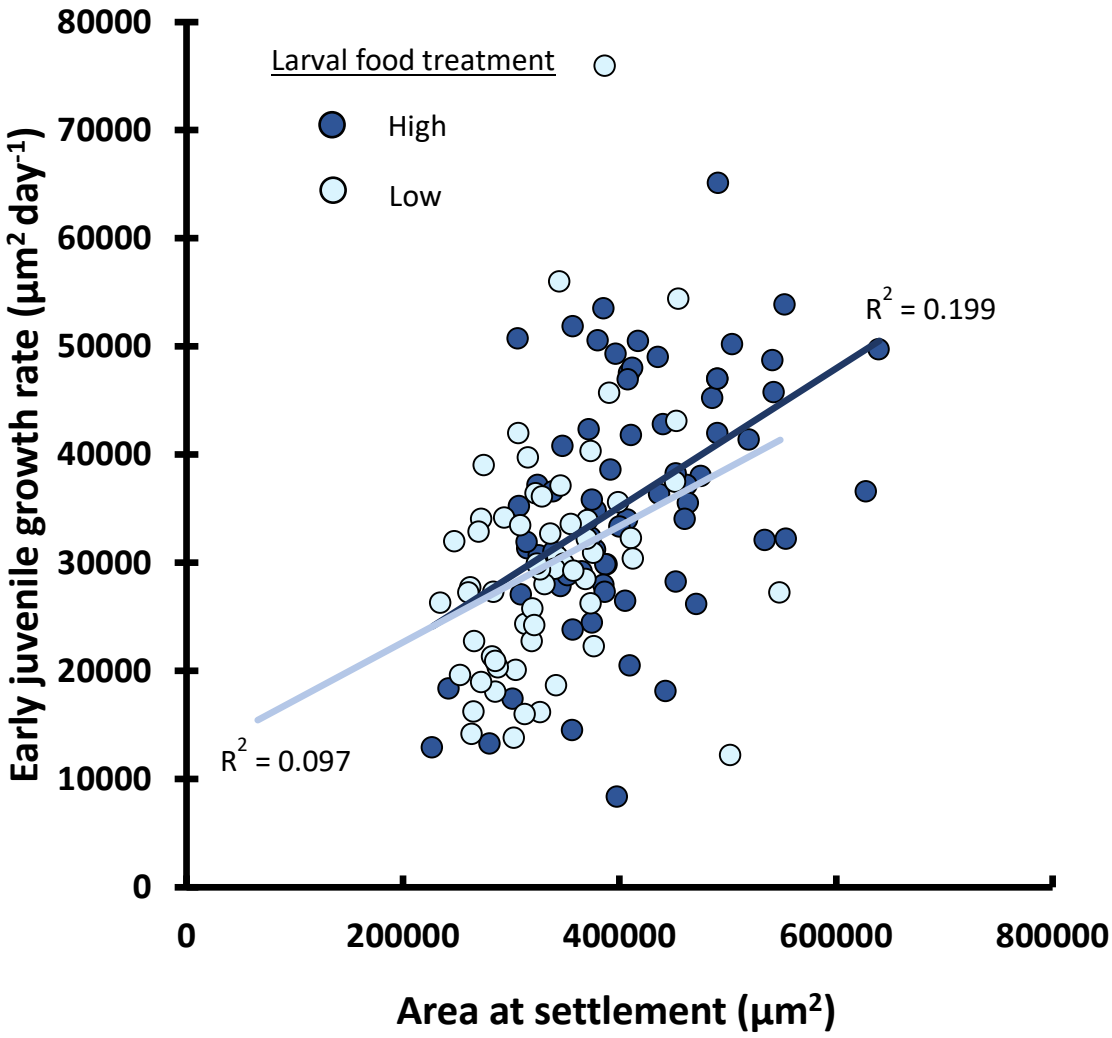

Figure 8. Early juvenile growth rate as a function of area at settlement for *Asterias forbesi* early settlers in the Juvenile Feeding Experiment (n = 75 treatment^{-1}). Area at settlement had a significant effect on early juvenile growth rate (linear mixed model: $p < 0.001$) but larval food treatment had no significant effect (linear mixed model: $p = 0.854$).

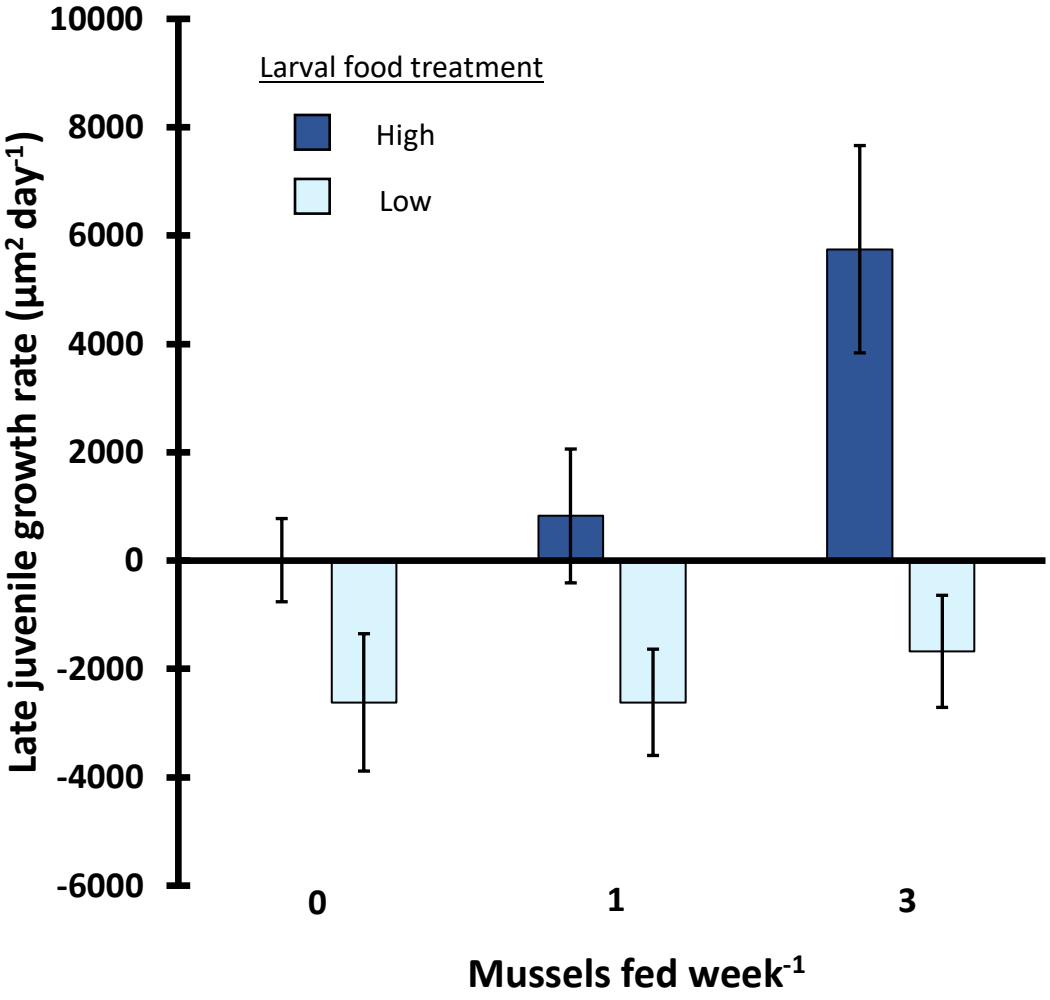

Figure 9. Late juvenile growth rate (mean ±SE) for *Asterias forbesi* early settlers in the Juvenile Feeding Experiment (n = 25 treatment^{-1}). Both larval food treatment (linear mixed model: $p < 0.001$), and juvenile food treatment (linear mixed model: $p = 0.019$) had a significant effect on late juvenile growth rate.

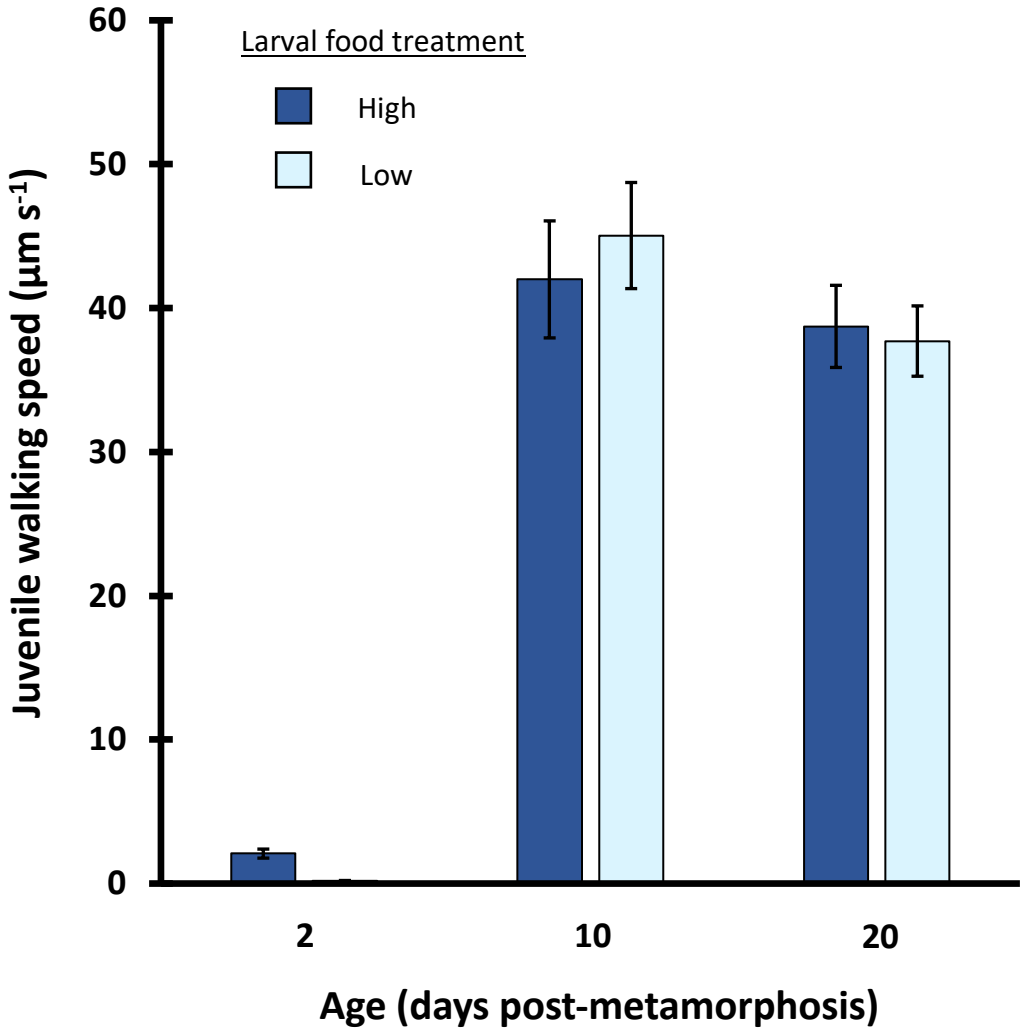

Figure 10. Juvenile walking speed (mean ±SE) for *Asterias forbesi* early settlers in the Juvenile Feeding Experiment (n = 75 treatment^{-1}). Walking speed was measured 2, 10, and 20 days post-metamorphosis. Age at filming had a significant effect on walking speed (linear mixed model: $p < 0.001$) but larval food treatment (linear mixed model: $p = 0.855$) and juvenile food treatment (linear mixed model: $p = 0.754$) did not significantly affect juvenile walking speed.

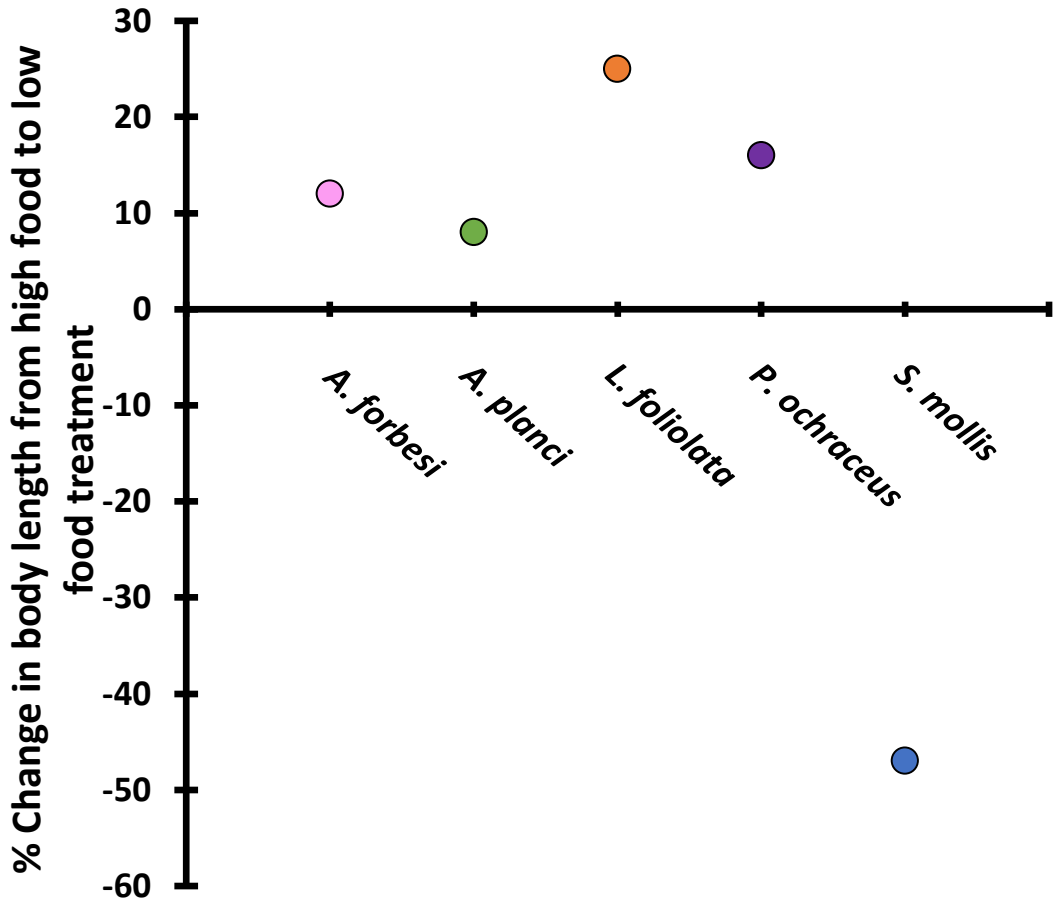

Figure 11. Comparison of *Asterias forbesi* larval plasticity results to published plasticity studies in asteroid species. (Data adapted from Wolfe et al. 2015; George 1994; George 1999; Poorbagher et al. 2010).

Table 1. Response variables measured at settlement for *Asterias forbesi* larvae reared to metamorphosis on high and low food concentrations. Percent survival in each beaker was analyzed using a one-way ANOVA with larval food treatment as a fixed effect. Age, juvenile area, and juvenile spine number were analyzed using a linear mixed model with larval food treatment as a fixed factor and beaker as a random factor. Significant effects ($p<0.05$) are in bold.

Response variable	*df*	*F*-ratio	*p*-value
a) Percent survival	1, 43	0.098	0.755
b) Age	1, 43	6.067	**0.018**
c) Juvenile area	1, 43	16.137	**<0.001**
d) Juvenile spine number	1, 43	7.118	**0.011**

Table 2. Two-way ANOVA table for *Asterias forbesi* larval morphological traits measured in the plasticity experiments in which larvae were reared under high and low food concentrations. Larval food treatment and day of measurement were modeled as fixed effects. Gut surface area and ciliated band length were square-root transformed prior to analysis to meet normality assumptions. Significant effects ($p<0.05$) are in bold.

Response variable	*df*	*F*-ratio	*p*-value
a) Body length			
Food	1, 36	5.759	**0.022**
Age	1, 36	754.599	**<0.001**
Food*Age	1, 36	0.005	0.942
b) Body width			
Food	1, 36	5.554	**0.024**
Age	1, 36	855.372	**<0.001**
Food*Age	1, 36	7.968	**0.008**
c) Posterior body width			
Food	1, 36	15.819	**<0.001**
Age	1, 36	657.549	**<0.001**
Food*Age	1, 36	0.919	0.344
d) Gut surface area			
Food	1, 36	4.367	**0.044**
Age	1, 36	534.459	**<0.001**
Food*Age	1, 36	2.712	0.108
e) Ciliated band length			
Food	1, 36	10.291	**0.003**
Age	1, 36	861.579	**<0.001**
Food*Age	1, 36	0.039	0.845

Table 3. Linear mixed model table for response variables measured for early settlers in the Juvenile Feeding Experiment. Juveniles from high larval food background and low larval background were reared under various juvenile food treatments. Larval food treatment, juvenile food treatment, area at settlement, and mussel mass consumption were modeled as fixed effects, depending on the model. Larval beaker was modeled as a random effect for every model. Significant effects ($p<0.05$) are in bold.

Response variable	*df*	*F*-ratio	*p*-value
a) Area at settlement			
Larval food	1, 32	24.699	**<0.001**
Juvenile food	1, 159	0.089	0.915
Larval*Juvenile	1, 159	2.523	0.083
b) Mussel mass consumption			
Larval food	1, 30	6.101	**0.020**
Juvenile food	2, 117	36.664	**<0.001**
Larval*Juveniles	2, 117	6.872	**0.002**
c) Total growth rate			
Larval food	1, 32	18.523	**<0.001**
Juvenile food	1, 112	7.591	**<0.001**
Larval*Juvenile	1, 112	2.107	0.127
d) Total growth rate			
Larval food	1, 46	12.940	**<0.001**
Mussel mass consumption	1, 113	71.024	**<0.001**
Larval*Mussel	1, 113	0.350	0.555
e) Early growth rate			
Larval food	1, 32	3.843	0.059
Juvenile food	1, 120	2.091	0.128
Larval*Juvenile	1, 120	0.432	0.650
f) Early growth rate			

Larval food	1, 124	0.034	0.854
Area at settlement	1, 129	10.757	**<0.001**
Larval*Area	1, 129	0.087	0.769
g) Late growth rate			
Larval food	1, 27	17.386	**<0.001**
Juvenile food	1, 122	4.097	**0.019**
Larval*Juvenile	1, 122	1.957	0.146

Table 4. Linear mixed model table for response variables measured for late settlers in the Juvenile Feeding Experiment. Juveniles from high larval food background and low larval background were reared under various juvenile food treatments. Larval food treatment, juvenile food treatment, and mussel mass consumption were modeled as fixed effects, depending on the model. Larval beaker was modeled as a random effect for every model. Significant effects (p<0.05) are in bold.

Response variable	*df*	*F*-ratio	*p*-value
a) Area at settlement			
Larval food	1, 76	1.360	0.247
Juvenile food	1, 151	1.460	0.229
Larval*Juvenile	1, 151	0.203	0.653
b) Mussel mass consumed			
Larval food	1, 62	0.366	0.548
Juvenile food	1, 140	198.850	**<0.001**
Larval*Juveniles	1, 140	0.259	0.612
c) Total growth rate			
Larval food	1, 74	0.234	0.630
Juvenile food	1, 150	84.892	**<0.001**
Larval*Juvenile	1, 150	0.021	0.885

Table 5. Linear mixed model table for walking speed of early settlers in the Juvenile Feeding Experiment. Larval food treatment, juvenile food treatment, and age at filming were modeled as fixed effects while larval beaker was modeled as a random effect. Significant effects (p<0.05) are in bold.

Response variable	*df*	*F*-ratio	*p*-value
Speed			
Larval food	1, 31	0.034	0.855
Juvenile food	2, 378	0.283	0.754
Age at filming	2, 370	150.322	**<0.001**

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