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ORIGINAL PAPER

# Carryover effects in a sea star: juvenile resource availability does not compensate for a poor larval environment

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## Abstract

Carryover effects are widespread in nature and can link early-life experiences to the regulation of populations. However, for organisms with complex life cycles, it is unclear whether offspring can overcome negative early-life experiences when provided with abundant post-metamorphic resources. We tested this by rearing larvae of the keystone sea star *Asterias forbesi*, under high or low food conditions, and then reared the juveniles for 2–3 weeks under one of four food treatments. Larvae reared under low food conditions took longer to reach metamorphosis and settled as smaller juveniles with fewer spines. For early settlers (mean age at settlement = 24.0 d), carryover effects of low larval food significantly reduced post-metamorphic size, mussel consumption and growth. However for late settlers (mean age at settlement = 29.3 d), there were no carryover effects of larval food availability detected post-metamorphosis. The differences between early and late settlers may indicate a trade-off between larval duration and the presence of carryover effects. Our data suggest that carryover effects mediated by body size at settlement could determine post-metamorphic survival, growth, and performance, ultimately impacting the recruitment of this keystone predator.

**Keywords** Asteroidea · Carryover effects · Juvenile · Larva · Metamorphosis

## Introduction

Carryover effects are characteristics that originate early in development and continue to impact an individual's phenotype later in life (in contrast to "latent effects" which manifest only in the juvenile or adult stages, see Pechenik 2006). Carryover effects are widespread across taxa including plants, insects, marine invertebrates, fish, amphibians, reptiles, birds and mammals (Miller et al. 1987; Pechenik and Cerulli 1991; Merila and Svensson 1997; Wendt 1998; Maldonado and Young 1999; Altwegg and Reyer 2003; Steinbrenner et al. 2012; Giovanoli et al. 2013; Hartmann et al. 2013; Touchon et al. 2013; Dingeldein and White 2016; Balogh and Byrne 2020). Phenotypic links among life history stages can have major ecological consequences for populations. For example, in marine bryozoans, colonizer phenotype, and not just offspring supply, affected population dynamics—individuals with short dispersal had greater reproductive yield compared to many individuals with long dispersal (Burgess and Marshall 2011). Carryover effects can also have evolutionary implications, because if one trait is expressed in multiple life stages, selection in one stage may be constrained by selection in another stage (reviewed by Marshall and Morgan 2011).

Carryover effects can impact a number of life history traits, such as survival, timing of stage transitions, body size and growth rate (reviewed by Pechenik 2006). Among these, body size is perhaps the most important trait affected by carryover effects, because it is correlated with predator avoidance, competitive ability and feeding success, among other performance measures (Werner and Gilliam 1984; Arendt 1997). Therefore, carryover effects impacting survival, growth rate and/or performance are likely mediated by body size. For example, tadpoles (*Agalychnis callidryas*) reared at high densities were smaller after metamorphosis, and juvenile frogs began feeding earlier (Bouchard et al. 2016). Similarly, reef fish (*Thalassoma bifasciatum*) larvae

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with high growth rates were larger post-settlement and also displayed predator-avoidance behavior that low-quality larvae did not display (Dingeldein and White 2016).

One mechanism used by some organisms to mitigate the negative effects of poor initial body condition or nutritional reserves is compensatory growth (i.e., increasing growth rate later in life; Metcalfe and Monaghan 2001). For example, juvenile Arctic charr (*Salvelinus alpinus*) initially reared in cold water, resulting in slow growth, significantly increased their growth rates after being transferred to warm water, and after five weeks, their body weights did not differ from controls (Mortensen and Damsgård 1993; Metcalfe and Monaghan 2001). However, compensatory growth does not always occur; when oyster larvae (*Ostrea lurida*) were reared in acidic conditions, they did not exhibit compensatory growth as juveniles when returned to normal pH conditions (Hettinger et al. 2013).

Evidence of compensatory growth in some animal systems but not others suggests the interaction between carryover effects and compensatory growth is complex. Studies in organisms with complex life cycles (CLCs), that also undergo metamorphosis, have mostly focused on whether ecological factors in the pre- or post-metamorphic stage are more important for determining offspring supply and recruitment (Underwood and Fairweather 1989; Zimmer et al. 2009). However, carryover effects across the metamorphic boundary demonstrate these life stages are not independent of one another (Pechenik et al. 1998). Therefore, despite numerous studies in organisms with CLCs, the connection between carryover effects, adult fitness and population dynamics is still unclear.

In this study we tested for carryover effects of food-limiting conditions in the sea star *Asterias forbesi*, and whether any resulting negative consequences can be overcome post-metamorphosis when individuals are well fed. Food availability and, by extension, growth rate, in early life has major ecological implications for populations, influencing sex ratios in sea lampreys (*Petromyzon marinus*; Johnson et al. 2017), morph determination and intraspecific competition in toads (*Scaphiopus multiplicatus*; Pfennig 1992), and migration condition in birds (*Parus caeruleaus*; Merila and Svenson 1997). Additionally, resource availability could influence whether compensatory growth occurs (Metcalfe and Monaghan 2001; Hector and Nakagawa 2012). Three studies in marine invertebrates found that low larval food conditions affect post-metamorphic growth, even when juveniles are fed (Phillips 2002; Emlet and Sadro 2006; Leung and McAfee 2020). Our aim is to build off of these studies and address whether compensatory growth occurs and if it depends on juvenile food supply. We addressed this knowledge gap by rearing sea star larvae through metamorphosis on high and low food levels. These experiments allowed us to assess the role of phenotypic plasticity in ciliary band length as a potential mechanism for compensatory growth. Then we reared juveniles from each larval food treatment on one of four juvenile food levels and evaluated their survival and growth, as well as performance, to try to explain why compensatory growth might not occur (e.g., low feeding rates, slow walking speeds).

## 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 1 L of 0.45-µm filtered seawater (FSW). Ten mL of dilute sperm from each of ten males were combined in a beaker and mixed well, and eggs were fertilized with 1 mL of dilute sperm from the combined sperm beaker. Prior to the pooled fertilization, to confirm 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 six females used in the experiment had fertilization scores > 90%.

Developing embryos reached the early gastrula stage after 24 h and were transferred to 45 glass beakers (250 mL volume) filled with 200 mL FSW at a density of 1 larva 10 $mL^{-1}$. Beakers were given a unique ID and 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, strain #LB999), *Isochrysis galbana* (National Center for Marine Algae and Microbiota, West Boothbay Harbor, ME, strain #CCMP1323), and *Rhodomonas lens* (National Center for Marine Algae and Microbiota, West Boothbay Harbor, ME, strain #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 Primatrode with NTC pH electrode (Metrohm, Riverview, FL) 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 and Hinegardner 1974) and a blue mussel shell (*Mytilus edulis*) was placed in each beaker to encourage larval settlement (Trackenberg et al. 2020). Shells and beakers were checked for settlement once per day and age at settlement was recorded. Juveniles were removed from the shell or beaker two days after they were first observed to ensure that juveniles had completed metamorphosis and to prevent damaging them upon removal. Once removed, the number of spines on each juvenile was counted under an Olympus CX41 compound microscope. Juveniles were then photographed at 40 × magnification, and two-dimensional area 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, ten beakers from the high food treatment and ten 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 100 × magnification (10 days post-fertilization) or 40 × 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, oral hood, gut hood, and larval sides (as in Wolfe et al. 2015a) 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

We conducted an experiment to evaluate the relative importance of the larval and juvenile food environments for post-metamorphic survival, growth, and performance. Juvenile sea stars from each larval food background were randomly assigned to a juvenile feeding treatment. Juvenile *A. forbesi* were fed juvenile *M. edulis* (300–1000 µm in length) that were removed from filamentous algae collected in the field at Giant Stairs, Bailey Island, Maine (43°43′36.09″N, 69°59′33.15″W). We completed two trials of the experiment, henceforth referred to as 'Trial 1' and 'Trial 2'. Juveniles used in Trial 1 were collected on days 22–27 post-fertilization and juveniles in Trial 2 were collected on days 27–32 post-fertilization. Juveniles in both trials were derived from the same population of larvae used in the Larval Feeding Experiment.

Immediately following metamorphosis, juvenile sea stars from each larval food treatment were randomly assigned to a juvenile food treatment (Fig. 1). Trial 1 juveniles were provided either 0, 1, or 3 juvenile *M. edulis* week$^{-1}$, resulting in six total treatments, each with 25 juvenile sea stars. Juveniles were reared for 18–24 days. For juveniles in Trial 2, an additional juvenile food treatment was added (6 juvenile *M. edulis* week$^{-1}$), yielding eight total treatments, each with 20 or 21 juvenile sea stars, and juveniles were reared for 13–15 days. The number of mussels eaten by each sea star was recorded at regular intervals—in Trial 1, three checks were conducted in the first week, and one check was conducted each week thereafter. In Trial 2, checks were conducted once per week. If a juvenile sea star had consumed a juvenile mussel, the empty shell was removed and the shell width was measured at 40 × magnification on a compound microscope. We found that mussel shell width was a significant predictor of mussel mass, so we converted all mussel shell widths to mussel mass for further analysis (Online Resource Fig. S1, Table S1). 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 also recorded throughout the experiment.

For all juvenile sea stars, photographs were taken at 40 × magnification on an Olympus CX41 compound

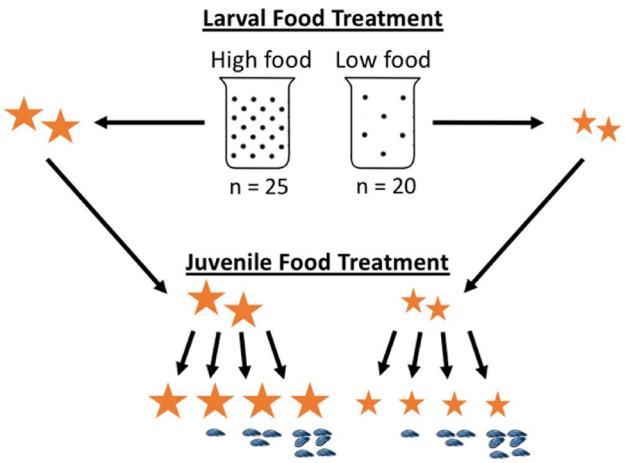


**Fig. 1** Experimental design for the Juvenile Feeding Experiment in which *Asterias forbesi* larvae were reared in beakers (1 larva 10 mL$^{-1}$) and fed either high ($n$ = 25 beakers, 7,500 algal cells species$^{-1}$ ml$^{-1}$) or low ($n$ = 20 beakers, 2500 algal cells species$^{-1}$ ml$^{-1}$) food concentration. After metamorphosis, juveniles were put in one of four food treatments ($n$ = 20–25 juveniles per treatment). Juvenile sea stars were fed zero, one, three or six juvenile mussels (*Mytilus edulis*) per week for 2–3 weeks

microscope at the beginning and the end of the experiment. These images were used to measure the two-dimensional area of each sea star in ImageJ64. The change in area (growth) was calculated as the difference between the size at settlement and the size at the end of the experiment.

### Juvenile performance experiment

To assess juvenile performance, we measured walking speed in juveniles from Trial 1 of the Juvenile Feeding Experiment. A Canon Vixia HFM52 video camera was mounted on a dissecting microscope at 20 × magnification. 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 a scale in view underneath. Juvenile sea stars were given a maximum time of five minutes to walk in any direction. Filming ended if the sea star walked out of the frame of the video or when 5 min elapsed, whichever came first. On days 10 and 21, each juvenile sea star's area was re-measured so that speed could later be correlated with body size.

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 scale in each frame, and juvenile speed was later calculated from the length of this path and the time elapsed.

### Statistical analyses

We used R (version 4.2.2, R Core Team 2022) and the 'lme4' (Bates et al. 2015) and 'car' (Fox and Weisberg 2019) packages for statistical analyses. We visually checked normality and homoscedasticity of residuals using Q–Q plots and residual plots, respectively, for each response variable (Quinn and Keough 2002).

For the Larval Plasticity Experiment, we used a repeated measures multivariate analysis of variance (MANOVA) to evaluate how larval food treatment (categorical, two levels: 'low' and 'high') and age at measurement (categorical, two levels: '10' and '17') affected eight larval morphological features (length, width, posterior width, gut surface area, oral hood, gut hood, sides, and ciliated band length). We calculated means within a beaker for each larval trait, and then used the beaker as a replicate for the analysis. Ciliated band length was square root transformed to meet normality assumptions. Larval beaker was included as a random effect to account for non-independence due to repeated measures.

For the Larval Feeding Experiment, beaker means were used as replicates for response variables measured at settlement. Survival to settlement was evaluated as the percentage of individuals in a beaker that successfully completed metamorphosis. A one-way ANOVA was used to analyze the effect of larval food treatment on survival, age, juvenile area and spine number at settlement.

For the Juvenile Feeding Experiment, we felt it was most appropriate to conduct separate analyses for Trial 1 and Trial 2. Our trials do not represent runs (i.e., blocks) of the experiment. Rather, juveniles in both trials were collected from the Larval Feeding Experiment and then reared under different conditions as juveniles—the trials differed in length of time and in the number of juvenile feeding treatments. First, to check whether juveniles began the experiment at the same size across juvenile food treatments, we evaluated juvenile area at settlement using a linear mixed model with larval food treatment and juvenile food treatment (categorical, four levels: 'unfed', 'low', 'medium', 'high') as fixed effects. Because we used individuals as replicates in this analysis, we accounted for the non-independence of juveniles coming from the same beaker by including larval beaker as a random effect.

For mussel mass consumption and change in juvenile area, we used a linear mixed model including larval food treatment, juvenile food treatment, experiment length (covariate, i.e., the number of days each juvenile was in the experiment) and all interactions as fixed effects. Again, we also included larval beaker as a random factor. Because some juveniles across different juvenile food treatments could come from the same larval beaker, we accounted for the non-independence by including juvenile food treatment nested within larval beaker as a random factor.

When we ran the full models for consumption and change in area across the two trials, all models were overfitted, except for the analysis of change in area in Trial 1. In the cases where the model was overfitted, the nested random effect (i.e., juvenile food treatment within larval beaker) was removed. For the consumption analysis in Trial 2, the model was still overfitted, so the random effect larval beaker was also removed. Across all models, non-significant interactions and the covariate 'experiment length' were removed from the model if $P > 0.25$ (Quinn and Keough 2002). The only interaction that was never removed from the models was that between larval food treatment and juvenile food treatment, because testing for this interaction was the goal of the study.

For juvenile survival, we used a binomial generalized linear mixed model with larval food treatment, juvenile food treatment and their interaction as fixed, categorical effects, and also included larval beaker, and juvenile food treatment nested within larval beaker as random effects. Models for both trials were overfitted, so both random factors were removed, and we conducted a binomial generalized linear model.

For the Larval Feeding Experiment and the Juvenile Feeding Experiment, we adjusted $P$ values using the false discovery rate (FDR) procedure from Benjamini and Hochberg (1995) to account for multiple non-independent response variables within each experiment. FDR procedures

control for the risk of Type I error, while retaining the power to identify significant effects, and have been deemed most appropriate for ecological and evolutionary data (Pike 2010).

For the Juvenile Performance Experiment, a repeated measures linear mixed model was used to evaluate the response variable walking speed, with larval food treatment, juvenile food treatment, and age at filming (categorical; '2', '10' and '20' days post-metamorphosis), as fixed, categorical effects. We also used a repeated measures linear mixed model to test the effects of juvenile food treatment, age at filming and juvenile area (covariate, fixed) on walking speed. For both models, we included juvenile identity, larval beaker and juvenile food treatment nested within larval beaker as random effects. The nested random effect was removed from both models due to overfitting. Again, non-significant interactions ($P > 0.25$; Quinn and Keough 2002) were removed, except for the larval food treatment by juvenile food treatment interaction.

## Results

### Larval Feeding Experiment

Across all beakers, 67.8% of larvae survived to settlement, with 66.8% survival among larvae reared in the low larval food treatment and 68.8% survival among larvae reared in the high larval food treatment (Fig. 2A). There was no effect of larval diet on the percent of larvae surviving to settlement (Fig. 2A; ANOVA: $F_{1,43} = 0.197$, $P = 0.659$). There was, however, a significant effect of larval diet on age at settlement (ANOVA: $F_{1,43} = 6.141$, $P = 0.023$) such that larvae reared on low food took 1.8 days longer to reach settlement (5.9% increase) than those reared on high food (Fig. 2B). Juveniles from the low larval food treatment also had a significantly smaller area (13.5% smaller; ANOVA: $F_{1,43} = 15.17$, $P = 0.001$) and significantly fewer spines (11.3% fewer; ANOVA: $F_{1,43} = 6.677$, $P = 0.023$) than did juveniles from the high larval food treatment (Fig. 2C, D).

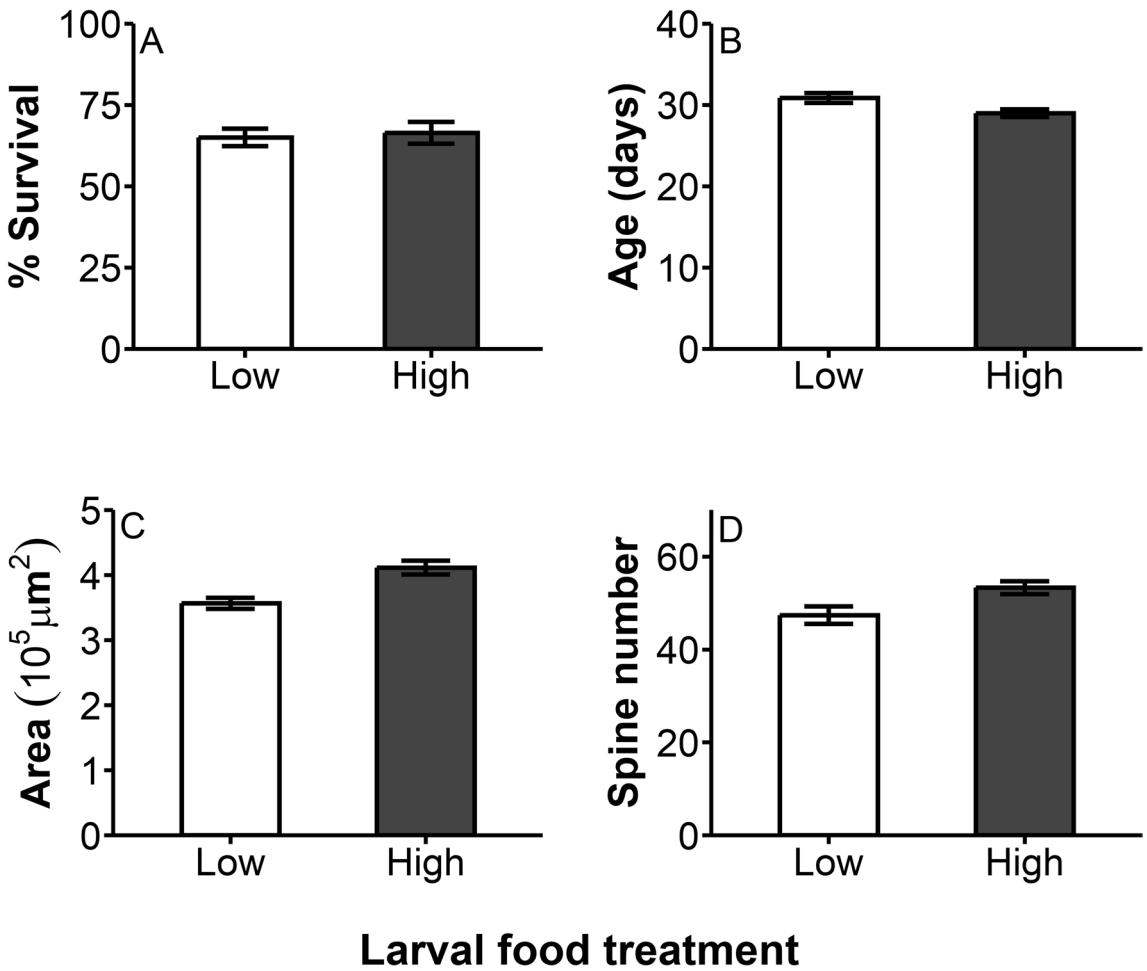


**Fig. 2** Mean (±SE) **A** larval survival, **B** age at settlement, **C** juvenile area and **D** juvenile spine number for individuals fed high larval food concentration (gray bars) and those fed low larval food concentration (white bars). Beaker means were used as replicates (low, $n = 20$; high, $n = 25$). Larvae reared on low food concentration settled later and were smaller juveniles with fewer spines

## Larval Plasticity Experiment

There was a significant interaction between larval diet and age at measurement on the size of larvae (Table 1). Overall, larvae grew through time, and larvae from the low larval food treatment were larger compared to well-fed larvae (Figs. 3, S2). However, the difference in size between larvae fed low food versus high food was greatest on day 10 (Fig. S2).

**Table 1** Repeated measures MANOVA results for eight larval morphological traits (length, width, posterior width, gut surface area, oral hood, gut hood, sides, ciliated band length) measured in the Larval Plasticity Experiment

| Source | *df* | *F* ratio | *P* value |
|---|---|---|---|
| Larval food | 8, 11 | 5.92 | **0.004** |
| Age | 8, 11 | 421.92 | **< 0.001** |
| Larval food*age | 8, 11 | 8.6 | **0.001** |

Larval food treatment, age at measurement and their interaction were included as fixed effects, and larval beaker as a random effect to account for non-independence due to repeated measures. Significant effects are bolded ($P < 0.05$)

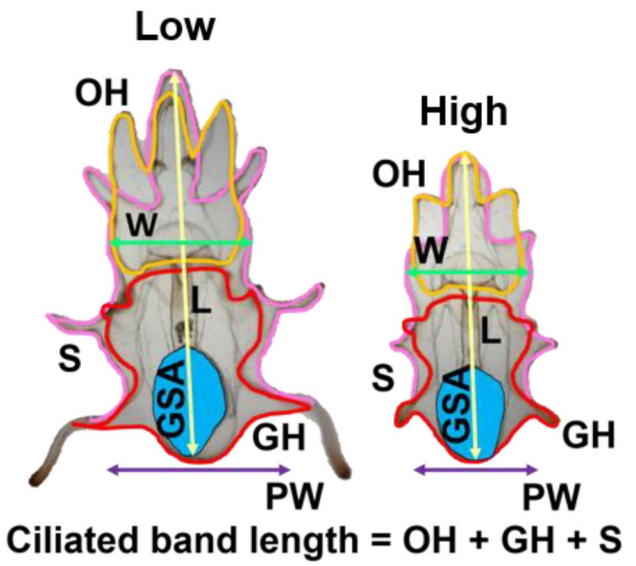


**Fig. 3** Larval morphological features measured 10 and 17 days post-fertilization to test plasticity in response to food concentration. Morphological features measured were length (L, yellow), width (W, green), posterior width (PW, purple), gut surface area (GSA, blue), oral hood (OH, orange), gut hood (GH, red), and sides (S, pink). Oral hood, gut hood, and side lengths were summed to find total ciliated band length. Larvae were reared in beakers (1 larva 10 $mL^{-1}$) and fed either low or high food concentration. Five larvae from each of ten beakers per treatment were measured. Beaker means were used as replicates for analyses. There was a significant interaction between age and larval food treatment—larvae fed low food concentrations were larger, and the greatest difference between food treatments was on day 10

## Juvenile Feeding Experiment

Juveniles from Trial 1 of the Larval Feeding Experiment settled on average 5 days sooner than those from Trial 2 (early: 22–27 days, mean = 24.0 days; late: 27–32 days, mean = 29.3 days). In Trial 1, juveniles reared on low food as larvae were significantly smaller at settlement (Fig. S3A, Table 2A). For Trial 2, there were no differences in mean area at settlement between juveniles from different larval food backgrounds (Fig. S3B, Table 2D). Size at settlement was not different among juvenile food treatments for either trial (Table 2A, D).

For Trial 1, juveniles from high larval food background, and those that were fed more as juveniles, gained more mass, but the interaction between larval and juvenile

**Table 2** Linear model results for response variables measured for Trial 1 of the Juvenile Feeding Experiment

| Response variable<br>Source | *df* | *F* ratio | *P* value |
|---|---|---|---|
| Trial 1 | | | |
| A) Area at settlement | | | |
| Larval food | 1, 26 | 18.29 | **0.001** |
| Juvenile food | 2, 111 | 0.062 | 0.94 |
| B) Change in area | | | |
| Larval food | 1, 30 | 18.52 | **0.001** |
| Juvenile food | 2, 44 | 6.73 | **0.008** |
| Larval*juvenile | 2, 44 | 2.88 | 0.355 |
| Experiment length | 1, 119 | 1.37 | 0.158 |
| C) Total consumption | | | |
| Larval food | 1, 28 | 5.92 | **0.047** |
| Juvenile food | 1, 77 | 11.63 | **0.004** |
| Larval*juvenile | 1, 77 | 5.34 | **0.047** |
| Trial 2 | | | |
| D) Area at settlement | | | |
| Larval food | 1, 34 | 1.45 | 0.521 |
| Juvenile food | 1, 138 | 1.81 | 0.521 |
| E) Change in area | | | |
| Larval food | 1, 39 | 0.64 | 0.589 |
| Juvenile food | 3, 142 | 20.56 | **0.001** |
| Larval*juvenile | 3, 142 | 1.12 | 0.543 |
| F) Total consumption | | | |
| Larval food | 1, 107 | 0.0004 | 0.991 |
| Juvenile food | 2, 107 | 46.16 | **0.001** |
| Larval*juvenile | 2, 107 | 1.07 | 0.543 |

Larvae were reared on either a low or high food treatment to settlement. Settled juveniles were assigned to one of four food treatments and reared for 2–3 weeks. Larval and juvenile food treatments were modeled as fixed effects and larval beaker was modeled as a random effect. For total consumption in Trial 2, the random effect was removed because the model was overfitted. Significant effects are bolded ($P < 0.05$)

food treatments was not significant (Fig. 4A; Table 2B). There was a significant interaction between larval and juvenile food treatments on total mussel mass consumption, reflecting that juveniles from the high larval food environment consumed more across juvenile food treatments (Fig. 5A; Table 2C). Finally, there was no effect of either larval (binomial GLM: $\chi^2 = 2.42$, $df = 1$, $P = 0.18$) or juvenile (binomial GLM: $\chi^2 = 0.87$, $df = 2$, $P = 0.777$) food treatments, or their interaction (binomial GLM: $\chi^2 = 0.51$, $df = 2$, $P = 0.844$), on juvenile survival (Fig. S4A).

For Trial 2, there was no effect of larval food on the change in area (Fig. 4B; Table 2E) or total mussel mass consumption (Fig. 5B; Table 2F). Juveniles that were fed more consumed significantly more and gained more mass during the experiment (Table 2E, F). Again, larval food treatment (binomial GLM: $\chi^2 = < 0.001$, $df = 1$, $P = 0.991$), juvenile food treatment (binomial GLM: $\chi^2 = 4.77$, $df = 3$, $P = 0.521$) and their interaction (binomial GLM: $\chi^2 = 1.83$, $df = 3$, $P = 0.743$), had no effect on juvenile survival (Fig. S4B).

## Juvenile Performance Experiment

For juveniles from Trial 1 of the Juvenile Feeding Experiment, age at filming significantly affected speed (mixed LM: $F_{2,252} = 134.74$, $P < 0.001$), with speed being slowest 2 days post-metamorphosis and fastest 10 days post-metamorphosis

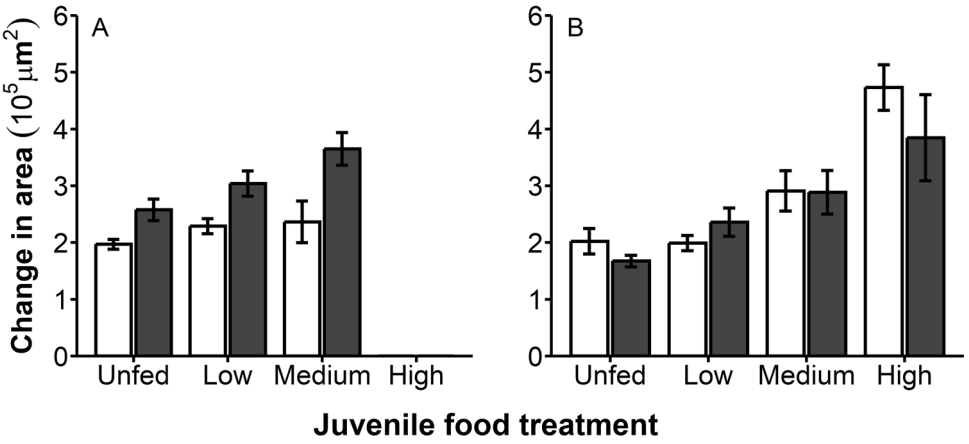


**Fig. 4** Mean (±SE) change in area (final area − area at settlement) for *Asterias forbesi* juveniles in **A** Trial 1 ($n = 25$ treatment$^{-1}$) and **B** Trial 2 ($n = 20$ or 21 treatment$^{-1}$) in the Juvenile Feeding Experiment. Larvae were reared in either a low or high food treatment to settlement. Settled juveniles were assigned to one of four food treatments—zero (unfed), one (low), three (medium) or six (high) mussels per week, for 2–3 weeks. In Trial 1, juveniles from low food background grew less, and juveniles grew the most when fed high densities of mussels. For juveniles in Trial 2, larval food treatment had no effect on change in area, but juveniles fed high numbers of mussels grew more

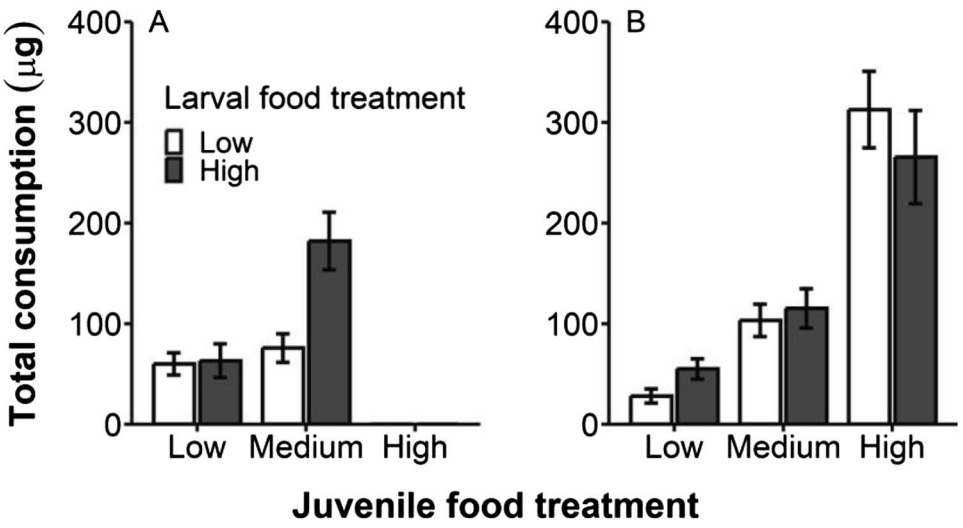


**Fig. 5** Mean (±SE) mussel mass consumed for juveniles from **A** Trial 1 ($n = 25$ treatment$^{-1}$) and **B** Trial 2 ($n = 20$ or 21 treatment$^{-1}$) in the Juvenile Feeding Experiment. For juveniles in Trial 1, there was a significant interaction between larval and juvenile food treatments on total consumption. In Trial 2, only juvenile food treatment affected total consumption

(Table S2A, Fig. S5). However, larval food treatment (mixed LM: $F_{1,32}=0.02$, $P=0.891$), juvenile food treatment (mixed LM: $F_{2,116}=0.65$, $P=0.524$), and their interaction (mixed LM: $F_{2,116}=0.47$, $P=0.629$) had no effect on speed (Table S2A; Fig. S5).

In a statistical model that included juvenile area, juvenile food treatment and age at filming, there was a significant effect of juvenile area on walking speed (mixed LM: $F_{1,138}=10.08$, $P=0.002$), such that larger juveniles were faster (Table S2B; Fig. S6).

## Discussion

We found that when larvae of the keystone predator *Asterias forbesi* are reared in a low larval food environment, they took longer to settle, were smaller at settlement and had fewer spines. Carryover effects of the low larval food environment affected traits of early settlers (Trial 1 age at settlement: 22–27 d)—juveniles fed less as larvae had lower survival, consumed fewer mussels and gained less mass, even when they were fed high densities of mussels. However, carryover effects of low larval food availability were not present among late settlers (Trial 2 age at settlement: 27–32 d), where there was no difference in size at settlement between individuals from different larval food treatments. These differences suggest that there may be a trade-off between larval duration and the occurrence of carryover effects. Overall, however, we observed that when carryover effects of low larval food availability were present at settlement, these effects persisted and were not mitigated by juvenile food availability, because individuals from the low larval food treatment had lower mass gain.

There were differences between the two trials in how larval food treatment affected mussel consumption and mass gain in the juvenile stage. One possible explanation is a limitation to our experimental design—juveniles in Trial 1 were on average younger and fed for 3 weeks while Trial 2 juveniles were older on average and fed for 2 weeks. However, we point out a few things in our data: (1) at settlement, juveniles from low larval food background in Trial 1 experienced carryover effects on body size, while in Trial 2, there was no evidence of carryover effects, and (2) juveniles in Trial 2 from the low larval food and medium juvenile food treatment consumed $103.23 \pm 16.16$ µg mussels and grew $2.91 \pm 0.36 \times 10^5$ µm$^2$ in just 2 weeks, while juveniles in Trial 1 of that same treatment had 3 weeks in the experiment, but consumed 26% less, or $75.83 \pm 14.17$ µg of mussels, and grew similarly in size ($2.36 \pm 0.37 \times 10^5$ µm$^2$). Given these two things in tandem, we suspect, though cannot conclusively state, that juveniles that settle later may be able to mitigate carryover effects of low larval food on body size and consumption, meaning there may be a trade-off between larval duration and the occurrence of carryover effects.

A trade-off between larval duration and the occurrence of carryover effects at settlement may be generated by larval plasticity, which is one mechanism organisms use to compensate for a poor food environment (Metcalfe and Monaghan 2001; McAlister and Miner 2018). In our study, larvae in the low food environment increased morphological traits, a phenomenon which has been demonstrated in a number of taxa including bivalves (Strathmann et al. 1993), polychaetes (Pawlik and Mense 1994), bryozoans (Strathmann et al. 2008) and echinoderms (Miner 2007; McAlister and Miner 2018), including asteroids (George 1994; George 1999; Wolfe et al. 2015a; but see Poorbagher et al. 2010). McAlister and Miner (2018) discuss three plastic responses of larvae to food availability: (1) morphological changes in feeding structures, (2) morphological changes in food-processing structures (e.g., stomach size) and (3) changes in development time (e.g., rudiment formation, stage duration). With respect to (3), a species that exhibits morphological changes in feeding structures and/or in food-processing structures may exhibit lower levels of plasticity in development time compared to a species that only exhibits plasticity in development time. We found evidence for plasticity in feeding structures and the small, yet statistically significant, delay in settlement time (~ 1.8 days) observed among larvae reared in the low food treatment may be one result of plasticity in morphological traits.

We found that low larval food background affected size at settlement in juveniles from Trial 1, and the carryover effects persisted for three weeks into the juvenile stage. Our results are similar to other studies in marine invertebrates that manipulated larval food environment (Pechenik et al. 1996; Phillips 2002; Emlet and Sadro 2006; Wolfe et al. 2015b). For example, in the sea star *Asterina miniata*, individuals reared on low food were smaller at metamorphosis and had poor body condition (e.g., low lipid content; Basch and Pearse 1996). Two other studies, one in mussels (Phillips 2002) and another in barnacles (Emlet and Sadro 2006), found no evidence for mitigation of carryover effects related to pre-metamorphic food environment during the juvenile stage, even after 2–3 weeks.

One possible explanation for why we did not observe compensatory growth is that there are trade-offs associated with rapidly increasing body size (Metcalfe and Monaghan 2001). Examples of traits that trade-off with high growth rates include body mass (when body dimensions are compensated for; Dmitriew and Rowe 2005), fecundity (Auer et al. 2010), age at maturity (Morgan and Metcalfe 2001) and life span (Dmitriew and Rowe 2007; Lee et al. 2013). Additionally, compensatory growth elicits costs including increased mortality risk because of a reduction in starvation

resistance (Gotthard et al. 1994) and increased predation risk due to increased foraging rates (Ali et al. 2003).

Another possible explanation for why carryover effects persisted in our study is that compensatory growth could occur in stages beyond those examined in our study. Growth rates are flexible over the whole life history, suggesting that there has been selection for optimizing growth rate, rather than maximizing it (Arendt 1997). For example, growth rate might accelerate during a particular season (Conover and Present 1990), when predation risk is low (reviewed by Dmitriew 2011; but see Werner and Gilliam 1984 for size-specific predation risks), when a size threshold must be met to reach maturity (Day and Rowe 2002) or when resources are high (Metcalfe and Monaghan 2001). Mortality rates in juvenile marine invertebrates are high (> 90%), particularly early in the juvenile period (Gosselin and Qian 1997), so we would expect to see fast juvenile growth rates to escape vulnerable sizes. In our study, juveniles in the highest juvenile food treatment were likely satiated—in Trial 2, which included a juvenile feeding treatment of six mussels fed week$^{-1}$, we found only one incidence of an individual consuming all six mussels each week. Regardless of whether juveniles in the high juvenile food treatments were food-limited or not, carryover effects of larval food background impacted mussel consumption in Trial 1—juveniles in Trial 1 from low larval food treatment consumed fewer mussels on average.

While we demonstrated carryover effects of larval food impacts size, consumption and growth, our Juvenile Performance Experiment was designed to test the mechanism. We hypothesized that juvenile body size impacts walking speed, handling time and consumption rates, as described in theory of size-selective predation (De Roos et al. 2003). Overall, larger individuals walked faster, as in other asteroids (Rumrill 1989; Montgomery 2014), but we found no support for larval food treatment impacting walking speed. In the sea star *Odontaster validus*, starved individuals began walking when they perceived chemical cues of prey items, presumably to facilitate resource acquisition (Kidawa 2001). One explanation for the low explanatory power of size on walking speed in our study is that it was difficult to know how motivated juvenile sea stars were to walk and especially whether they were walking close to their maximum speeds.

In addition to contributing to life history theory, understanding the relationship between carryover effects and recruitment success is particularly important in sea stars, because as keystone species, their population dynamics can have remarkable consequences for community structure in rocky shore (e.g., Witman et al. 2003) and coral reef systems (e.g., De'ath et al. 2012; Kayal et al. 2012). The boom–bust nature often associated with echinoderm recruitment (e.g., Hart and Scheibling 1988) is particularly well understood in the genera *Acanthaster* and *Asterias* (Uthicke et al. 2009). Although these two genera are tropical and temperate, respectively, they share certain reproductive features in common, including the production of large numbers of eggs that develop into planktotrophic larvae, phenotypic plasticity of larvae (Wolfe et al. 2015a; this study) and the ability to clone during the larval stage (Allen et al. 2018, 2019). Even for these well-known genera, however, triggers of outbreaks are complex and numerous (e.g., fluctuations in fertilization rates, larval survival, juvenile prey abundance, intraspecific cannibalism) and identifying one or even a few overriding factors that predict outbreaks may be challenging (see review by Pratchett et al. 2017 for *Acanthaster*). Studies of carryover effects may be the most effective way of testing the strength of links between larval nutrition, juvenile performance, and recruitment rates in these species that influence benthic community structure.

In species with feeding larvae, planktonic duration may increase risk of predation and exposure to physiological stress (Pechenik 1999; Vaughn and Allen 2010), but can sometimes improve juvenile phenotype and fitness (Pechenik and Eyster 1989). It is also possible that rapid growth of new juveniles is more critical to post-metamorphic survival than is size or timing of settlement, as predation has been shown to be size selective in juvenile urchins (Scheibling and Robinson 2008). If true, carryover effects of larval food background that impact juvenile growth may be especially important in determining recruitment success as larval food affects both juvenile abundance and quality. The general principles suggested by our data can likely be applied to other organisms with CLCs that are under similar constraints related to selection across the life history (Marshall and Morgan 2011). To extend this research to recruitment and population dynamics, empirical tests of theory related to mortality and growth rates are needed to fully understand whether there could be selection for a trade-off between larval duration and carryover effects of body size.

An interesting finding in our study was that not only did juveniles from the low larval food treatment experience carryover effects throughout our experiment (early settlers only, Fig. 2), but the impact of the carryover effects was magnified through time via differences in juvenile growth rate (i.e. change in area). We expected to observe compensatory growth in juveniles in response to carryover effects on body size, because post-settlement mortality is strongly correlated with body size (Metaxas 2013). However, because mussel consumption was significantly correlated with initial area at settlement in our study, carryover effects on size at settlement reduced the number of mussels consumed by juvenile sea stars from the low larval food treatment, suggesting that body size may be important for capturing and handling prey items. Because juveniles from the low larval food treatment had low mussel consumption rates, they also had low growth

rates. According to Podolsky and Moran (2006), carryover effects can be compensated for, persist, or be amplified through time. If we had observed compensation or persistence of carryover effects, growth rates for juveniles from the low larval food treatment would have been greater than or equal to growth rates of juveniles from the high larval food treatment, respectively. However we found that juveniles from the low larval food treatment always had lower growth rates, even when juveniles were unfed, meaning that the difference in size between juveniles from high and low larval food treatments was greatest at the end of the experiment, providing evidence for the amplification of carryover effects. Amplification suggests that carryover effects of size likely impact prey handling capabilities and growth, and could therefore influence competitive interactions and drive population fluctuations in accordance with resource supply (Persson et al. 1998).

In addition to being important for mussel consumption and growth rates, we found that size at settlement was the main difference between early and late settlers. There were no differences between treatments in area at settlement among late settlers, and by extension, we found no evidence of carryover effects in the other response variables we measured: survival, consumption rates and growth rates. Body size is an important life history trait that predicts fitness, because it is correlated with almost all other life history traits (Werner 1986) and is central to theories on the evolution of complex life cycles (Day and Rowe 2002; Werner 1986). We have demonstrated yet another important characteristic of body size—larval duration is correlated with the presence of carryover effects via their correlation with body size. Indeed, carryover effects of larval food environment were not present in individuals that settled later, likely because, for planktotrophic species, including asteroids (Basch and Pearse 1996; George 1999), food accumulation by larvae is critical for determining larval duration and size at metamorphosis (e.g., Basch and Pechenik 1996; Byrne et al. 2008). Increased larval duration may increase risk of predation and exposure to physiological stress (Pechenik 1999; Vaughn and Allen 2010), but can sometimes improve juvenile phenotype and fitness (Pechenik and Eyster 1989). For example, *A. forbesi* juvenile body size is important—one study found that large newly metamorphosed juveniles cannibalize smaller juveniles, emphasizing the relationship between size and mortality in this species (Brocco French and Allen 2021). We therefore propose that the trade-off between larval duration and the presence of carryover effects might be explained by theory (Werner 1986)—settlement time may be determined by larvae perceiving mortality risk and growth rate conditions in the planktonic and benthic environments. Therefore, carryover effects related to body size are important for determining survival and performance of juveniles, because size is correlated with many life history traits (e.g., competitive ability, predation risk, foraging rates, etc., reviewed by Werner and Gilliam 1984) and suggests these two ratios are non-independent.

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**Data availability** The data files and R code for this article are available on Dryad https://doi.org/10.5061/dryad.w9ghx3fsm.

## Declarations

**Conflict of interest** The authors declare no conflict of interest.

**Compliance with ethical standards** As this study uses invertebrates, no ethical approval was required. We used government-issued permits for collection.



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