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The larval legacy: cascading effects of recruit phenotype on post-recruitment interactions

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For organisms with complex life-cycles, the abundance of individuals in a given stage is driven by the quantity of individuals in the previous stage. The successful recruitment of juveniles to adult populations is, however, the product of both recruit quantity and quality. Previous studies on recruit quality have revealed that better quality individuals have higher growth and survival, yet few studies have considered how recruit quality and quantity interact. In a sessile marine invertebrate, we experimentally tested whether the larval food environment causes variation in recruit quality and affects post-metamorphic performance. We found that larvae that were fed higher concentrations of phytoplankton had higher survivorship, but that this higher survivorship meant recruit density was higher in this treatment, intensified intraspecific competition and lowered post-metamorphic growth. Our results highlight the complex repercussions that the presence of phenotypic links among life-history stages can have for population dynamics and the interdependence of pre-and post-recruitment processes in shaping populations. Overall, we suggest that pre-recruitment events can shape the post-recruitment environment independently of recruit number.

For organisms with complex life-cycles, the population dynamics of different life-history stages are tightly linked (Gaines and Roughgarden 1987, Roughgarden et al. 1988, Berven 1990, Vonesh and De la Cruz 2002). At the simplest level, abundance in one life-history stage determines abundance in the subsequent stage (Gaines et al. 1985, Berven 1990, Schupp 1990), but in most cases the demographic influences of one stage on another are less straightforward (Vonesh and De la Cruz 2002). First, environmental factors can mediate the number of individuals that successfully complete development to the next stage, and these factors may act independently of population density (Roughgarden et al. 1988, Desante 1990, Schupp 1990, Vonesh and De la Cruz 2002). Second, variation in recruitment density may generate density-dependent interactions in the adult population (Roughgarden 1986). For example, high recruitment of juveniles into an adult population may initially increase abundance, but increased recruitment can also increase the intensity of intraspecific competition, the risk of predation, or the risk of disease, which may ultimately cause a population to idle or decline (Roughgarden 1986, Fairweather 1988, Webb and Peart 1999, Vonesh and De la Cruz 2002, Bell et al. 2006). Populations are therefore shaped by both the pre-recruitment processes that affect initial recruit abundance and the interactions between individuals post-recruitment (Menge 2000).

Understanding the demographic impact of variation in the number of individuals recruiting from one life-history stage to another has long been a major goal of ecologists. This focus on variation in the number of recruits to populations is appropriate given the high levels of variation in recruitment that are observed in natural populations and the lasting influences of this recruitment on further ecological processes (Gaines and Roughgarden 1985). Accordingly, most models of population dynamics treat recruiting individuals as having equal chance of surviving to reproduction (Roughgarden et al. 1985, Hanski and Gilpin 1991, Cowen et al. 2006). Recently however, it has emerged that populations may experience variation not only in the quantity of recruits they receive, but also in the quality of recruits (Semlitsch et al. 1988, Berven 1990, Taylor et al. 1998, Jarrett 2003, Hamilton et al. 2008, Johnson 2008, Shima and Swearer 2009).

Across a variety of taxa, the quality of recruits can vary dramatically among individuals, cohorts and populations (Fox and Czesak 2000, Einum and Fleming 2002, Marshall and Keough 2008). Variation in recruit quality may arise when experiences during one life-history stage carry-over and strongly affect performance in subsequent stages (Roach and Wulff 1987, Mousseau and Fox 1998, Pechenik et al. 1998, Padilla and Miner 2006). For example, for the frog *Bombina orientalis*, exposure to a cooler embryonic environment leads to larger larvae that have higher survival (Kaplan 1992). Similarly, increases in maternal investment or larval nutrition can greatly increase adult survival, growth and reproduction (Fox et al. 1997, Taylor et al. 1998, Phillips 2002, Marshall

et al. 2003). The consequences of variation in the quantity of recruits for the population dynamics of subsequent life-history stages are well recognized, but whether variation in the quality of recruits has similar consequences across life-history stages remains unclear. Initial indications suggest that recruit quality can affect ecologically relevant traits, including survival (Berven 1990, Phillips 2002, Hamilton et al. 2008, Johnson 2008), but beyond this, the effects of recruit quality remain largely unknown. If recruit quality affects population dynamics in a simple way, we might expect increases in recruit quality to simply increase adult abundance. However, previous studies investigating recruit quantity suggest that the relationship between recruitment and adult population dynamics are likely to be more complex than a simple 'increase recruit quantity – increase adult abundance' relationship (Roughgarden 1986, Menge 2000). For example, increases in recruit quality could make them more attractive prey items (Brewer 2001) or intensify post-recruitment competition (Marshall et al. 2006) – both of which could result in increases in recruit quality having a negative effect on subsequent adult population abundance. If we hope to understand how variation in the quality of recruits affects adult population dynamics, more examinations of these effects, particularly in the field where studies are scarce, are necessary.

Here, we examine the effect of larval nutrition on post-metamorphic survival and growth under field conditions for a sessile marine invertebrate – the tubeworm *Hydroides diramphus*. We found that well fed larvae survived better but grew less as adults than poorly fed larvae. The reduction in growth appeared to be an indirect effect – well fed larvae had higher survival, and appeared to suffer higher levels of post-metamorphic competition because they grew less. Our results suggest that variation in larval quality has complex consequences for the population dynamics of adult stages and that the strong phenotypic links among life-history stages can have important ecological repercussions throughout the life-history.

Material and methods

Study species and field site

Hydroides diramphus is a polychaete tube worm found in invasive benthic marine assemblages around the world. *Hydroides diramphus* was collected locally from the floating docks at the Scarborough Marina, Redcliffe, Queensland, Australia (27°10'45"S, 153°06'18"E) between November 2008 and March 2009. Worms were collected and transported to the laboratory for spawning and larval culture. The sexes are separate, fertilization occurs externally and hatched larvae have an obligate planktonic feeding period.

Obtaining gametes and fertilization

Gametes were obtained with a similar spawning method used by Hadfield et al. (1994) for *Hydroides elegans*. The calcareous tubes containing worms were gently broken and the worm placed into individual petri dishes (30 mm diameter) containing < 5 ml of sterilized seawater (seawater microwaved at 1000 watts for 3 min past boiling, water was aerated by brief shaking of the vessel). Upon removal from the tube, worms immediately released gametes. Fertilization was achieved in the lab by mixing eggs with a few drops of sperm in a large 3-l beaker. After approximately 12–14 h at 22°C, trochophore larvae hatched and began to feed. Larvae were fed *Isocrysis galbana* – Tahitian strain.

Larval food environment and post-metamorphic performance

The aim of this experiment was to determine the effects of the larval food environment on post-metamorphic performance. A consequence of manipulating food availability in larval cultures is that larval development takes longer in lower phytoplankton concentrations (Pechenik et al. 2002, Phillips 2002). We therefore knew a priori that we would need to control for deployment date, if we were to measure post-metamorphic performance in the field without confounding deployment date. In pilot studies, we found when larvae were reared at 50 larvae ml^{-1} and fed 100 000 cells ml^{-1} of *Isocrysis* (our 'high-food' treatment), >75% of larvae had reached competency at 10 days after hatching. When fed 10 000 cells ml^{-1} (our 'low-food' treatment), >75% of larvae reached competency at 15 days after hatching. To control for the confounding effects of development time, we staggered the starting date of our larval cultures so that larvae from each of the two treatments settled on the same day, and were therefore deployed into the field on the same day (Fig. 1). To reduce confounding start date and family identity, we had four lines of food trial in total (two high- and two low-food treatments) starting as follows: low food at time 1, high and low food at time 2, and high food at time 3 (Fig. 1). In doing so, larvae from the low-food treatment at time 1 were ready to settle with the high-food larvae from time 2 (settlement day A, Fig. 1). Also, larvae from the low-food treatment at time 2 were ready to settle with the high-food larvae from

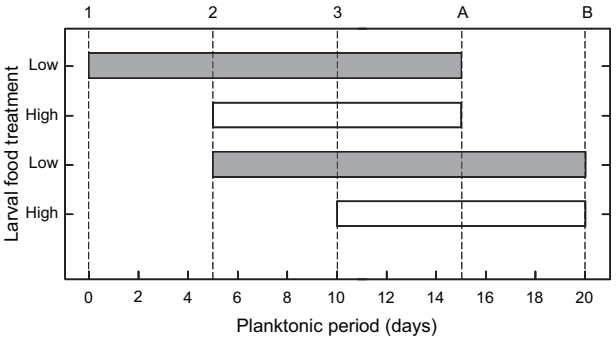

Figure 1. A schematic diagram of the experimental manipulations to control for the effects of larval food concentration on the feeding planktonic period in *Hydroides diramphus*. The x-axis represents the total planktonic development time, and the y-axis represents the four groups of treatments within a run. High food is shown as white bars, and low food shown as grey bars. There are two groups for each food treatment, with ten replicate larval culture jars per treatment. Dashed vertical lines represent the point in time when each treatment was commenced and when each treatment was deployed into the field. Labels (1), (2), and (3) indicate the commencement times, and (A) and (B) represent the day larvae were settled and deployed into the field.

time 3 (settlement day B, Fig. 1). Each line of treatment initially contained 10 replicate jars of larval culture; that is 40 jars per experimental run.

For each of the four groups, a stock source of larvae was created by spawning 20 mothers (80 mothers total). The eggs of these mothers were pooled and fertilized with a few drops of sperm from five males. Once hatched, larvae were split into ten replicate 600 ml beakers containing 300 ml of sterilized seawater with the appropriate phytoplankton concentration, and the concentration of larvae was adjusted to 50 larvae ml^{-1}. Phytoplankton concentrations were determined by three replicate counts of a stock phytoplankton solution on a haemocytometer. Larval concentrations were determined by three replicate counts of three replicated samples for each jar using an S-well. Beakers were covered with perforated plastic wrap and kept at 22°C for the duration of the larval period and the water was changed, with fresh phytoplankton added every two days. Larval competency was determined by morphological examination of larvae in three 1 ml samples (Scheltema et al. 1981). We repeated the above procedure three times, for three experimental runs. Run 1 was completed in October 2008, and run 2 and 3 were completed in January and February 2009.

Field deployment

At competency, larvae from each beaker were settled in individual 60 mm petri dishes. These petri dishes were conditioned to maximize settlement by roughing the plastic surface, and submerging dishes in fresh seawater for five days to allow the development of a biofilm (Unabia and Hadfield 1999). Larvae were allowed 48 h to settle and metamorphose. Once settled, the settler density was reduced to 25 individuals per dish (settlers culled haphazardly), and each settler was circled with a graphite pencil. A 6 mm hole was drilled in each dish and the dishes were taken to the field where they were attached to a submerged 500×500 mm PVC backing panel with plastic plugs. Each run was deployed onto a single backing panel.

Measurements

After 10 days in the field, the dishes were returned to the lab and survival was scored as the proportion of juveniles alive per dish after the 10 days. The surviving worms were then photographed for measurements using PixeLINK Capture SE ver. 1.0. Each image was analyzed with Image-Pro express ver. 5.1. We measured the maximum length of the tube for the surviving worms, with the unit of replication the mean length of all the worms per dish.

Statistical analysis

The effect of larval food treatment on post-metamorphic survival and growth was analyzed using multi-factorial analysis of variance. Here, the larval-food treatments were applied to each jar, and therefore jar was our unit of replication. Our initial design had three factors: larval food, date of deployment and experimental run. Our main hypothesis tested whether larval-food treatment influenced post-metamorphic survival and growth, but we also included date of deployment and run as crossed factors in the model to see if the effects of larval-food treatment were temporally dependent. Larval food was treated as a fixed factor with two levels: high and low food. Date of deployment (two levels within each run) and experimental run (three levels) were treated as random factors. We checked that both response variables had a normal frequency distribution: growth data was normal, however, the survival data was not, hence it was normalized by square-root arcsine transformation.

In run 1, the entire first group of the high-food treatment suffered 100% unexplained mortality during larval culture, as did 80% of the second low-treatment of run 2. The unexplained mortality was likely due to infected larval culture. Hence, we could not produce complete crosses for the effects of deployment date and larval food concentration for runs 1 and 2. We could therefore only test for an interaction between food treatment and deployment time for run 3. The interaction between food treatment and deployment date was non-significant for both survival ($F_{1,36}=0.003$, $p=0.953$) and growth ($F_{1,35}=2.367$, $p=0.133$), therefore these terms were omitted from the model (see Quinn and Keough 2002 for details on model reduction).

Our results from the previous analysis revealed that higher survival may be causing reduced post-metamorphic growth via increased competition. To test whether recruit density was correlated to growth, we used Person's correlation analysis to investigate the relationship between the number of recruits that survived and the size of those recruits after 10 days. Our predictor variable was the proportion of recruits that had survived, which essentially represents the number of recruits in the post-metamorphic environment. Our response variable was the average growth of recruits per petri dish. Each run was analyzed separately.

Results

Larval food environment and post-metamorphic performance

After 10 days in the field, individuals that were fed a high concentration of phytoplankton as larvae suffered less mortality (23.6% ± SE 4.8) than individuals that were fed a low concentration of phytoplankton as larvae (45.5% ± SE 5.1). In run 2 and 3, food treatment significantly influenced survival (Table 1): individuals fed high food as larvae had higher survival than larvae fed the low-food treatment (Fig. 2a). The differential survivorship between the high- and low-food treatments caused the average density of post-metamorphic worms to be reduced to 19.1 and 13.7 worms per 30 mm petri dish, respectively. In run 1, juveniles from the high food treatment had lower survival on average than juveniles from the low-food treatment (11.3% ± SE 4.2 and 16.1% ± SE 4.6 respectively), however this effect was non-significant (Table 1). The date that the settlers were deployed into the field did not affect survival in run 1 or run 3, but was marginally significant in run 2 (Table 1).

After 10 days in the field, juveniles that were fed the high concentration of phytoplankton as larvae were, on

Table 1. Two-way ANOVA results for the effect of the concentration of food fed to larvae during planktonic development and the date of deployment on post-metamorphic survival after 10 days in the field for the tube worm *Hydroides diramphus*. The interaction term is omitted from run 3 due to non-significance, and is also omitted from run 1 and 2 due to incomplete crosses caused by larval culture mortality.

	Source	DF	MS	F	p
Run 1	larval food	1	0.012	0.143	0.709
	deployment date	1	0.002	0.028	0.869
	error	23	0.081		
Run 2	larval food	1	0.758	22.05	<0.001
	deployment date	1	0.145	4.229	0.049
	error	29	0.034		
Run 3	larval food	1	0.25	5.85	0.021
	deployment date	1	0.058	1.365	0.250
	error	37	0.043		

Table 2. Two-way ANOVA results for the effect of the concentration of food fed to larvae during planktonic development and the date of deployment on post-metamorphic growth after 10 days in the field for the tube worm *Hydroides diramphus*. The interaction term is omitted from run 3 due to non-significance, and is also omitted from run 1 and 2 due to incomplete crosses caused by larval culture mortality.

	Source	DF	MS	F	p
Run 1	larval food	1	8.741	0.47	0.507
	deployment date	1	46.28	2.488	0.143
	error	11	18.602		
Run 2	larval food	1	60.463	11.537	0.002
	deployment date	1	22.196	4.235	0.049
	error	27	5.241		
Run 3	larval food	1	47.458	9.492	0.004
	deployment date	1	152.637	30.528	<0.001
	error	36	5		

average, 22.93% smaller than worms fed the low phytoplankton concentration as larvae (Table 2, Fig. 2b). In run 1, however, we found no significant effect of larval food on juvenile size (Table 2). Across all of our experiments, post-metamorphic survival within each petri dish was negatively correlated with post-metamorphic growth (Fig. 3; run 1, R=–0.623, p=0.017; run 2: R=–0.423, p=0.02; and run 3: R=–0.403, p=0.011).

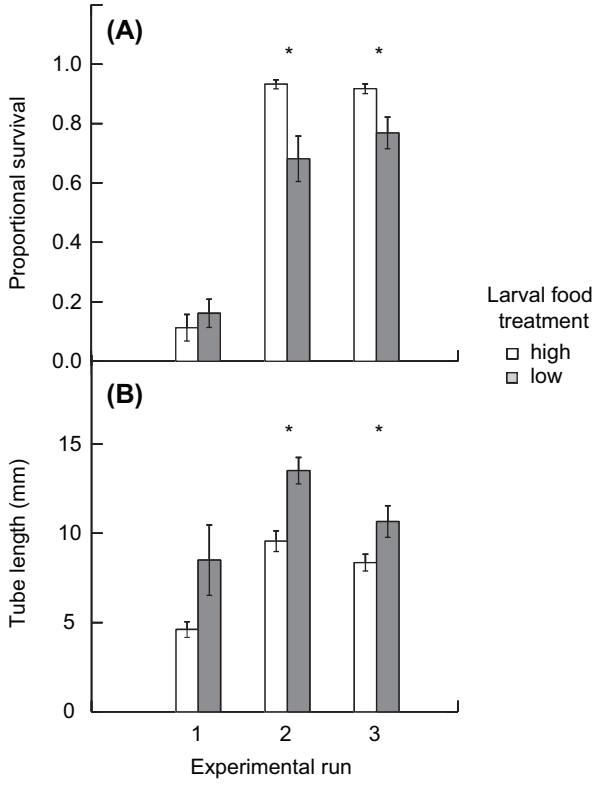

Figure 2. Post-metamorphic performance after 10 days in the field for *Hydroides diramphus* fed either high (100 000 cells ml^{-1} of *Isocrysis*) or low (10 000 cells ml^{-1}) food concentrations as larvae. (A) Mean proportion of surviving juveniles per petri dish. (B) Mean post-metamorphic growth of juveniles. The x-axis represents the experimental runs, and the y-axis represents the performance metric. Figure legend indicates high food as white bars, and low food as grey bars. Asterix above bars indicate a significantly different mean between food treatments for the performance measure in that particular run. For the survival analysis n=26, 32 and 40 for runs 1, 2 and 3, respectively; for the growth analysis n=15, 30 and 39 for runs 1, 2 and 3 respectively. Error bars are SE.

Discussion

In the past, there has been much debate on the relative strength of pre- and post-recruitment processes in shaping adult populations (Olafsson et al. 1994, Menge 2000). In the tubeworm *Hydroides diramphus*, environmental heterogeneity during development has cascading effects across life-history stages, resulting in variable survivorship and density-dependent interactions that ultimately affect juvenile population dynamics. Our results further support previous studies that show both pre- and post-settlement factors can influence population dynamics, and our results also provide new insight because population level effects occur not just from a simple numerical perspective – factors that change the mean phenotype of the larval pool result in complex ecological interactions. Hence,

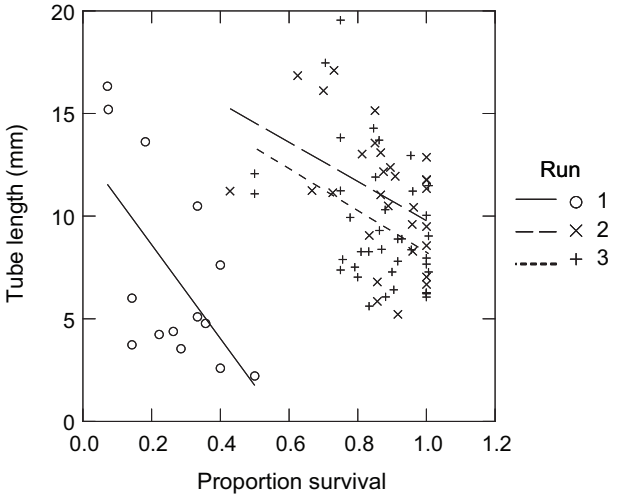

Figure 3. The correlation between post-metamorphic survival and growth of *Hydroides diramphus* after 10 days in the field for three experimental runs.

pre- and post-recruitment processes may not be independent. Importantly, complexity is added to this relationship because pre-settlement factors may not manifest as ecologically relevant influences on populations until after recruitment. First, our study demonstrates that the pre-settlement environment caused larvae that were fed higher concentrations of phytoplankton to have a shorter planktonic period, such results have previously been reported (Basch and Pearse 1996, Pechenik et al. 2002, Phillips 2002, Reitzel et al. 2004). Given that mortality in the plankton is strongly determined by the length of the larval period, increasing larval food is likely to increase the number of recruiting larvae (Strathmann 1985, Morgan and Christy 1995). Second, variation in the availability of food during the planktonic larval stage transcended metamorphosis and affected survival in the benthic adult stage: well-fed larvae survived better as juveniles. Third, the effects of larval diet on post-metamorphic dynamics were not straightforward: increasing recruit quality did not simply increase adult performance. Instead, because larval diet increased juvenile survival, density-dependent competition appeared to reduce the growth of juveniles. Therefore, this cascade of events, originating from a simple manipulation of the conditions larvae experienced during planktonic development, may influence the post-recruitment environment indirectly. Few theoretical explorations of these issues have considered how variation in larval quality can lead to changes in the intensity of interactions during the adult stage and can have complex consequences for post-recruitment population dynamics (but see Roughgarden 1986).

In previous studies, increasing larval condition positively affects post-metamorphic performance. For example, in terrestrial systems there is evidence of such positive phenotypic links across life-history stages (Alford and Harris 1988, Berven 1990, Audo et al. 1995), and similar trends are reported in marine invertebrates where larvae in better condition (as larger lecithotrophic larvae or well fed planktotrophic larvae) have higher post-metamorphic growth (Phillips 2002, Marshall et al. 2003). Our finding that well fed larvae grew relatively poorly, contradicts this trend. We suggest the likely cause of reduced growth in the well fed treatment was due to an increase in density-dependent competition in the post-metamorphic environment, where resource limitation for food the likely mechanism. In our study, tubes were often overlapping indicating that contacting tubeworms were likely to infringe the feeding ability of neighbours, and also may have limited the amount of free-space available for growth. Competition among benthic marine invertebrates can be intense for resources such as space and food (Connolly and Roughgarden 1999). Competition for space can cause reduced performance in numerous species (Connell 1961, Russ 1982). In suspension feeding species, increasing competitor density can cause individuals to withdraw from feeding (Levin 1982), and also directly reduce the amount of planktonic food available to individuals (Dalby 1995). For example under conditions of flowing water, bryozoans that were upstream of their conspecifics removed food particles from the water, therefore reduced the amount of food available to the downstream bryozoans, which resulted in poor growth in the downstream individuals (Okamura 1984).

The effect of larval feeding environment on post-metamorphic performance was not consistent across all experimental runs. It is not clear why the larval-food environment did not increase larval survival in run 1, but did in runs 2 and 3. We can only attribute this difference to random sources of variation, but can speculate that it may be due to temporal variability due to seasonal change. The two runs that were similar were conducted close together in the austral summer, as where the run that differed was conducted in spring of the preceding year. Interestingly, even though the role of larval nutrition was not consistent across runs, a negative relationship between survival and worm length was maintained in all runs.

While we suspect our result is due to the indirect ecological effects of density-dependence, mediated through variation in recruit survival, we cannot rule out the possibility that high larval nutrition directly reduces post-metamorphic growth. The mechanism that causes this effect is not obvious, but we offer three alternative hypothesis. 1) In natural fish populations, larval history can cause significant differences in recruit growth and survival (Hamilton et al. 2008, Shima and Swearer 2009), but in these studies, certain larval environments may select for genetically superior individuals that eventually recruit to a population (Hamilton et al. 2008). In our study, conditions of low food may have limited successful development of genetically inferior larvae so that only those genetically superior individuals could develop to settlement and these individuals may therefore have higher growth. 2) Post-metamorphic growth may be higher in individuals fed higher food rations, but may be context dependent and masked by an interaction with density. However, this hypothesis is not supported when both larval condition and density are simultaneously manipulated in a reef fish (Johnson 2008). 3) The larval food environment may induce irreversible developmental plasticity in the ability of individuals to assimilate exogenous resources. Such that larvae fed lower phytoplankton concentrations can assimilate resources more efficiently, leading to faster growth when the availability of food is constant in the post-recruitment environment, independent of larval history (Nicieza and Metcalfe 1997, Moran and Manahan 2004). Regardless of the mechanism, the ecological consequences at the population level are the same: changes in the larval environment lead to seemingly non-intuitive changes in the growth of juveniles.

Evidence from recruitment in natural populations supports the cascading effects observed in our study, but is perhaps higher in magnitude. Spatial and temporal variation in upwellings off the west-coast of North America can cause large variation in primary production that leads to variation in food available to developing larvae and eventually high variation in the subsequent recruitment of larvae to the benthic adult populations (Leslie et al. 2005, Barth et al. 2007). The intensity of post-recruitment competition under such conditions is likely to be high in such systems for two reasons. First, planktonic mortality is proportional to the time spent in the plankton (Strathmann 1985), and under conditions of high food availability larvae are likely to suffer less planktonic mortality when development is faster. Therefore, cohorts of larvae that experience these conditions are likely to settle in high densities and density-dependent competition in the post-recruitment environment should

be high (Roughgarden 1986). Secondly, as our results suggest, those larvae that experience high levels of food are also in better condition and less likely to die post-recruitment, compounding the intensity of post-recruitment competition. Therefore, natural variability in recruit quality caused by heterogeneous environments are likely to compound the effects of variability in recruit quantity on subsequent population-level interactions post-recruitment.

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