Vol. 545: 147–160, 2016
doi: 10.3354/meps11586

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published March 8

Persistent and context-dependent effects of the larval feeding environment on post-metamorphic performance through the adult stage

Gabriela Torres[1,*], Luis Giménez[1], Amanda Kate Pettersen[1], Mathilde Bue[1], Michael Timothy Burrows[2], Stuart Rees Jenkins[1]

[1]School of Ocean Sciences, Bangor University, LL59 5AB Menai Bridge, UK
[2]Scottish Association for Marine Science, Scottish Marine Institute, PA37 1QA Oban, UK

ABSTRACT: One of the central issues in ecology is the identification of processes affecting the population structure and dynamics of species with complex life cycles. In such species, variation in both the number of larvae that enter a population and their phenotype are important drivers of survival and growth after metamorphosis. Larval experience can have strong effects on key post-metamorphic traits, but the temporal scale of such 'trait-mediated effects' may be short, and their magnitude may depend on the environment experienced after metamorphosis. We used an intertidal barnacle to study the long-term consequences of trait-mediated effects under different post-metamorphic conditions by manipulating larval food concentration and monitoring patterns of survival and growth in juveniles at 2 intertidal levels over a 5 mo period. In 2 replicated experiments, higher food levels resulted in increased body size, mass and reserves (measured from elemental composition) in the settling larval stage and increased body size of newly metamorphosed juveniles. In Expt 1, high food concentration reduced juvenile mortality at low intertidal levels, while on the upper intertidal, mortality was high for all larval food concentrations. By contrast, in Expt 2, low larval food concentration decreased juvenile survival at both shore levels. When present, effects were established early (Weeks 1 or 2) and persisted for over 10 wk in Expt 1 and 22 wk in Expt 2. Interactive effects of the larval and juvenile environments can have important implications for population size: trait-mediated effects may persist for long periods, helping to explain patterns of adult abundance.

KEY WORDS: Benthic invertebrate · Food limitation · Larval environment · Trait-mediated effect · Recruitment

INTRODUCTION

For species with complex life cycles, a better understanding of processes affecting the structure and dynamics of populations and communities is achieved if studies consider both pre- and post-metamorphic stages (Thorson 1950, Grosberg & Levitan 1992, Caley et al. 1996, Jenkins 2005, Allen & Marshall 2010, Marshall & Morgan 2011). In marine invertebrates, the number of individuals successfully settling and metamorphosing, as well as the patterns of recruitment, can vary enormously over a number of spatial and temporal scales (e.g. Jenkins et al. 2000, Navarrete et al. 2002, Broitman et al. 2008). In barnacles, such variation has been attributed to patterns of predation (Gaines & Roughgarden 1987), behaviour (Jenkins 2005) and transport by currents (Roughgarden et al. 1988). While for many decades benthic ecologists focused on post-settlement processes to explain patterns of community structure,

*Corresponding author: g.torres@bangor.ac.uk

the discovery of the role of pre-settlement processes changed views about the organisation of marine communities, which now recognise the balance between the roles of pre- and post-metamorphic processes operating on cohort dynamics (Connell 1985, Gaines & Roughgarden 1985, Menge 2000, Jenkins et al. 2008). On a wider scale, the consideration of pre-settlement processes on connectivity has contributed to the development of the field of marine metapopulation dynamics (Armsworth 2002, Shima & Swearer 2009). In addition, a growing body of work has also shown that the environmental conditions experienced by larval stages can affect phenotype and eventually performance and survival after metamorphosis (Prout & McChesney 1985, Giménez 2004, Pechenik 2006, Aguila et al. 2013). These effects, called 'trait-mediated effects' (Giménez 2004, Kerby et al. 2012), are part of a wider type of plastic response where traits of organisms are altered in response to biotic and abiotic pressures (Miner et al. 2005). These effects are widespread among organisms and have important consequences for the organisation of communities (Schmitz et al. 2003, Werner & Peacor 2003, Ohgushi et al. 2012).

The most widely studied type of trait-mediated effect is perhaps that operating top-down, where morphological or behavioural traits of a consumer are modified by the presence of predators (Kerby et al. 2012). In tri-trophic food chains, the response of the consumer to predator cues can modify the abundance of the producer. There are also bottom-up effects where, for instance, food availability or the physical environment experienced by early (e.g. larval) stages affect physiological or morphological traits of advanced stages, and subsequently their chances of survival, and recruitment (Giménez 2004, Pechenik 2006). Here, the emphasis is on the consequences of modified traits as they propagate through the life cycle. We know that the larval environment can have a profound influence on individual size and available reserves at the time of metamorphosis. A range of studies have clearly demonstrated that, over the first days of post-metamorphic life, the larval environment can determine metamorphic success (e.g. Tremblay et al. 2007), survival (Pechenik et al. 1993) and the ability to tolerate food limitation (Thiyagarajan et al. 2003a,b) or physical stress (Phillips 2002). However, we still do not clearly understand the long-term consequences of trait-mediated effects propagating through the life cycle, for instance, if effects of early (e.g. larval) experience will reach beyond a few days after metamorphosis. Strong effects, i.e. those that can influence population dynamics, should have long-term consequences on fecundity or on the number of individuals reaching reproductive maturity. The strength of such effects may be restricted to species with a short post-metamorphic phase. In species with a short juvenile phase (<4 wk), the larval environment can affect fecundity (Prout &McChesney 1985, Wendt 1998). An extreme case of this is the holometabolous insects, in which feeding larvae eclose into an adult stage whose energy reserves largely depend on larval history (Aguila et al. 2013).

In addition, environmental conditions experienced after metamorphosis modify the strength of a trait-mediated effect, leading to context-dependent effects. For instance, environmental stochasticity experienced at advanced stages may also limit the strength of trait-mediated effects because it may blur the relationship between the larval environment, post-metamorphic phenotype and survival. In species with long post-metamorphic phases (months to years), laboratory studies where environmental conditions are kept constant have shown that effects of larval experience on phenotype are still found approximately 3 mo after metamorphosis (Giménez et al. 2004, Giménez 2010). However, relationships between early and late phenotypes are sometimes weak in the wild (Lindholm et al. 2006, Auer et al. 2010), where conditions in the post-metamorphic environment can re-shape phenotypes (and modify fitness) or produce immediate effects on mortality, irrespective of the phenotype.

Context-dependent effects are important even in the absence of environmental stochasticity, but the lack of research (Allen & Marshall 2013) still precludes the formulation of specific predictions about which environmental contexts enable trait-mediated effects to influence recruitment. While some studies have shown trait-mediated effects when post-metamorphic conditions are harsh (Spight 1976, McGinley et al. 1987, Hutchings 1991, Tamate & Maekawa 2000, Phillips 2002, Allen & Marshall 2013), the opposite pattern has also been reported (Moran & Emlet 2001). Most likely, contradictory results reflect different types of stressors (Moran 1999) or non-linear responses to a stressor (Allen et al. 2008), i.e. the fact that under extremely harsh conditions all organisms die irrespective of traits while trait-mediated advantages are too small in benign conditions. In the first case, some specific stressors may select for particular body sizes, while other stressors may not (Moran 1999). In the latter case, trait-mediated effects may arise if environmental conditions are intermediate between the extremes described above (Allen et al.

2008). More complex responses that have been found in field studies evaluating larval responses to egg size and thermal conditions, i.e. across another life history boundary, suggest that complex patterns are possible. For example, in the frog *Bombina orientalis*, larvae hatching from large eggs perform better at low temperatures or under low variability in temperature, but the patterns reverse at high temperatures (Kaplan 1992, Kaplan & Phillips 2006).

In marine benthic invertebrates, observations suggest mortality is generally high throughout a range of taxa over the period following metamorphosis (Gosselin & Qian 1997, Hunt & Scheibling 1997, Underwood & Keough 2001, Gosselin & Jones 2010). However, mortality at advanced juvenile stages can also be high if intraspecific competition increases as individuals use more resources (Jenkins et al. 2008, Giménez & Jenkins 2013), and modelling output indicates that juvenile/adult survival is critical to local dynamics (Svensson et al. 2004). These results suggest that a longer term perspective of trait-mediated effects, integrating across life stages, is required.

In this paper, we address the long-term consequences of trait-mediated effects under different post-metamorphic contexts. We studied the effect of larval food environment on larval quality and subsequent long-term post-metamorphic survival and growth of an intertidal acorn barnacle in 2 habitats characterised by different levels of environmental stress over a period of 22 to 25 wk. The study addressed the following questions: (1) What is the relationship between the larval environment and the phenotype before and after metamorphosis? (2) Do we see trait-mediated effects? (3) Do these trait-mediated effects propagate through time or alternatively does stochastic variation override the signal? (4) If present, do trait-mediated effects depend on the environmental context (tidal elevation)?

MATERIALS AND METHODS

Model species

Intertidal barnacles are a useful model system for addressing trait-mediated effects on population dynamics. They develop through a series of pelagic larval feeding stages, the nauplius, followed by a non-feeding larval stage, the cyprid, which settles and metamorphoses. Food conditions experienced by nauplius stages determine the amount of reserves available to the cyprids to search for an appropriate settlement site and undergo metamorphosis (West & Costlow 1987, Hentschel & Emlet 2000, Thiyagarajan et al. 2003a,b). Metamorphosis requires a considerable amount of total available reserves (e.g. 30% in *Semibalanus balanoides*; Lucas et al. 1979), and feeding does not start until 2 to 5 d after metamorphosis (Rainbow & Walker 1977). Hence, it is not surprising that both laboratory (Thiyagarajan et al. 2003a) and short-term field studies (Jarrett 2003, Tremblay et al. 2007) have found that metamorphic success and early post-metamorphic survival are influenced by the larval food environment and positively correlate with the amount of cyprid reserves (Jarrett & Pechenik 1997, Miron et al. 1999). However, the long-term effects of the larval environment and how this interacts with levels of post-larval environmental stress are not known.

Austrominius modestus, a non-native species originally from Australasia, was first recorded in the UK in 1945 (Crisp 1958), and since then it has spread rapidly throughout the European continent (Harms 1986). The duration of larval development, through 6 naupliar stages followed by the cyprid, depends on temperature: in the Irish Sea, larvae are expected to take approximately 15 d (Harms 1998) to reach the first juvenile stage. In the study area, larval development and settlement takes place mainly during the summer through to early autumn. Juveniles feed on plankton at high tide, grow rapidly and are able to breed within 12 wk (Crisp & Davies 1955).

Laboratory and field procedures

Adult *A. modestus* were collected from the mid intertidal zone of Menai Bridge (Isle of Anglesey, UK) and maintained in the laboratory in seawater. In 2 separate experiments, in September and October 2011, larval release was stimulated by detaching the adults from the rock. For each experiment, freshly hatched larvae from approximately 100 adults were pooled and then divided among 18 vessels (5 l). Nauplii were mass-reared at an initial density of 0.8 to 1.0 ind. ml^{-1} at 3 different food concentrations (6 replicate vessels per food treatment), using the diatom *Skeletonema costatum* as food (Harms 1987). Larvae were reared following Harms (1987) at low (1×10^5 cells ml^{-1}), medium (2×10^5 cells ml^{-1}) and high (3×10^5 cells ml^{-1}) food concentrations at 16°C under gentle aeration. These concentrations produced low larval mortalities in preliminary experiments. Water and food were changed every second day and dead larvae discarded. Towards the end of each experiment, water was changed daily and cul-

tures were inspected for cyprids. When cyprids amounted to 50–80% of larvae present (in most cases ca. 24 to 48 h from when the first cyprids were observed), the contents of each culture vessel were transferred to a separate settlement vessel made of PVC, each containing 6 natural slate tiles of 3 × 3 cm each (i.e. there was a settlement vessel associated with each replicate culture vessel). After 48 h, tiles with settlers were out-planted to the field and remaining swimming cyprids were discarded to avoid confounding food treatment effects with effects of delayed metamorphosis. Development time to reach the cyprid stage varied slightly among food treatments, such that transfer to the settlement vessel and subsequent settlement was delayed by 1 and 2 d in the intermediate and low food concentrations, respectively, compared to high food. Rather than maintain settlers from different food treatments under laboratory conditions for differing periods, out-planting was performed at the end of the settlement period, and hence out-plant dates differed by a maximum of 2 d among food treatments. Most tiles (90%) had densities below 5 ind. cm^{-2}; the maximum density of settlers per tiles was 93 (~10 ind. cm^{-2}). Density did not vary in any consistent way among food treatments. Observations showed that settled individuals were unlikely to compete for space or resources since there was enough free space between settlers until the end of the experiment. Therefore food effects were not confounded with density effects.

Tiles were out-planted (Expt 1: 21 to 23 September 2011; Expt 2: 17 to 19 October 2011) on a rocky intertidal outcrop under the suspension bridge in the Menai Strait (ca. 800 m from the laboratory) at 2 tidal levels, 4.8 and 3.0 m above chart datum, corresponding to the upper and lower distribution of *A. modestus*. Three PVC frames were used at each tidal level and tiles (2 to 3 from each vessel) were attached at random across these frames using a 5 mm pre-drilled hole through the tile centre. In total, between 100 and 400 individuals were out-planted per treatment combination.

All tiles were photographed, to determine survival and growth rates, before out-planting and then at bi-weekly (Weeks 2 to 10) intervals and at the end of the experiments in March 2012 (Expt 1: 25 wk and Expt 2: 22 wk). In addition, in Expt 2, tiles were also sampled 1 wk after out-planting. During the first 2 wk, tiles were photographed under a dissecting microscope (Leica Microscope MZ 6) by transporting tiles, attached to the PVC frames, to the laboratory during low tide, and returning before the incoming tide. Subsequently, barnacle sizes were large enough to allow appropriate estimations of body size through *in situ* photography (Pentax Optio W60 camera mounted on a PVC frame). Digital images were processed using Image J software. All surviving individuals were counted and the basal and operculum length measured in 5 individuals from each replicate settlement vessel. Body size measurements ended when less than 5 individuals per replicate vessel remained on the tiles (Week 10 for Expt 1 and Week 22 for Expt 2).

Body size, dry mass and elemental composition of swimming cyprids

In both experiments, cyprid body size was determined by measuring 20 cyprids per replicate vessel under the microscope. Cyprids were collected as swimming individuals within the first 48 h of the first cyprids being observed. In Expt 2, dry mass and elemental composition were also determined by sampling 100 swimming cyprids from each replicate vessel. Sample processing followed Anger & Harms (1990): 100 individual cyprids were pipetted out of each replicate vessel, quickly rinsed in distilled water, blotted dry with filter paper, placed in aluminium cartridges and frozen at –20°C for later analysis; 20 randomly chosen individuals per sample were measured under the microscope before being placed in the cartridges. Samples were freeze-dried (Edwards Supermodulyo 12 k freeze-drier) and weighed using a microbalance (Mettler Toledo, precision = 1 µg). Elemental composition (carbon and nitrogen content) was determined using a CHNS-O Analyser (Thermo Electron Flash EA 1112 Series).

Statistical analysis

We used each culture vessel, and corresponding settlement vessel, as a replicate unit, such that all tiles originating from each vessel were considered as 1 replicate. A minimum of 5 vessels from each food treatment produced suitable tiles. Statistical tests were run for each experiment separately. We first tested if food concentration affected cyprid body size, dry mass or elemental carbon and nitrogen content. For body size, we obtained data from individual cyprids; therefore, a nested ANOVA was used with food concentration as a fixed factor and culture vessel nested within food concentration (replicate unit = individual larvae sampled from within each vessel). A 1-way ANOVA was used for dry mass and elemental composition where 1 sample per vessel (made up

of 100 cyprids) was obtained. After significant differences in ANOVA, differences among treatments were tested here and in subsequent analyses using Student-Newman-Keuls (SNK) post hoc tests.

We tested if the body size of metamorphs (basal and operculum length) varied between intertidal level and larval food using a 2-way ANOVA. Our analyses confirmed that body size did not differ among intertidal levels at the time of out-planting (see 'Results').

The effects of larval food concentration, intertidal level and time on survival were tested through a 3-way repeated measures ANOVA using each of the settlement vessels as our replicate unit (i.e. values from tiles within each settlement vessel were combined). Variances were homogeneous (Cochran's test) and residuals did not show any serious deviations from the normal distribution.

Since the highest mortality rates were observed during the first 2 wk (see 'Results'), we also tested for potential effects of initial densities of post-metamorphs on the proportion of barnacles surviving the first 2 wk in the intertidal. This test considered interactions of initial barnacle numbers, larval food and intertidal level and was made using tiles (instead of vessels) as this was the natural replicate unit to express densities. Tests were run using general least square (gls function in the nlme package; Pinheiro et al. 2015) with the varPower constructor function (variance depended on barnacle density). Pearson residuals showed homogeneity and did not show serious deviations from normal.

The effects of larval food concentration, intertidal level and time on body size of metamorphs (basal and operculum length) were tested using generalised linear modelling (GLM) with Gamma distribution and logarithmic link function. ANOVA was not used because variances were heterogeneous and did not follow a normal distribution even after data transformation.

RESULTS

Effect of food concentration levels on traits of swimming cyprids and metamorphs

For both Expts 1 and 2, larval food concentration significantly affected cyprid body length (Table 1), with low food concentration resulting in a 4 to 7% reduction in size compared with those from the high food level. Intermediate food concentrations resulted in cyprid lengths equivalent to the high food treatment in Expt 1 but an intermediate size in Expt 2 (Fig. 1).

Table 1. *Austrominius modestus*. Two-way nested ANOVAs evaluating the effect of food concentration (F) and replicate vessel (V), nested in food concentration, on body length of swimming cyprids for 2 different experiments. Significant effects are in **bold**. The *F*-statistic of the food effect was calculated using the MS of the vessel effect as denominator; the corresponding df was used for the calculation of the p-value

	df	MS	*F*	p
Expt 1				
Food (F)	2	5003	17.0	**<0.0001**
Vessel (V(F))	15	294	0.5	0.92
Error	162	556		
Expt 2				
Food (F)	2	48889	47.4	**<0.0001**
Vessel (V(F))	14	1032	1.8	**0.038**
Error	323	574		

Dry mass (dry wt, DW) and elemental composition were only measured in Expt 2. Cyprid DW was 41% lower at low food concentrations than at intermediate and high food levels (significant food effect, Table 2, Fig. 2a). Significantly lower carbon (C) and nitrogen (N) content per individual were also found under low food levels (data not shown). The amount of carbon per individual cyprid, for example, was 47% lower at low food concentrations compared to high. Levels of C and N relative to DW also responded to food treatments: %C was significantly greater in the high food treatment with 9.5% and 7% lower values in low and intermediate food treatments, respectively (Table 2, Fig. 2b). In contrast to all other patterns, %N was highest in the low food treatment, and significantly lower in the mid and high treatments (11 to 13% lower than in high food treatment, Fig. 2c). The strong food effects on C compared to N led to significant differences in the C:N ratio among all treatments (high to mid to low food). In larvae reared

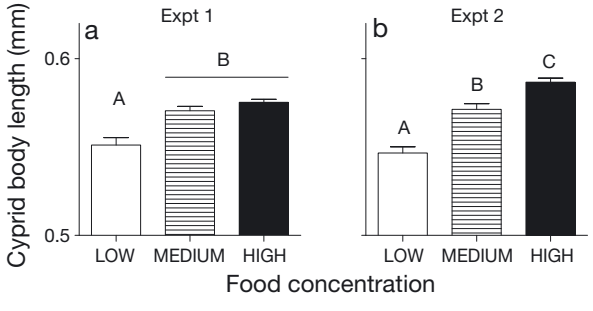

Fig. 1. *Austrominius modestus*. Effect of larval food concentration on body size of swimming cyprids. (a) Expt 1, (b) Expt 2. Different capital letters indicate significant differences between treatments after Student-Newman-Keuls (SNK) post hoc test; error bars are SE among replicate vessels

Table 2. *Austrominius modestus*. One-way ANOVAs evaluating the effect of food concentration on dry mass (dry wt, DW) and elemental composition (C:N ratio, %C and %N) of swimming cyprids for Expt 2 (degrees of freedom of Food and Error were 2 and 13, respectively). Significant effects are in **bold**

	Dry mass (DW)			C:N ratio			C (%)			N (%)		
	MS	*F*	p	MS	*F*	p	MS	*F*	p	MS	*F*	p
Food	4.20	13.87	**0.0006**	3.10	13.50	**0.0007**	27.46	7.18	**0.008**	1.57	5.27	**0.021**
Error	0.30			0.23			3.83			0.30		

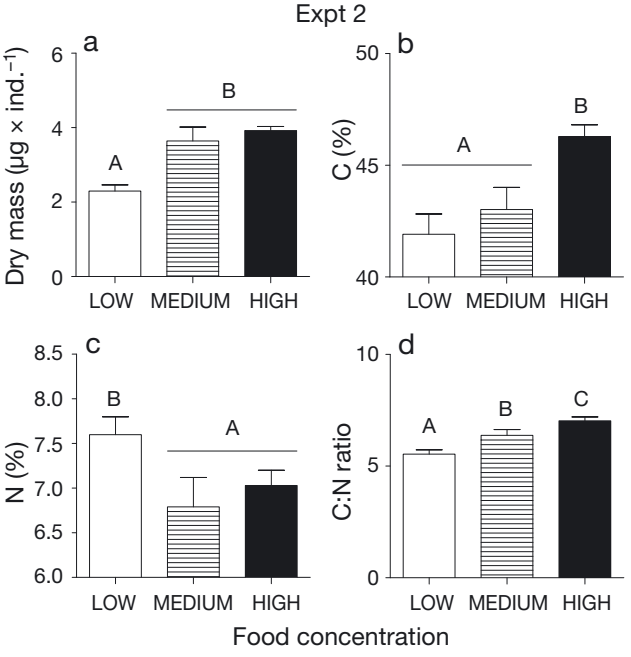

Fig. 2. *Austrominius modestus*. Effect of larval food concentration on dry mass and elemental composition (C and N content) of swimming cyprids. (a) Dry mass, (b) % carbon, (c) % nitrogen, (d) C:N ratio. Different capital letters indicate significant differences between treatments after SNK post hoc test; error bars are SE among replicate vessels

Table 3. *Austrominius modestus*. Two-way ANOVAs evaluating the effect of food concentration on size of metamorphs (measured as basal and operculum length) out-planted at different intertidal levels during 2 different experiments. Significant effects are in **bold**

	df	Basal length			Operculum length		
		MS	*F*	p	MS	*F*	p
Expt 1							
Intertidal level (I)	1	235	0.18	0.68	1816	1.52	0.23
Food (F)	2	37029	27.67	**<0.0001**	8179	6.83	**0.004**
F × I	2	395	0.29	0.75	340	0.28	0.76
Error	27	1338			1198		
Expt 2							
Intertidal level	1	599	0.31	0.58	673	0.62	0.44
Food	2	10010	5.17	**0.012**	3769	3.50	**0.043**
F × I	2	1381	0.71	0.50	301	0.28	0.76
Error	30	1935			1078		

under low food concentrations, this ratio was 21% lower than in those reared under the highest food concentration (Fig. 2d).

At the time of out-planting, body size (basal and operculum length) of metamorphs (within 24 h of metamorphosis) varied among food concentrations but not between intertidal levels (Table 3, Fig. 3) showing that individuals of different sizes were effectively allocated randomly among intertidal levels. In both experiments, the highest food concentration resulted in the longest basal length after metamorphosis (Fig. 3a,b). Low food concentration resulted in metamorphs that had 15% (Expt 1) and 8% shorter (Expt 2) basal lengths than those from the high food concentration. The operculum length was longest for individuals metamorphosed from larvae reared under high food concentrations in Expt 1 (Fig. 3c), but similar sizes were found between individuals reared under high and medium food concentrations in Expt 2 (Fig. 3d).

It is interesting to note the way in which cyprid size and metamorph size responded differently to food treatments in Expt 1 (Fig. 1a vs. Fig. 3a). The medium food concentration produced cyprids equivalent in body length to those at high food concentrations. However, this size advantage over the low food treatment was not maintained in metamorphs, where the medium food concentration clearly produced metamorphs equivalent to those from the low food treatment, with basal and opercular lengths 16 and 13% smaller on average, respectively, than those from the high food treatment.

Post-metamorphic survival

In both experiments, the percentage of out-planted barnacles surviving to a specific week (cumulative survival) decreased strongly during the first 2 wk and then remained steady over the study period (Fig. 4). In Expt 1 (Fig. 4a,b), the effect of larval food environment on cumu-

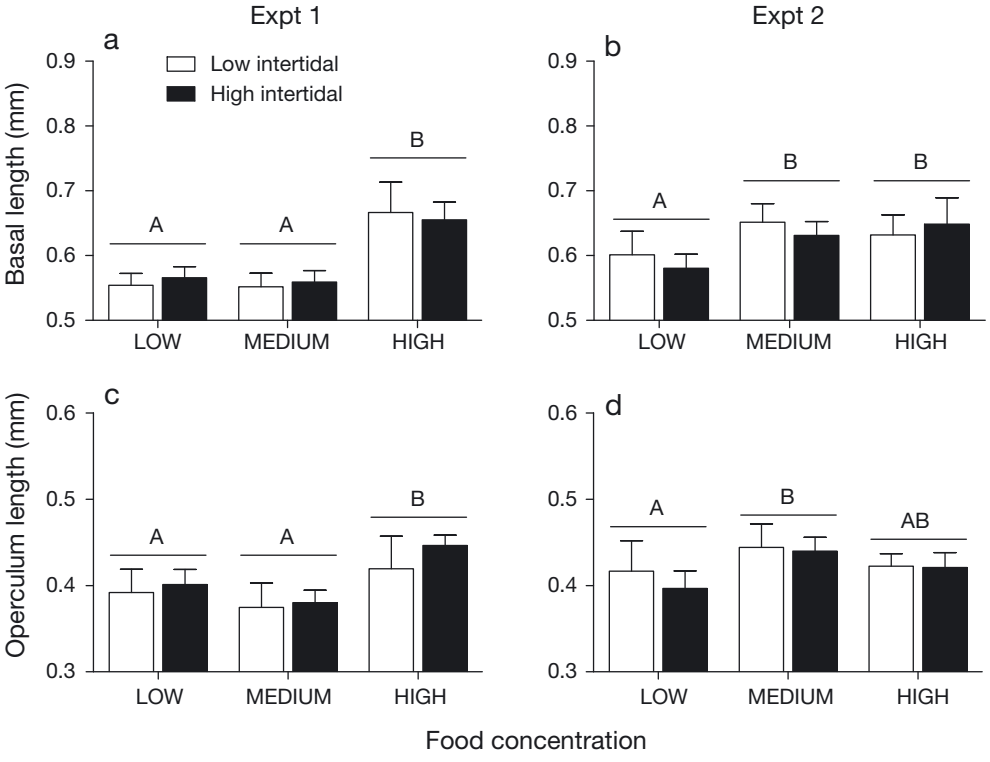

Fig. 3. *Austrominius modestus*. Effect of larval food concentration on body size (basal and operculum length) of out-planted metamorphs at the time of out-planting (Day 0). Basal length in (a) Expt 1, (b) Expt 2; operculum length in (c) Expt 1, (d) Expt 2. Different capital letters indicate significant differences between treatments after SNK post hoc test; error bars are SE among replicate vessels. Note that no differences between intertidal levels are presented, showing that the sizes at metamorphosis were evenly distributed among intertidal levels

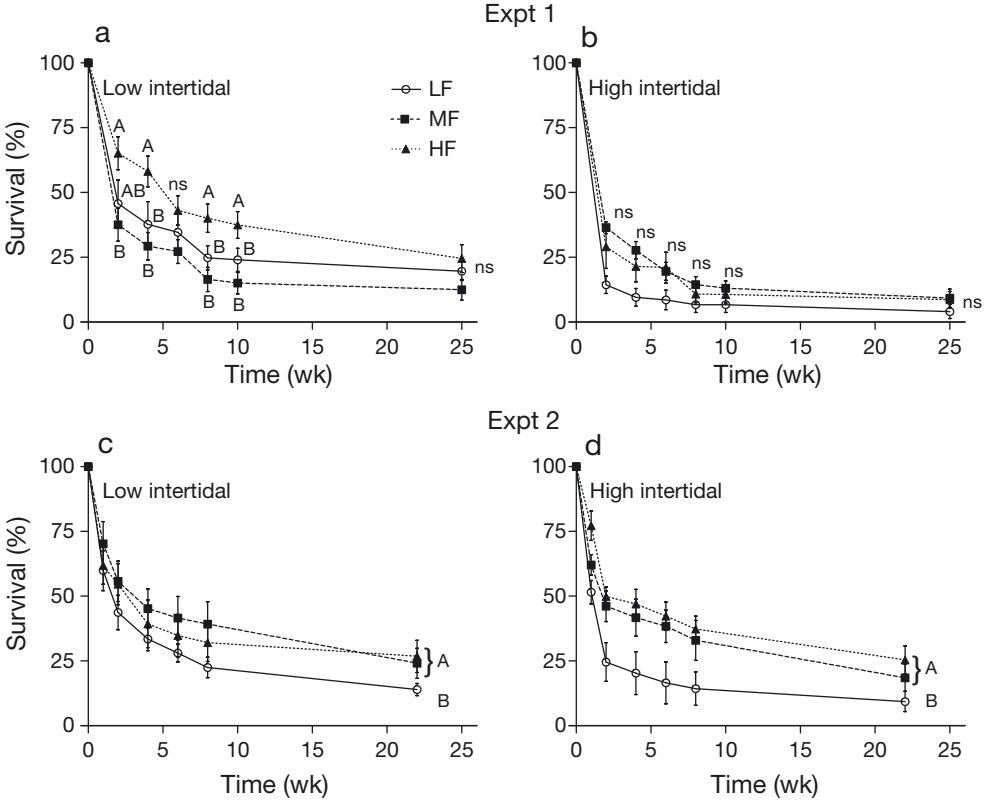

Fig. 4. *Austrominius modestus*. Effect of larval food concentration and intertidal level on survival of settlers through time. Expt 1 (a) low intertidal, (b) high intertidal; Expt 2 (c) low intertidal, (d) high intertidal. Food concentration: LF, low; MF, medium; HF, high. Error bars are SE among replicate vessels. For Expt 1, SNK post hoc tests were run for week, food and intertidal level combinations. Different capital letters indicate significant differences each week among food treatments; ns: no significant difference. For Expt 2, a SNK post hoc test was run after a main food effect (interactions were not significant); different letters (panels c and d) indicate overall differences between food treatments

Table 4. *Austrominius modestus*. Three-way repeated measures ANOVAs evaluating the effect of food concentration, intertidal level and time on cumulative barnacle survival for 2 different experiments. Significant effects are in **bold**

	Expt 1				Expt 2			
	df	MS	*F*	p	df	MS	*F*	p
Food (F)	2	0.153	2.28	0.123	2	0.752	5.84	**0.0082**
Intertidal level (I)	1	1.271	18.93	**<0.001**	1	0.003	0.02	0.88
F × I	2	0.259	4.81	**0.035**	2	0.05	0.41	0.67
Error	25	0.067			25	0.129		
Time (T)	5	0.282	57.45	**<0.0001**	5	0.665	153.96	**<0.0001**
T × F	10	0.004	1.315	0.52	10	0.007	1.65	0.10
T × I	5	0.012	4.035	**0.034**	5	0.011	2.67	**0.025**
T × F × I	10	0.007	1.94	0.12	10	0.004	0.95	0.49
Error	125	0.004			125	0.004		

lative survival depended on intertidal level (significant 2-way interactions, Table 4). Significant effects of larval food concentration were restricted to the lower intertidal: high larval food concentrations resulted in the highest survival. The differences between low and intermediate food concentrations were not significant. This effect of food on survival on the lower intertidal was established between the time of out-planting and Week 2 (6 October 2011). On average, 65% of metamorphs originating from the high food level survived the first 2 wk after out-planting; only 37 to 46% of those from the intermediate and low food level survived that period (Fig. 4a, SNK post hoc tests). By contrast, survival was low in the upper intertidal, irrespective of the larval food treatment (on average, 25% of the out-planted metamorphs, Fig. 4b).

Further examination of Expt 1 showed that the effect of food observed in the low intertidal at Week 2 remained (except in Week 6) until Week 10 (Fig. 4a, SNK post hoc test) owing to a bi-weekly survival (percentage surviving any 2 wk period) which was consistently high (>70%) irrespective of food treatment. By Week 10, the cumulative survival was 37% on average in juveniles metamorphosed from larvae reared at high food concentrations, significantly higher than in those from intermediate and low food concentrations, which showed an average survival of 15 and 24%, respectively (Fig. 4a). At Week 25 (16 March 2012), the effect of larval food concentration on cumulative survival was not significant, but the trend was still present (Fig. 4a). The loss of significance was most likely due to loss of power in the test since very few individuals (<5 per tile) remained alive at that time. In summary, the effect of larval food on barnacle density in Expt 1, found at the low intertidal level, was established in the first 2 wk. These differences in barnacle density due to the effect of larval food were maintained from Week 2 until Week 10.

In Expt 2, there was a significant main effect of larval food concentration which was consistent across both intertidal levels (Table 4). Cumulative survival was lowest in metamorphs which originated from the lowest food concentrations, while those from intermediate and high food concentration showed similar levels of survival (Fig. 4c,d, SNK post hoc test). In this experiment, the effect of larval food conditions on survival was apparent 1 wk after settlement (24 October 2011), and these differences remained over the whole 22 wk study period. The percentage survival after 2 wk was 34% on average for the metamorphs from the low food level and 52% for those from the high and intermediate food levels. After the second week, bi-weekly survival was high (>80% on average), irrespective of food treatment. Thus, the differences in barnacle density related to larval food environment were established during the first 2 wk and remained for the 22 wk of the study period.

Examination of survival as a function of density revealed inconsistent patterns. For Expt 1, initial density (D) and proportion of survivors (S) after 2 wk were weakly but negatively correlated ($S = 0.48 - 0.0022D$, $p = 0.016$), irrespective of the food and intertidal level. For Expt 2, the correlation of initial density and survival depended on the intertidal level: for the high level, the correlation was positive ($S = 0.54 + 0.0025D$, $p = 0.04$), while for the low level, the correlation was not significant.

Post-metamorphic growth

Overall, barnacles grew from approximately 0.55 to 4–5 mm in basal length (Fig. 5) and from 0.39 to 1.5–2.5 mm in operculum length (data not shown). In Expt 1, an effect of food concentration was only found in the lower intertidal (intertidal level × food interaction, Table 5). Here, high food concentration led to significantly larger body size (basal length, Fig. 5a) and longer operculum length (not shown) than the intermediate and lower food concentrations (SNK post hoc test). These differences were established at the time of out-planting (see Fig. 3 for details) and appeared to increase with time (Fig. 5a).

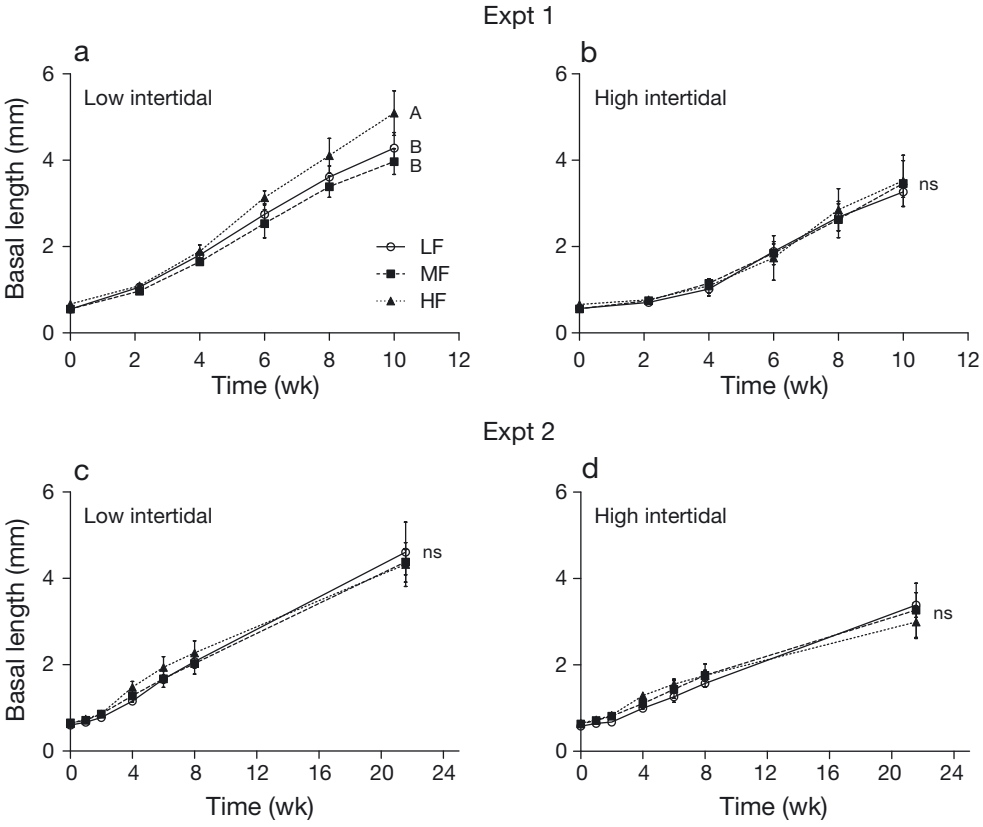

Fig. 5. *Austrominius modestus*. Effect of larval food concentration and intertidal level on growth (basal length) of settlers through time. Expt 1 (a) low intertidal, (b) high intertidal; Expt 2 (c) low intertidal, (d) high intertidal. Food concentration: LF, low; MF, medium; HF, high. Error bars are SE among replicate vessels. Different capital letters indicate significant overall differences among food treatments after 10 wk (SNK post hoc test); ns: no significant difference

Initially, the basal length of metamorphs from the low and intermediate food treatments were 0.12 mm smaller on average than those from the high food treatment (0.55 vs. 0.67 mm); this difference increased to 1 mm after 10 wk. By contrast, proportional differences varied little between the time of outplanting (17%) and after 10 wk (19%). There was no effect of food treatment on growth in Expt 2.

Table 5. *Austrominius modestus*. Generalised linear models (GLM) evaluating the effect of food concentration, intertidal level and time on barnacle growth (basal and operculum length) for 2 different experiments. Significant effects are in **bold**

	df	Basal length χ^2	Basal length p	Operculum length χ^2	Operculum length p
Expt 1					
Intertidal level (I)	1	16.78	**<0.0001**	17.79	**<0.0001**
Food (F)	2	0.57	0.75	1.14	0.56
Time (T)	4	404.93	**<0.0001**	375.80	**<0.0001**
I × F	2	9.92	**0.007**	8.69	**0.013**
I × T	4	13.88	**0.008**	7.87	0.096
F × T	8	2.64	0.95	6.07	0.64
I × F × T	8	4.06	0.85	9.44	0.31
Expt 2					
Intertidal level	1	7.59	**0.006**	7.46	**0.006**
Food	2	1.84	0.40	2.95	0.23
Time	5	613.94	**<0.0001**	562.78	**0.0001**
I × F	2	1.85	0.40	0.45	0.80
I × T	5	29.37	**<0.0001**	28.09	**<0.0001**
F × T	10	27.05	**0.0026**	19.25	**0.037**
I × F × T	10	3.09	0.98	2.24	0.99

DISCUSSION

In species with complex life cycles, spatial and temporal variation in the timing of metamorphosis can be important in determining the structure and dynamics of populations and communities (Gaines & Roughgarden 1985, Caley et al. 1996, Connolly et al. 2001, Jenkins et al. 2008), and metapopulation persistence (Armsworth 2002). However, recent work has shown that variations in traits (e.g. body size, nutritional reserves), at or after metamorphosis, also affect subsequent survival or reproduction (Pechenik 2006) and can translate into effects on recruitment (Giménez 2004) and reproductive potential for a population (Burgess & Marshall 2011). Such trait-mediated effects may be strong in species with a short post-metamorphic phase. However, the situation for species with longer post-metamorphic life is not so straightforward (Pechenik et al. 1998) because post-metamorphic conditions (i.e. stochasticity, biotic interactions, stress, disturbance or density-dependent

effects) may prevail over any effect produced by the pre-metamorphic environment. Using an intertidal barnacle as a model we found: (1) that effects of the larval environment on performance, when present, had long-term consequences, affecting the abundance and size of individuals reaching reproductive maturity; (2) context-dependent effects of the larval environment on performance, mediated by changes in larval and post-metamorphic traits. In addition, we found: (3) variable responses among experiments that may reflect variations in the environmental context or other sources (e.g. genotype × environment interactions). Long-term but variable effects (context-dependent or not) add to the complex ways in which trait-mediated effects can affect natural communities (Werner & Peacor 2003, Ohgushi et al. 2012).

The persistence of trait-mediated effects is critical in demonstrating that larval traits can have a strong influence on population level processes. We showed persistence of effects from the time of settlement in autumn until the spring (an age at which *Austrominius modestus* can be reproductively mature; Crisp & Davies 1955). Most studies demonstrating effects of larval history on performance focus on the first 2 to 3 wk after metamorphosis (Pechenik et al. 1993, Phillips 2002, Thiyagarajan et al. 2003a,b). Temporal persistence of larval effects is not widely known for marine invertebrates (but see Allen et al. 2008), and we are not aware of any field study tracking cohorts of invertebrates for several months after manipulating the larval environment. Previous studies of species with short maturation times have shown important effects of the larval environment on adult cohorts (e.g. Prout & McChesney 1985, Wendt 1998) or effects of the natal habitat on population dynamics over several generations (Van Allen & Rudolf 2013). Our results extend those carried out with short post-metamorphic phases and point to the potentially widespread effect of the larval environment on recruitment. There is now an important body of work that highlights the contributory role of oceanographic conditions in determining the recruitment of individuals to adult stages through effects on larval settlement (Connolly et al. 2001). In addition, variations in oceanographic conditions leading to, for example, changes in food availability may also contribute to changes in recruitment through modifications of traits at or after metamorphosis.

During our study, it was striking to observe that patterns in survival, once established, persisted over a long period, irrespective of biotic and abiotic processes operating after metamorphosis. These patterns were established during the first 2 wk, when mortality in invertebrate juveniles is known to be particularly high (Gosselin & Qian 1997, Hunt & Scheibling 1997, Underwood & Keough 2001, Gosselin & Jones 2010). On average, 58% of the outplanted juveniles were lost during that period. In the case of barnacles, the level of reserves at metamorphosis is critical, since they cannot feed for the following few days (Rainbow & Walker 1977). Therefore, it is likely that there is a critical window where effects of larval experience on post-metamorphic survival are highest.

A potential process leading to high early mortality is density-dependence, for instance through competition. In our case, however, density-dependence did not seem to be an overall explanation for the high mortality observed in both experiments. Significant negative correlations between densities and survival were only found in Expt 1. Competition was unlikely because metamorphs were distributed randomly over the plates, at low densities (max. density = 10 ind. cm^{-2}) and at such distances that they would not have the opportunity to engage in competition. A previous study on barnacle density-dependence, also carried out on Welsh intertidal shores (Jenkins et al. 2008), suggested that this process requires higher densities (above 20 ind. cm^{-2}). This study looked at 1 mo old juvenile *Semibalanus balanoides*, which are larger and occupy more space than 2 wk old *A. modestus*.

Patterns established early in the benthic phase persisted because actual mortality rates did not vary further among food treatments (only 16% were lost in any subsequent 2 wk period), leading to the so-called Type III trajectory (Caley 1998). We can only speculate about the reasons behind the maintenance of the patterns. The timing of our experiments meant that surviving juveniles developed through autumn–winter conditions, when low temperatures may reduce the strength of biotic interactions or metabolic requirements. Perhaps the timing of settlement in relation to seasonality in the environment is an important factor determining the extent of trait-mediated effects. In addition, a reduction in sensitivity to environmental conditions through ontogeny could also be important (McCormick & Hoey 2004).

It is important to understand the physiological mechanisms leading to trait-mediated effects in order to progress toward a predictive theoretical framework. In this particular case, the mechanisms leading to trait-mediated effects may involve processes occurring before, during and after metamorphosis. First, low larval food concentration resulted in a reduction in cyprid size, %C content and body mass

(DW), as well as a reduced C:N ratio, effects which are consistent with findings for other barnacles (Thiyagarajan et al. 2002b, Emlet & Sadro 2006). Most of the changes in C content may result from reductions in the proportion of total lipids or triacylglycerols, which have been linked with variations in growth and survival of early barnacle stages (Thiyagarajan et al. 2002a,b, Tremblay et al. 2007). Second, important changes appeared to occur during metamorphosis because differences in body size among larval food treatments were not fully equivalent between pre-metamorphic (cyprid) and post-metamorphic juvenile stages. For example, in Expt 1, intermediate levels of food produced larger cyprids which were equivalent in size to the high food treatments but metamorphs that were smaller and equivalent to individuals raised on low food concentration; a similar mismatch occurred in Expt 2. In addition, examination of standardised average values of cyprid and metamorph size and early survival show clearly that survival was fully linked to metamorph, but not cyprid size (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m545p147_supp.pdf). Overall, these findings emphasise the importance of the interaction between physiological processes determining larval traits and the process of metamorphosis in establishing early post-metamorphic traits, which appeared to underpin the patterns of survival.

Another important result was the context-dependent nature of the trait-mediated effects. In Expt 1, the effects of larval environment on survival were only evident in the lower intertidal. In the upper intertidal, where conditions are expected to be more stressful (longer daily periods of desiccation, extreme temperatures and lower food supply), survival was strongly depressed, irrespective of food quality. Most related studies argue that the benefits of better quality larval phenotype will be expressed in poorer quality environments (e.g. Spight 1976, McGinley et al. 1987, Hutchings 1991, Tamate & Maekawa 2000, Phillips 2002, Allen & Marshall 2013), yet our work did not show this. Observations similar to our own have been made by Moran & Emlet (2001), who showed that hatching size of the gastropod *Nucella ostrina* positively affected early survival in a benign shaded habitat but not in a stressful sun-exposed environment. It is likely that under the conditions tested in our first experiment, the feeding/desiccation conditions were too harsh in the upper intertidal, but not in the lower intertidal. The limited number of studies and contradictory results still preclude making any generalisation about how variations in traits of metamorphs affect recruitment along the intertidal gradient.

The still limited capacity for generalisation is further shown by our results from the second experiment, where trait-mediated effects were found at both levels. This is relevant as a warning for interpreting results of studies lacking any level of repetition. We can only speculate that either environmental variability or variability among cohorts of settling larvae may drive trait-mediated effects. Evidence in favour of an environmental effect, in particular thermal stress, comes from naturally occurring differences in temperature experienced by juveniles outplanted in the different experiments. Temperature records (Hilbre Island meteorological station) show that the average air temperature during the first 2 wk after the out-planting in September (17.8°C) was 5°C higher than that experienced by barnacles outplanted in October (13.2°C). During the same period, daily temperature maxima (September: 25°C; October: <20°C) coincided with midday/early afternoon low water periods. These data, combined with the laboratory observations of Foster (1971) of 50% mortality rates of *A. modestus* recruits at 20°C, suggest that high intertidal level out-plants in Expt 1, where larval food treatment effects were not observed, would have been exposed to potentially much higher levels of emersion stress than those in Expt 2, where trait-mediated effects were clear. An alternative view of our results is that the different outcomes of the 2 experiments may reflect variations in larval phenotypes among cohorts. Evidence in favour of this hypothesis is that the effect of the larval food concentration on basal and operculum diameter was weaker in the cohort out-planted in October than that outplanted in September; hence, that cohort would have been better suited to tolerate the conditions existing in the upper intertidal level. Variations in phenotypes may reflect genetic variability or maternal effects on egg size and embryonic development. Variations in egg size within populations are important in intertidal barnacles in particular (Barnes & Barnes 1965). Significant spatial and temporal variations in larval size at hatching among parents have been recorded recently for *A. modestus* in our study area (Griffith 2013), but we still do not know if these are carried over to the cyprid stage.

We conclude that trait-mediated effects can be important for understanding the patterns of recruitment of organisms to the adult cohorts. Early effects of the larval environment on post-settlement survival can persist for months and eventually define the number and quality of adults. Our data showed that

this persistence was maintained through low levels of late juvenile mortality occurring over the winter. Specific trait responses are central to the understanding of the nature of trait-mediated effects across gradients of thermal and nutritional stress. The key trait responsible for the patterns of survival appears to be size at metamorphosis, which may affect the capacity to cope with food limitation or other stress during the first days of post-metamorphic life. This trait is shaped at the time of metamorphosis and did not fully correlate with larval traits, which were also affected by larval nutritional conditions. We also conclude that trait-mediated effects can be context-dependent but that such phenomena also depend on the level of habitat harshness or the variability among cohorts in the phenotypic responses to environmental conditions.

Acknowledgements. Special thanks are due to Dr. Katherine Griffiths for her help in rearing the microalgae. We also thank Dr. Joachim Harms (Forschungszentrum Jülich, Rostock-Warnemünde, Germany) for advice on barnacle rearing at early stages of the experiment. This research was funded by a Natural Environment Research Council (NERC) grant NEH006702/1 (UK) to S.R.J., L.G., M.T.B. and G.T.

LITERATURE CITED

Aguila JR, Hoshizaki DK, Gibbs AG (2013) Contribution of larval nutrition to adult reproduction in *Drosophila melanogaster.* J Exp Biol 216:399–406

Allen RM, Marshall DJ (2010) The larval legacy: cascading effects of recruit phenotype on post-recruitment interactions. Oikos 119:1977–1983

Allen RM, Marshall DJ (2013) Phenotypic links among life-history stages are complex and context-dependent in a marine invertebrate: interactions among offspring size, larval nutrition, and post-metamorphic density. Funct Ecol 27:1358–1366

Allen RM, Buckley YM, Marshall DJ (2008) Offspring size plasticity in response to intraspecific competition: an adaptive maternal effect across life-history stages. Am Nat 171:225–237

Anger K, Harms J (1990) Elemental (CHN) and proximate biochemical composition of decapod crustacean larvae. Comp Biochem Physiol B 97:69–80

Armsworth PR (2002) Recruitment limitation, population regulation, and larval connectivity in reef fish metapopulations. Ecology 83:1092–1104

Auer SK, Arendt JD, Chandramouli R, Reznick DN (2010) Juvenile compensatory growth has negative consequences for reproduction in Trinidadian guppies (*Poecilia reticulata*). Ecol Lett 13:998–1007

Barnes H, Barnes M (1965) Egg size, nauplius size, and their variation with local, geographical and specific factors in some common cirripedes. J Anim Ecol 34:391–402

Broitman BR, Blanchette CA, Menge BA, Lubchenco J and others (2008) Spatial and temporal patterns of invertebrate recruitment along the West Coast of the United States. Ecol Monogr 78:403–421

Burgess SC, Marshall DJ (2011) Are numbers enough? Colonizer phenotype and abundance interact to affect population dynamics. J Anim Ecol 80:681–687

Caley MJ (1998) Age-specific mortality rates in reef fishes: evidence and implications. Aust J Ecol 23:241–245

Caley MJ, Carr MH, Hixon MA, Hughes TP, Jones GP, Menge BA (1996) Recruitment and the local dynamics of open marine populations. Annu Rev Ecol Syst 27: 477–500

Connell JH (1985) The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. J Exp Mar Biol Ecol 93:11–45

Connolly J, Menge BA, Roughgarden J (2001) A latitudinal gradient in recruitment of intertidal invertebrates in the northeast Pacific Ocean. Ecology 82:1799–1813

Crisp DJ (1958) The spread of *Elminius modestus* Darwin in north-west Europe. J Mar Biol Assoc UK 37:483–520

Crisp DJ, Davies PA (1955) Observations *in vivo* on the breeding of *Elminius modestus* grown on glass slides. J Mar Biol Assoc UK 34:357–380

Emlet RB, Sadro SS (2006) Linking stages of life history: how larval quality translates into juvenile performance for an intertidal barnacle (*Balanus glandula*). Integr Comp Biol 46:334–346

Foster BA (1971) Desiccation as a factor in the intertidal zonation of barnacles. Mar Biol 8:12–29

Gaines S, Roughgarden J (1985) Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidal zone. Proc Natl Acad Sci USA 82:3707–3711

Gaines SD, Roughgarden J (1987) Fish in offshore kelp forests affect recruitment to intertidal barnacle populations. Science 235:479–481

Giménez L (2004) Marine community ecology: importance of trait-mediated effects propagating through complex life cycles. Mar Ecol Prog Ser 283:303–310

Giménez L (2010) Relationships between habitat conditions, larval traits and juvenile performance in a marine invertebrate. Ecology 91:1401–1413

Giménez L, Jenkins SR (2013) Combining traits and density to model recruitment of sessile organisms. PLoS ONE 8: e57849

Giménez L, Anger K, Torres G (2004) Linking life history traits in successive phases of a complex life cycle: effects of larval biomass on early juvenile development in an estuarine crab *Chasmagnathus granulata.* Oikos 104: 570–580

Gosselin LA, Jones LA (2010) Effects of solar radiation on barnacle settlement, early post-settlement mortality and community development in the intertidal zone. Mar Ecol Prog Ser 407:149–158

Gosselin LA, Qian PY (1997) Juvenile mortality in benthic marine invertebrates. Mar Ecol Prog Ser 146:265–282

Griffith K (2013) Climate-driven changes in the recruitment success of marine invertebrates: the role of food supply and temperature. PhD dissertation, School of Ocean Sciences, Bangor University

Grosberg RK, Levitan DR (1992) For adults only? Supply-side ecology and the history of larval biology. Trends Ecol Evol 7:130–133

Harms J (1986) Effects of temperature and salinity on larval development of *Elminius modestus* (Crustacea, Cirripedia) from Helgoland (North Sea) and New Zealand. Helgol Meersunters 40:355–376

Harms J (1987) Energy budget for the larval development of *Elminius modestus* (Crustacea: Cirripedia). Helgol Meersunters 41:45–67

Harms J (1998) The neozoan *Elminius modestus* Darwin (Crustacea, Cirripedia): possible explanations for its successful invasion in European water. Helgol Meersunters 52:337–345

Hentschel BT, Emlet RB (2000) Metamorphosis of barnacle nauplii: effects of food variability and a comparison with amphibian models. Ecology 81:3495–3508

Hunt HL, Scheibling RE (1997) Role of early post-settlement mortality in recruitment of benthic marine invertebrates. Mar Ecol Prog Ser 155:269–301

Hutchings JA (1991) Fitness consequences of variation in egg size and food abundance in brook trout *Salvelinus fontinalis.* Evolution 45:1162–1168

Jarrett JN (2003) Seasonal variation in larval condition and postsettlement performance of the barnacle *Semibalanus balanoides.* Ecology 84:384–390

Jarrett JN, Pechenik J (1997) Temporal variation in cyprid quality and juvenile growth capacity for the barnacle *Semibalanus balanoides.* Ecology 78:1262–1265

Jenkins SR (2005) Larval habitat selection not larval supply determines settlement patterns and adult distribution in two chthamalid barnacles. J Anim Ecol 74:893–904

Jenkins SR, Åberg P, Cervin G, Coleman RA and others (2000) Spatial and temporal variation in the settlement and recruitment of the intertidal barnacle *Semibalanus balanoides* (L.) (Crustacea: Cirripedia) over a European scale. J Exp Mar Biol Ecol 243:209–225

Jenkins SR, Murua J, Burrows MT (2008) Temporal changes in the strength of density-dependent mortality and growth in intertidal barnacles. J Anim Ecol 77:573–584

Kaplan RH (1992) Greater maternal investment can decrease offspring survival in the frog *Bombina orientalis.* Ecology 73:280–288

Kaplan RH, Phillips PC (2006) Ecological and developmental context of natural selection: maternal effects and thermally induced plasticity in the frog *Bombina orientalis.* Evolution 60:142–156

Kerby J, Wilmers CC, Post E (2012) Climate change, phenology and the nature of consumer-resource interactions: advancing the match-mismatch hypothesis. In: Ohgushi T, Schmitz OJ, Holt RD (eds) Trait-mediated indirect interactions: ecological and evolutionary perspectives. Cambridge University Press, New York, NY, p 508–525

Lindholm AK, Hunt J, Brooks R (2006) Where do all the maternal effects go? Variation in offspring body size through ontogeny in the live-bearing fish *Poecilia parae.* Biol Lett 2:586–589

Lucas MI, Walker G, Holland DL, Crisp DJ (1979) An energy budget for the free-swimming and metamorphosing larvae of *Balanus balanoides* (Crustacea: Cirripedia). Mar Biol 55:221–229

Marshall DJ, Morgan SG (2011) Ecological and evolutionary consequences of linked life-history stages in the sea. Curr Biol 21:R718–R725

McCormick M, Hoey A (2004) Larval growth history determines juvenile growth and survival in a tropical marine fish. Oikos 106:225–242

McGinley MA, Temme DH, Geber MA (1987) Parental investment in offspring in variable environments: theoretical and empirical considerations. Am Nat 130:370–398

Menge BA (2000) Top-down and bottom-up community regulation in marine rocky intertidal habitats. J Exp Mar Biol Ecol 250:257–289

Miner BG, Sultan SE, Morgan SG, Padilla DK, Relyea RA (2005) Ecological consequences of phenotypic plasticity. Trends Ecol Evol 20:685–692

Miron G, Boudreau B, Bourget E (1999) Intertidal barnacle distribution: a case study using multiple working hypotheses. Mar Ecol Prog Ser 189:205–219

Moran AL (1999) Size and performance of juvenile marine invertebrates: potential contrasts between intertidal and subtidal benthic habitats. Am Zool 39:304–312

Moran AL, Emlet RB (2001) Offspring size and hatchling performance of an intertidal gastropod under variable field conditions. Ecology 82:1597–1612

Navarrete SA, Broitman B, Wieters EA, Finke GR, Venegas RM, Sotomayor A (2002) Recruitment of barnacles and mussels in the southeast Pacific during and after the 1997–1998 El Niño. Limnol Oceanogr 47:791–802

Ohgushi T, Schmitz O, Holt RD (eds) (2012) Trait-mediated indirect interactions: ecological and evolutionary perspectives. Cambridge University Press, New York, NY

Pechenik JA (2006) Larval experience and latent effects — metamorphosis is not a new beginning. Integr Comp Biol 46:323–333

Pechenik JA, Rittschof D, Schmidt AR (1993) Influence of delayed metamorphosis on survival and growth of juvenile barnacles *Balanus amphitrite.* Mar Biol 115:287–294

Pechenik JA, Wendt DE, Jarrett JN (1998) Metamorphosis is not a new beginning. Bioscience 48:901–910

Phillips NE (2002) Effects of nutrition-mediated larval condition on juvenile performance in a marine mussel. Ecology 83:2562–2574

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2015) nlme: Linear and nonlinear mixed effects models. R package version 3.1-122, http://CRAN.R-project.org/package=nlme

Prout T, McChesney F (1985) Competition among immatures affects their adult fertility: population dynamics. Am Nat 126:521–558

Rainbow PS, Walker G (1977) The functional morphology of the alimentary tract of barnacles (Cirripedia: Thoracica). J Exp Mar Biol Ecol 28:183–206

Roughgarden J, Gaines S, Possingham H (1988) Recruitment dynamics in complex life cycles. Science 241: 1460–1466

Schmitz OJ, Adler FR, Agrawal AA (2003) Linking individual-scale trait plasticity to community dynamics. Ecology 84:1081–1082

Shima JS, Swearer SE (2009) Larval quality is shaped by matrix effects: implications for connectivity in a marine metapopulation. Ecology 90:1255–1267

Spight TM (1976) Ecology of hatching size for marine snails. Oecologia 24:283–294

Svensson CJ, Jenkins SR, Hawkins SJ, Myers AA and others (2004) Models of open populations with space-limited recruitment in stochastic environments: relative importance of recruitment and survival in populations of *Semibalanus balanoides.* Mar Ecol Prog Ser 275:185–197

Tamate T, Maekawa K (2000) Interpopulation variation in reproductive traits of female masu salmon, *Oncorhynchus masou.* Oikos 90:209–218

Thiyagarajan V, Harder T, Qian PY (2002a) Effect of the physiological condition of cyprids and laboratory-mimicked conditions on the metamorphic success of *Balanus amphitrite* Darwin (Cirripedia: Thoracica). J Exp Mar Biol Ecol 274:65–74

Thiyagarajan V, Harder T, Qian PY (2002b) Relationship between cyprid energy reserves and metamorphosis in the barnacle *Balanus amphitrite* Darwin (Cirripedia; Thoracica). J Exp Mar Biol Ecol 280:79–93

Thiyagarajan V, Harder T, Qiu JW, Qian PY (2003a) Effects of TAG/DNA ratio and age of cyprids on post-metamorphic growth and survival in the barnacle *Balanus amphitrite.* J Mar Biol Assoc UK 83:83–88

Thiyagarajan V, Harder T, Qiu JW, Qian PY (2003b) Energy content at metamorphosis and growth rate of the juvenile barnacle *Balanus amphitrite.* Mar Biol 143:543–554

Thorson G (1950) Reproductive and larval ecology of bottom marine invertebrates. Biol Rev Camb Philos Soc 25:1–45

Tremblay R, Olivier F, Bourget E, Rittschof D (2007) Physiological condition of *Balanus amphitrite* cyprid larvae determines habitat selection success. Mar Ecol Prog Ser 340:1–8

Underwood AJ, Keough MJ (2001) Supply-side ecology: the nature and consequences of variations in recruitment of intertidal organisms. In: Bertness MD,Gaines SD, Hay ME (eds) Marine community ecology. Sinauer Associates, Sunderland, MA, p 183–200

Van Allen BG, Rudolf VHW (2013) Ghosts of habitats past: environmental carry-over effects drive population dynamics in novel habitat. Am Nat 181:596–608

Wendt DE (1998) Effect of larval swimming duration on growth and reproduction of *Bugula neritina* (Bryozoa) under field conditions. Biol Bull 195:126–135

Werner EE, Peacor SD (2003) A review of trait-mediated indirect interactions in ecological communities. Ecology 84:1083–1100

West TL, Costlow JD (1987) Size regulation in larvae of the crustacean *Balanus eburneus* (Cirripedia: Thoracica). Mar Biol 96:47–58

Editorial responsibility: Susanne Schüller, Oldendorf/Luhe, Germany

Submitted: May 6, 2015; Accepted: December 18, 2015
Proofs received from author(s): February 23, 2016