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RESEARCH ARTICLE

Temperature-induced maternal effects and environmental predictability

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SUMMARY

Maternal effects could influence the persistence of species under environmental change, but the adaptive significance of many empirically estimated maternal effects remains unclear. Inferences about the adaptive significance of maternal effects depend on the correlation between maternal and offspring environments, the relative importance of frequency- or density-dependent selection and whether absolute or relative fitness measures are used. Here, we combine the monitoring of the environment over time with a factorial experiment where we manipulated both the maternal and offspring environment in a marine bryozoan (*Bugula neritina*). We focused on temperature as our environmental variable as temperature commonly varies over short time scales in nature. We found that offspring from mothers kept in warmer water were smaller and more variable in size, but had increased dispersal potential and higher metamorphic success than offspring from mothers kept in cooler water. Our results suggest that, under frequency- or density-independent selection, mothers that experienced higher temperatures compared with lower temperatures were favoured. Under frequency- or density-dependent selection, there were indications that mothers that experienced higher temperatures would be favoured only if their offspring encountered similar (warmer) temperatures, though these results were not statistically significant. Analysis of time series data on temperature in the field shows that the maternal thermal environment is a good predictor of the temperatures offspring are likely to experience early in life. We suggest that future studies on maternal effects estimate environmental predictability and present both absolute and relative estimates of maternal fitness within each offspring environment.

Key words: climate change impact, dispersal, larval quality, offspring size, phenotypic plasticity.

INTRODUCTION

Maternal effects are one of the most important influences on the phenotype and performance of offspring (Wade, 1998). Maternal effects occur when the environment or phenotype of the mother influences the phenotype of their offspring (Mousseau and Fox, 1998; Marshall and Uller, 2007). Maternal effects can buffer offspring from the impacts of environmental heterogeneity because mothers can adjust the phenotype of their offspring to match the environment that offspring are likely to experience (Fox et al., 1997; Mousseau and Fox, 1998; Agrawal et al., 1999; Benton et al., 2005; Plaistow et al., 2007; Allen et al., 2008; Marshall et al., 2008; Latzel et al., 2010). When maternal effects increase the fitness of offspring in the presence of environmental change, they are sometimes called 'adaptive transgenerational phenotypic plasticity' or 'anticipatory maternal effects' (Fox et al., 1997; Agrawal et al., 1999; Marshall and Uller, 2007). For example, mothers exposed to predators can produce predation-resistant offspring such that both maternal and offspring fitness are maximised (Agrawal et al., 1999). More generally, phenotypic plasticity (of which maternal effects are just a subset) is thought to play a major role in the persistence of species in the face of human-induced changes (Ghalambor et al., 2007; Chevin et al., 2010). Nevertheless, the adaptive significance of many maternal effects remains unclear.

Mothers can only match the phenotype of their offspring to the offspring's local environment if they can anticipate the environment their offspring will experience (Marshall and Uller, 2007). Thus, maternal manipulations of the offspring phenotype will only be favoured if the maternal environment is a good predictor of the offspring environment in space or time. Studies of phenotypic plasticity have emphasised that, in the absence of explicitly estimating the reliability of environmental cues, the adaptive significance of plasticity remains unclear (Lechowicz and Bell, 1991; Stratton, 1994; Kelley et al., 2005; Baythavong et al., 2009). Although there have been repeated calls for similar estimates of environmental predictability in studies of transgenerational plasticity (i.e. maternal effects), very few studies have addressed this issue (Donohue and Schmitt, 1998; Einum and Fleming, 2004; Galloway, 2005; Fischer et al., 2010). In a rare example, Galloway showed that the scale of seed dispersal in a short-lived understory herbaceous plant was less than the typical distance between light gaps (Galloway, 2005), suggesting that the maternal light environment was a good predictor of the offspring light environment and that anticipatory maternal effects occurred in this species (Galloway and Etterson, 2007). To understand the ecological context and adaptive significance of maternal effects, it is necessary to estimate both the maternal and offspring environments, and the correlation (or predictability) between them, under natural settings and across appropriate scales (Donohue and Schmitt, 1998; Galloway, 2005).

Importantly, maternal effects do not always increase offspring fitness and so the interaction between environmental change and maternal effects may not always be straightforward (Marshall and Uller, 2007; Plaistow et al., 2007). Although maternal effects influence the fitness of both mothers and offspring, selection typically acts to maximise maternal fitness (Kirkpatrick and Lande,

1989; Bernado, 1996; Marshall and Uller, 2007) [but see Wolf and Wade (Wolf and Wade, 2001) for important caveats]. Thus, under some circumstances, environmental change can induce mothers to reduce the fitness of their offspring in order to increase maternal lifetime fitness (Cunningham and Russell, 2000; Kudo, 2006). Furthermore, when environmental conditions are spatially or temporally unpredictable, selection may favour mothers that produce a range of offspring phenotypes (Einum and Fleming, 2004; Crean and Marshall, 2009; Fischer et al., 2010). Thus, maternal effects can protect offspring from environmental change, or transmit negative environmental influences through the maternal phenotype into the next generation, thereby increasing the challenging of predicting the biological impacts of environmental change.

Estimating the fitness benefits of a maternal effect is not as straightforward as it may seem. Inferences about the adaptive significance and population consequences of maternal effects in heterogeneous environments depend on the relative importance of frequency- or density-dependent selection and whether absolute or relative fitness measures are used (Schmitt and Antonovics, 1986; Kelley et al., 2005; Stanton and Thiede, 2005; Kokko and Lopez-Sepulcre, 2007; Orr, 2009; Fischer et al., 2010). When frequency- or density-independent selection predominates, absolute fitness of mothers should be compared across the whole population. Under this scenario, offspring environments containing a higher absolute mean fitness contribute more to the next generation than environments with lower absolute mean fitness (Stanton and Thiede, 2005). When frequency- or density-dependent selection predominates, fitness variation should be estimated using relative maternal fitness calculated within each offspring environment. Under this scenario, the contribution of offspring in a particular environment to the next generation is affected by the probability that offspring encounter each environment (Lechowicz and Bell, 1991; Kelley et al., 2005). Therefore, mothers influencing their offspring to achieve high absolute fitness in the best offspring environment are favoured under frequency- or density-independent selection, whereas mothers influencing their offspring to achieve relatively higher fitness across environments are favoured by frequency- or density-dependent selection (Stanton and Thiede, 2005). Consequently, inferences from absolute *versus* relative fitness make different assumptions about how population density and the frequency of offspring environments in space or time affect the outcome of selection and its consequences to subsequent population numbers (Galloway, 2005; Stanton and Thiede, 2005; Saccheri and Hanski, 2006). Evolutionary biologists have long been aware of the different evolutionary interpretations of absolute *versus* relative fitness (e.g. Lande and Arnold, 1983; Via and Lande, 1985; Kawecki and Ebert, 2004; Stanton and Thiede, 2005; Saccheri and Hanski, 2006; Orr, 2009), but studies on maternal effects usually draw inferences from only the absolute fitness benefits of a particular maternal effect (e.g. Marshall, 2008).

A powerful way to determine the adaptive significance of maternal effects is to use a factorial experiment where both the offspring and maternal environments are manipulated (Donohue and Schmitt, 1998; Galloway, 2005; Latzel et al., 2010). Importantly, when assessing the fitness benefits of maternal effects, both absolute and relative estimates of maternal fitness should be provided, and the correlation between the maternal environment and the offspring environment in the field should be estimated. As far as we are aware, very few studies on maternal effects utilise all of these elements.

Here, we address these issues by combining the monitoring of the environment over time with a manipulative factorial experiment. We then compare our estimates of absolute and relative fitness of the maternally induced phenotypic changes within each offspring environment. We focused on temperature as our environmental variable because temperature commonly varies in nature, is known to induce maternal effects in a range of taxa (e.g. Huey and Kingsolver, 1989; Blanckenhorn, 2000; Angilletta et al., 2003; Fischer et al., 2003c; Seko and Nakasuji, 2006) and there is growing interest in the role of phenotypic plasticity in mitigating the impact of climate change (Chevin et al., 2010; Chown et al., 2010). Specifically, we examined the influence of temperature on the size of offspring that mothers produce, as well as the dispersal potential and metamorphic success (the latter being an important component of fitness) of offspring in different water temperatures. These three traits (larval size, dispersal potential and metamorphic success) are important determinants of individual performance, are sensitive to environmental change and strongly influence the dynamics of marine populations (Hoegh-Guldberg and Pearse, 1995; Stachowicz et al., 2002; Marshall and Keough, 2008; Burgess and Marshall, 2011).

MATERIALS AND METHODS

Study species

Bugula neritina (Linnaeus 1758) (Bryozoa: Cheilostomata) is an arborescent bryozoan that grows by asexual budding of zooids to form branches. *Bugula neritina* has a global distribution and colonies often grow on man-made structures (e.g. pontoons, pilings and jetties) in protected harbours around the coast of Australia. Colonies are hermaphroditic and larvae are brooded inside ovicells (specialised zooids) for approximately 1 week, during which time they receive nutrients from the colony *via* a placenta-like transport system and increase 500-fold in size from egg to larva (Woollacott and Zimmer, 1975). Larvae are competent to settle after release from the maternal colony and typically settle within a few hours in the laboratory when offered an appropriate settlement surface. At our field site, *B. neritina* are particularly common from November to July (personal observation).

Characterising the temperature regime in the field

In order to characterise the temperature regime that mothers and offspring experience in the field, we placed a temperature data logger (Odyssey temperature/salinity data recorder, Burnside, Christchurch, New Zealand) at our field site (East Coast Marina, Brisbane, Australia) adjacent to established adult colonies within the population. The data recorder was attached to a weighted rope, which was attached to the floating pontoon and hung 1 m below the water surface. Data were collected throughout four deployments between 17 July 2008 and 4 March 2009 (Fig. 1). Data were logged every 6 h during each deployment (at 00:00, 06:00, 12:00 and 18:00 h each day).

Temperature manipulation experiment

The experiments were performed at the CSIRO Marine and Atmospheric Research aquaculture facility at Cleveland (Brisbane, Australia) from 12 to 29 May 2009. Healthy, fecund colonies of *B. neritina* were collected from the sides of floating docks at the East Coast Marina at Manly (Brisbane, Australia) and transported to the aquaculture facility in insulated aquaria. Adult colonies were kept in four plastic 50 l experimental tanks at water temperatures of either 19 or 25°C. These temperatures are within the annual range of water temperatures recorded at our field site (Fig. 1), and were 3°C lower or higher than the water temperature measured in the field during the experiment (which was approximately 22°C). A change of 3°C over a few hours (as colonies experienced when relocated from the field to the tanks) is also within the natural range of day/night temperature variability in the field (Fig. 2A).

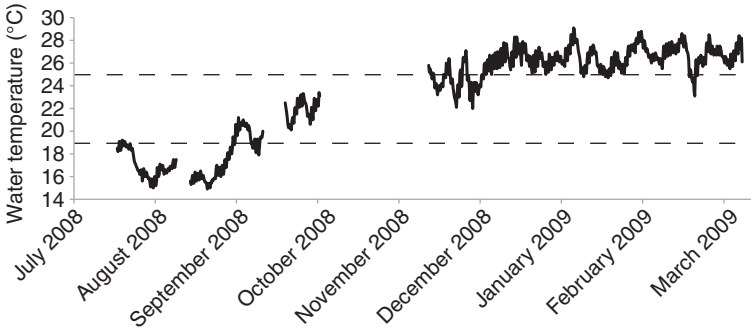

Fig. 1. Profile of water temperature where *Bugula neritina* were collected (East Coast Marina, Brisbane, Australia). Temperature data were recorded every 6 h. Dashed lines indicate the treatment temperatures used in the tank experiments and are plotted here as reference points. Experiments were conducted in May 2009 when the average water temperature was approximately 22°C.

Each tank was aerated and continuously supplied with filtered seawater (FSW; 20 µm screen size) at a rate of 1 l min^{-1}. To manipulate water temperature, we used a water bath technique. The tubing that supplied filtered seawater to the experimental tanks was placed in header tanks filled with 150 l of freshwater that was either heated or cooled. By sitting 30 m of 13 mm aquarium tubing in header tanks of either warmer or cooler water, the ambient temperature (~22°C) of the FSW in the tubing was effectively changed to the required temperatures *via* conduction. Water in one header tank was warmed using aquarium heaters whereas water in the other header tank was cooled using a water cooler (Hailer, MC150A, Raoping, Guangdong, China). Circulation within each header tank was achieved with a small submersible aquarium pump. This technique was effective in maintaining the temperature of the FSW in the experimental tanks at 19.36±0.025 or 24.83±0.003°C (mean ± s.e.m.).

All tanks were insulated with tinted polycarbonate sheets and covered with 15 mm polystyrene lids. The polystyrene lids also served the purpose of maintaining colonies in the dark to avoid (or minimise) the likelihood of colonies releasing larvae, as light is a known spawning cue in *B. neritina*. The colonies in each tank were fed ~150 ml of cultured microalgae (*Isochrysis galbana* or *Pavlova salina*) at ~5 to 7 million cells ml^{-1} every 2 days (on each day, the same concentration was injected into each tank). Each colony was individually attached to a 10×10×3 mm PVC plate by wrapping a small piece of sponge around the base of the colony and inserting it into a 4 mm hole. Plates were then threaded onto rods, which held the plates vertically so colonies were not touching any surfaces.

Experimental procedures and measurements

In each of two runs, 40 colonies (i.e. 80 colonies in total) were collected from the field and placed in each of the four tanks (10 colonies per tank per run). Colonies in run 2 were collected 10 days after those in run 1. Colonies were kept in tanks for a period of 1 week, similar to the time required for embryogenesis (Woollacott and Zimmer, 1975), after which time they were removed from the tanks and placed in individual containers with 1 l of FSW (FSW came from the same tank that they came from) under bright light to stimulate larval release. Previous studies have shown that *B. neritina* at our field site do not release immature larvae (Allen et al., 2008; Marshall, 2008), so we are confident that the larvae used in our experiments were those that were brooded from the beginning of our thermal manipulations.

Larval size

Sixty-three out of 80 colonies released larvae (percent of colonies that released larvae: 19°C$_{run1}$=70%; 25°C$_{run1}$=55%; 19°C$_{run2}$=95%; 25°C$_{run2}$=95%). Most larvae from each colony were placed in a vial containing 2% formalin. Larval size was later estimated by photographing larvae under a dissecting microscope and measuring the cross-sectional area of 10 larvae from each colony using Image Pro Plus 5.1 (Media Cybernetics, Bethesda, MD, USA). Six out of the 63 colonies that spawned produced less than 10 larvae, and so for these colonies all larvae were measured.

Dispersal potential

The time a larva takes to settle is often used as a proxy for dispersal potential in marine invertebrates with non-feeding larvae (Marshall and Keough, 2003). To estimate the effects of maternal temperature and offspring temperature on the dispersal potential of offspring, we placed larvae in 24 well cell culture plates (one larva per 3 ml well) and recorded whether individuals had settled 2.5 h after being released. The well walls had been roughened with sandpaper and had no biofilm, so represented a poor but suitable settlement habitat. Our measures of settlement time therefore estimate maximum dispersal potential.

Four colonies from each maternal temperature (two colonies from each of four tanks; eight colonies in total) were used. From each colony, 24 larvae were divided into the larval temperature treatments and allowed to settle: 12 larvae were allocated to water at 19°C and 12 larvae were allocated to water at 25°C. Within each larval temperature, the 12 larvae were divided into two tanks. Within each tank, the six larvae were divided between two cell culture plates. A larva was recorded as settled if it was attached to the surface of the well and could not be removed by a gentle jet of water from a pipette.

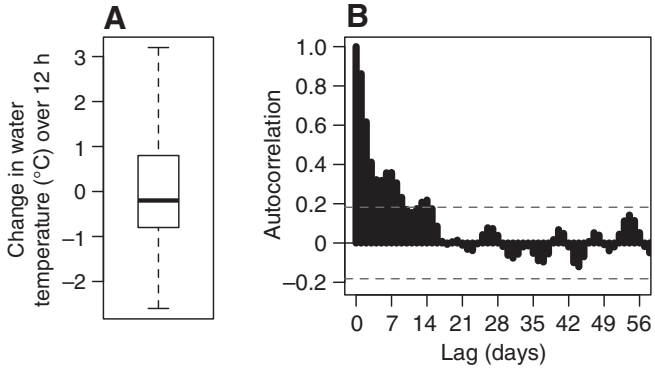

Fig. 2. (A) The change in water temperature over 12 h periods, which were 06:00 to 18:00 h and 18:00 to 06:00 h. (B) Predictability of temperature in the field. Correlogram shows the amount of dependency (autocorrelation) of values in the series on values found at a distance of *k* lags (1 lag=1 day). The mean temperature per day between 9 November 2008 and 4 March 2009 was used for this analysis (see Fig. 1). The dashed lines are approximate 95% confidence limits for an independent series for which the autocorrelation is zero.

A water bath technique was used to maintain water temperatures in the wells in which settlement was measured. Wells were filled with tank water (from the tank to which they were allocated) 1 h prior to putting larvae into them. The plates were floated on the surface of the water in each tank so that the wells were immersed in the tank water at the prescribed temperature.

Metamorphic success

To estimate metamorphic success, we used larvae from all colonies that produced enough larvae to allow meaningful analyses (resulting in 12 colonies, six from each maternal temperature). From each colony, 34±2.3 larvae were transferred to seven to eight Petri dishes (four to five larvae per 90 mm Petri dish) and allowed 4 h to settle. We then transferred Petri dishes with the newly attached offspring to the experimental tanks so that there were approximately eight offspring from each colony in each larval temperature treatment. The proportion of offspring from each colony in each larval temperature that had metamorphosed (defined as present with a normally developed lophophore) was recorded 48 h after settlement. The duration of metamorphosis at 20°C ranges from approximately 42 to 45 h (Wendt, 1996).

Data analysis

Predictability of temperature in the field

Correlograms were used to assess the systematic component of temperature variation in the field (Box et al., 1994; Legendre and Legendre, 1998). Correlograms are plots of the autocorrelation between successive terms in a data series, which measures the dependence of values in the series on the values before it (at a distance of k lags). Out of the four time periods where temperature was recorded continuously, only the last period (9 November 2008 to 4 March 2009) was used to quantify predictability because the other periods were too short for meaningful autocorrelation analyses (Legendre and Legendre, 1998). This time period also covers the period when *B. neritina* are particularly common at our field site (personal observation). Autocorrelation was calculated using the 'acf' function in R (v. 2.10.1, www.r-project.org). Data were averaged by day prior to analysis, so the observational window for this data series was 2 to 58 days [N=116 days, Δ=1 day (Legendre and Legendre, 1998)]. The average lifespan of our study species at our field site is in the order of weeks to months (personal observation) (Keough and Chernoff, 1987), so our estimates of thermal predictability cover a biologically relevant time scale for *B. neritina*. The raw time series exhibited stationarity (Shapiro–Wilk normality test, W=0.98, P=0.20), which is a statistical requirement for autocorrelation analyses on time series, and so were not detrended (Legendre and Legendre, 1998).

Temperature manipulation experiments

ANOVA was used to test for the effects of maternal temperature (fixed factor), offspring temperature (fixed factor), run (random factor) and tank nested within maternal temperature (random factor) plus all interactions. Analyses were done in Systat 11.0 (Systat Software, Chicago, IL, USA) and R. The effects of tank (within maternal temperature treatments), and interactions between run and tank, were assessed by comparing ANOVA models with and without the particular term of interest, starting with the highest order interactions (Quinn and Keough, 2002). In cases where these terms were not significant, they were removed from the final model. For each colony used in the estimates of dispersal potential, the proportion of larvae that settled was calculated at the offspring temperature level (i.e. the number of larvae settled out of 12; colony was the unit of replication).

Relative fitness

We calculated the relative fitness of offspring from mothers kept at high or low temperatures using frameworks developed in other areas of evolutionary biology (e.g. Kawecki and Ebert, 2004; Stanton and Thiede, 2005; Orr, 2009). Our estimate of fitness was offspring metamorphic success, which is an important component of maternal fitness in sessile marine invertebrates. At each larval temperature [LT(A) or LT(B)], the metamorphic success of offspring from each mother ['absolute fitness'; $W_{\mathrm{LT(A),MT(A)}}$] was calculated relative to the mean metamorphic success of offspring from all mothers kept at both temperatures [$\overline{W}_{\mathrm{LT(A),MT(A,B)}}$] as: $W_{\mathrm{LT(A),MT(A)}}/\overline{W}_{\mathrm{LT(A),MT(A,B)}}$. This calculation eliminates mean fitness differences between larval temperatures, so that a main effect of maternal temperature indicates that mothers experiencing a particular temperature differ in mean relative fitness across all offspring temperatures. A significant interaction between maternal temperature and offspring temperature indicates that mothers from a particular temperature will be favoured differently within each offspring temperature.

RESULTS

Predictability of temperature in the field

Temperature in the field on any given day in the data series was a good predictor of the temperature for up to 15 days into the future, though the strength of autocorrelation declined rapidly by four days (Fig. 2B). Because the duration of embryogenesis in *B. neritina* is approximately 1 week (Woollacott and Zimmer, 1975) and larval durations are in the order of hours, the maternal temperature environment at our field site was a good predictor of the offspring environment during the larval stage and early post-metamorphosis. After offspring metamorphose, the temperature they experience is likely to become increasingly independent of the temperature their mothers experienced during embryogenesis, and the temperature they experienced as larvae (Fig. 2B).

Temperature manipulation experiment

Offspring size

Colonies in colder water produced larger offspring than colonies from warmer water (Fig. 3A). Colonies kept at 19°C for 1 week produced a mean offspring size that was 3076 μm^2 (95%CI=1000–5152) larger than that produced by colonies kept at 25°C ($F_{1,60}$=8.78, P=0.004), and this was consistent between the two runs (run × temperature: $F_{1,59}$=0.72, P=0.4).

The size of offspring produced by colonies in colder water was also less variable than the size of offspring produced by colonies from warmer water (Fig. 3B). The standard deviation in offspring size was 895 (95%CI=95–1694) smaller in colonies kept at 19°C compared with colonies kept at 25°C ($F_{1,61}$=5.01, P=0.029), and this was also consistent between runs ($F_{1,60}$=2.04, P=0.159).

Dispersal potential.

The effects of maternal temperature on dispersal potential differed among runs (run × maternal temperature: $F_{1,22}$=5.17, P=0.03), so each run was analyzed separately. In run 1, offspring from mothers kept at lower temperatures tended to settle sooner, though this was not significant. However, larvae in cooler water settled sooner (Table 1, Fig. 4), indicating reduced dispersal potential compared with larvae in warmer water. In run 1, there were also significant differences in dispersal potential between larvae in different tanks

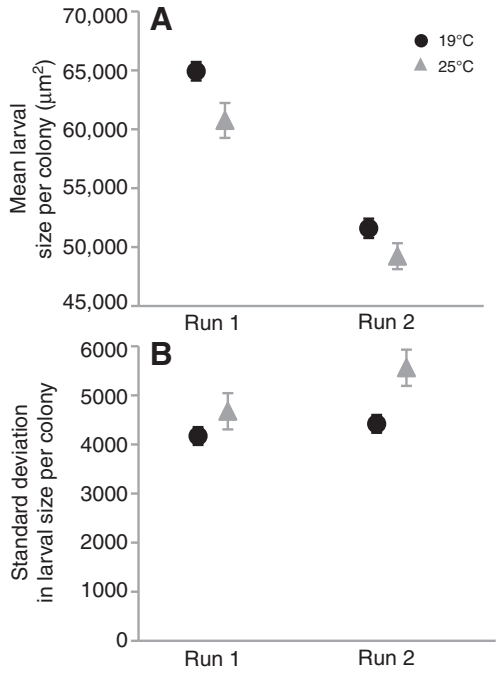

Fig. 3. (A) Mean offspring size per *B. neritina* colony and (B) the standard deviation of variation in offspring size per colony for colonies kept at either 19°C (N_{run1}=14; N_{run2}=19) or 25°C (N_{run1}=11; N_{run2}=19) for 1 week. Each run is plotted separately, though there were only additive effects of run for mean offspring size ($F_{1,60}$=138.99, P<0.001). Errors bars are ±s.e.m. calculated at the level of individual colony because there were no differences between tanks.

(nested within each maternal temperature, Table 1). In run 2, maternal temperature had a significant effect on the dispersal potential of offspring (Table 1). A higher proportion of offspring from mothers that experienced warmer water were still swimming after 2.5 h compared with offspring from mothers that had experienced cooler water (Fig. 4).

Absolute metamorphic success (absolute fitness)

The metamorphic success of offspring from mothers that had experienced warmer water was 14% (95%CI=3–24) greater than offspring from mothers that had experienced cooler water (maternal temperature effect: $F_{1,21}$=7.3, P=0.013; Fig. 5A). Larvae had greater metamorphic success (by 44%; 95%CI=34–55) in cooler water than in warmer water (offspring temperature effect: $F_{1,21}$=76.56, P<0.001; Fig. 5A). There was no interaction between maternal and offspring temperature ($F_{1,20}$=0.5, P=0.49).

Relative metamorphic success (relative fitness)

Mothers from each temperature were not favoured differently within each offspring temperature (maternal × larval temperature: $F_{1,20}$=1.22, P=0.28), but mothers from each temperature differed in mean relative fitness across all offspring temperatures (maternal temperature: $F_{1,21}$=4.54, P=0.04). At the higher offspring temperature of 25°C, there were indications that the relative metamorphic success of offspring from mothers kept at 25°C was greater than that for offspring from mothers kept at 19°C (Fig. 5B). In contrast, the relative metamorphic success of offspring from mothers kept at 19°C was similar to that for offspring from mothers kept at 25°C (Fig. 5B).

DISCUSSION

The effects of water temperature on larvae depended on the temperature that their mothers experienced. Offspring from mothers kept in warmer water were smaller and more variable in size, but had increased dispersal potential and higher metamorphic success than offspring from mothers kept in cooler water. Our results indicate that, under frequency- or density-independent selection, mothers that experienced higher temperatures compared with lower temperatures were favoured, regardless of the temperature in the offspring environment. Ecologically, however, we would predict that increases in water temperature between the maternal and offspring generation would be more detrimental to populations (in terms of the proportion of individuals that successfully metamorphose; Fig. 5A) than decreases in water temperature between generations. Under frequency- or density-dependent selection, there were indications that mothers that experienced higher temperatures were favoured only if their offspring encountered similar (warmer) temperatures, though these results were not statistically significant. Analysis of time series data on temperature in the field indicated that offspring are likely to experience the same (or similar) thermal environments as their mother, particularly during the larval and very early post-metamorphic life-history stages. In offspring environments with lower ('benign') temperatures, there were indications that frequency-

Table 1. Partially nested between-subjects ANOVA testing the effects of maternal temperature and offspring temperature on the proportion of *Bugula neritina* larvae swimming after 2.5 h

Source	d.f.	Mean square	*F*	*P*
Run 1				
Maternal temperature	1	0.047	0.783	0.469
Offspring temperature	1	0.133	44.33	**<0.001**
Maternal × Offspring temperature	1	0.002	0.033	0.872
Tank (Maternal temperature)	2	0.060	20	**<0.001**
Error	10	0.003		
Run 2				
Maternal temperature	1	0.336	42	**0.023**
Offspring temperature	1	0.00017	0.01	0.922
Maternal × Offspring temperature	1	0.000017	0.002	0.967
Tank (Maternal temperature)	2	0.008	0.471	0.638
Error	10	0.017		

Bold *P*-values indicate significant effects at the P=0.05 level.
Note: model was reduced after finding no effect of Offspring temperature × Tank (Maternal temperature).

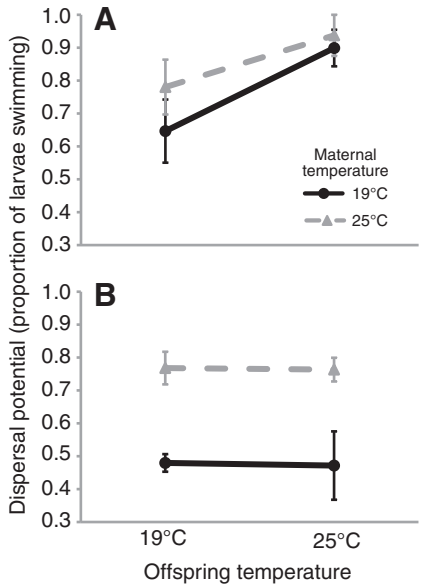

Fig. 4. The proportion of *B. neritina* larvae swimming (an estimate of dispersal potential) in water temperatures of 19 or 25°C (offspring temperature) after 2.5 h in (A) run 1 and (B) run 2 that originated from colonies kept at 19 or 25°C (maternal temperature). Lines join maternal temperature treatments and have been shifted slightly for ease of display. Error bars are ±s.e.m. calculated at the level of tank.

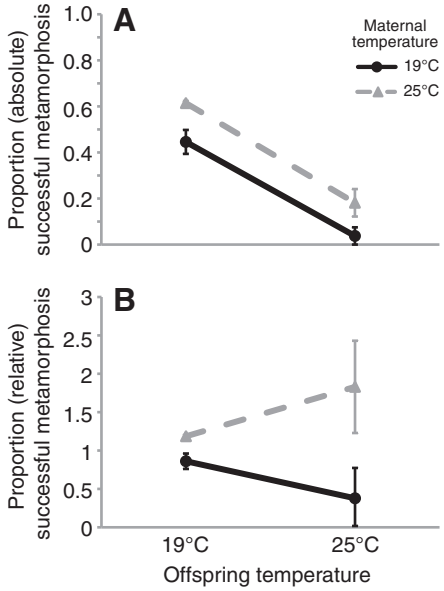

Fig. 5. (A) Absolute and (B) relative fitness (proportion of larvae that successfully metamorphosed) of *B. neritina* in water temperatures of 19 or 25°C (offspring temperature) that originated from colonies kept at 19 or 25°C (maternal temperature). Lines join offspring temperature treatments. Error bars are ±s.e.m.

or density-dependent selection would not favour mothers from either low or high temperatures and there was no evidence of any maternal effects. Because the relative importance of frequency- or density-dependent selection can vary both across space and over time (Gomulkiewicz and Kirkpatrick, 1992; Sinervo and Calsbeek, 2006), we suggest that future studies on maternal effects present both absolute and relative estimates of maternal fitness in order to better understand the adaptive significance of transgenerational plasticity (Stanton and Thiede, 2005).

Maternal effects are increasingly recognised as an important way for organisms to cope with changes in environmental temperature (Landa, 1992; Fischer et al., 2003b; Gagliano et al., 2007; Stillwell et al., 2008). More generally, phenotypic plasticity is thought to be important for population persistence in new environments *via* adaptation without genetic change (Ghalambor et al., 2007; Chevin et al., 2010; Chown et al., 2010) and may be particularly important in the context of climate change (Coles and Brown, 2003; Munday et al., 2008; Chown et al., 2010). Ocean temperature is expected to change significantly over the next few decades as a result of climate change (Coles and Brown, 2003; Harley et al., 2006; Munday et al., 2008). Maternal effects have evolved under predictable environmental variation and it remains to be tested whether maternal effects are adaptive under rapid change to novel environments (Visser, 2008; Fischer et al., 2010). Accurately predicting the impact of rising ocean temperatures will be difficult, but future studies that consider adaptive maternal effects, in addition to constraints and trade-offs that limit phenotypic responses (DeWitt et al., 1998), will be needed to make progress in this area.

Our finding that offspring size increased in colder water is consistent with a large body of literature on ectotherms showing that mothers produce larger offspring at lower temperatures (but see Blanckenhorn, 2000; Stillwell et al., 2008). The temperature-dependent shift in offspring size can be an adaptive response (Landa, 1992; Fischer et al., 2003b; Seko and Nakasuji, 2006; Bownds et al., 2010) or a physiological constraint (Blanckenhorn, 2000), though the underlying developmental mechanisms for either cause still remain unclear (Fischer et al., 2003c; Karl and Fischer, 2008). Whether the shift in offspring size that we observed is adaptive depends on whether selection on offspring size (or some correlate) is stronger at higher temperatures than at lower temperatures (Fox, 2000; Fischer et al., 2003a; Gagliano et al., 2007; Bownds et al., 2010). Regardless of the underlying causes of the offspring size–temperature relationship, offspring size often has far-reaching consequences for individuals and populations across a range of taxa [and in particular our study species (Marshall and Keough, 2003)], and we show that temperature-induced maternal effects can be a major source of variation in offspring size.

Temperature influenced the length of the larval period (an estimate of dispersal potential) of *B. neritina* offspring, but in counterintuitive ways. Larval duration within a species typically declines with increasing temperature as a result of increased metabolic and developmental rate (Brown et al., 2004), or an increase in the willingness of non-feeding larvae to settle (Thiyagarajan and Qian, 2003; David et al., 2010), thereby decreasing dispersal potential (O'Connor et al., 2007). In contrast to previous studies, we found that larvae in warmer water tended to have a greater dispersal potential (fewer larvae had settled within 2.5 h). Furthermore, mothers kept at higher temperatures produced smaller larvae (with presumably lower energetic reserves), and smaller, non-feeding larvae generally have reduced dispersal potential compared with larger larvae (Marshall and Keough, 2003). So we would expect that, even if temperature had little direct influence on larval settlement times, smaller offspring produced by mothers at higher temperatures would have reduced dispersal potential than offspring from mothers kept at lower temperatures; again this is contrary to our results.

The increased dispersal potential in warmer water could be a way for mothers to increase the probability that their offspring disperse out of unfavourable environments. Larvae had higher metamorphic success in cooler water, and creating more dispersive offspring (perhaps through changes in the composition of maternal investment) may be another way to offset the costs of offspring settling in warmer environments. Previous studies have shown that when local conditions degrade, mothers can produce more dispersive offspring that are more likely to colonise better habitats (Roff, 1994; Krug and Zimmer, 2004; Allen et al., 2008; Marshall, 2008). In aquatic environments, water temperature is likely to change more quickly with depth than over the same distance horizontally, and dispersive larvae could access habitats in deeper, cooler water if the spatial scale at which temperature changes with depth is within the spatial scale of dispersal. Of course there are other factors (e.g. light, food, pressure and predators) associated with depth that may also influence the success of larvae and our speculation requires furthers testing. Although the explanation for our counterintuitive results remains unclear, the consequences of temperature on the dispersal potential of *B. neritina* are complex – the dispersal potential of *B. neritina* was greater in warmer water (whether experienced in the maternal or larval environment) and the temperature that mothers experience can mediate the dispersal potential in *B. neritina* independently of the temperature that their offspring experience.

Our inferences about environmental predictability between maternal and offspring environments assume that the nature of the temperature autocorrelation is representative of other seasons and years (i.e. is independent of the mean temperature) and that autocorrelation reflects the ability of mothers to respond to thermal cues. At our field site, there is no upwelling or other obvious sources of fluctuations in water temperature that might influence thermal predictability over the time scales relevant to our study species. Therefore, estimates of autocorrelation from November to March are likely to apply to the time of year that *B. neritina* are common at our field site (November to July). At other sites, however, upwelling events can cause temperature to fluctuate at different frequencies at different times of the year. On the coasts of California and Nova Scotia, for example, water temperatures fluctuate significantly more during some months of the year than others (Saunders and Metaxas, 2007; Garcia-Reyes and Largier, 2010). At these sites, we would expect the strength of autocorrelation in temperature to be dependent on the time of year and, depending on the ability of individuals to respond to environmental cues, this would influence the adaptive significance of any maternal effects. Analyses of environmental predictability should therefore be conducted in the season, and at the time scale, relative to the reproductive schedule of the focal species. Furthermore, although we found a statistically significant autocorrelation of up to 15 days at our field site, it still remains unclear whether the strength of autocorrelation up to this point is also biologically significant.

In conclusion, we estimated the intergenerational correlation between maternal and offspring environment and found that it was a good predictor of the early offspring environment. We recommend the use of our approach for those interested in testing whether maternal environmental cues are reliable predictors of the offspring environment. Furthermore, we estimated the absolute and relative fitness benefits of maternally induced changes in offspring phenotype and found evidence that the benefits of transgenerational plasticity in our species depend on the relative importance of frequency- or density-dependent selection on maternal effects in the field. We found that temperature-induced maternal effects influence a range of offspring traits: warmer water was associated with smaller, more variable offspring sizes, yet greater dispersal potential. Clearly, the presence of complex maternal effects will exacerbate the challenge of making accurate predictions about the ecological and evolutionary impacts of environmental change, but the challenge should nonetheless be considered.

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