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Trans-generational plasticity in physiological thermal tolerance is modulated by maternal pre-reproductive environment in the polychaete *Ophryotrocha labronica*

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ABSTRACT

Maternal temperature is known to affect many aspects of offspring phenotype, but its effect on offspring physiological thermal tolerance has received less attention, despite the importance of physiological traits in defining organismal ability to cope with temperature changes. To fill this gap, we used the marine polychaete *Ophryotrocha labronica* to investigate the influence of maternal temperature on offspring upper and lower thermal tolerance limits, and assess whether maternal influence changed according to the stage of offspring pre-zygotic development at which a thermal cue was provided. Measurements were taken on adult offspring acclimated to 18 or 30°C, produced by mothers previously reared at 24°C and then exposed to 18 or 30°C at an early and late stage of oogenesis. When the shift from 24°C was provided early during oogenesis, mothers produced offspring with greater cold and heat tolerance whenever mother–offspring temperatures did not match, with respect to when they matched, suggesting the presence of an anticipatory maternal effect triggered by the thermal variation. Conversely, when the cue was provided later during oogenesis, more tolerant offspring were observed when temperatures persisted across generations. In this case, maternal exposure to 18 or 30°C may have benefited offspring performance, while limitations in the transmission of the thermal cue may account for the lack of correlation between maternal experiences and offspring performance when mother–offspring environments did not match. Our results provided evidence for a trans-generational effect of temperature on physiological performance characterised by a high context dependency, and are discussed in the light of maternal pre-reproductive experiences.

KEY WORDS: Ectotherms, Maternal effects, Oogenesis, Polychaetes, Thermal tolerance limits

INTRODUCTION

In most natural environments, abiotic conditions show multi-dimensional variation, changing temporally and/or spatially over short or long time scales or distances (Levins, 1968). Species have evolved different strategies to cope with environmental heterogeneity, including the production of variable phenotypes across multiple environments (e.g. Bradshaw, 1965; DeWitt and Langerhans, 2004; Gotthard and Nylin, 1995; Meyers and Bull, 2002; Pigliucci, 2001; Stearns, 1989).

When changes occur on an adequate regular scale, organisms can rely on one or more correlations between environmental cues and

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windows of optimal performance, and are able to adjust their phenotype, or behaviour, to suit the prevailing conditions (McNamara et al., 2011; Uller et al., 2013; Visser et al., 2010). This ability, known as phenotypic plasticity, is a key strategy to optimise individual fitness in fluctuating environments: not only does it allow a genotype to have a broader tolerance across multiple environments both within (e.g. Bonduriansky et al., 2012; Gianoli and Valladares, 2012; Kingsolver and Huey, 1998; West-Eberhard, 2003) and across generations (e.g. Lacey, 1998; Meylan et al., 2012) but also it may be shaped by selection leading to adaptive responses when novel environments are encountered (Agrawal, 2001; Draghi and Whitlock, 2012; Ghalambor et al., 2007; Price et al., 2003; Via and Lande, 1985).

Environmentally induced maternal effects are particular forms of phenotypic plasticity by which offspring responses to abiotic and biotic changes are mediated by the environment experienced by their mother (Lacey, 1998; Mousseau and Fox, 1998a; Uller, 2008). Maternal experiences may be translated into phenotypic variations in the progeny and may affect many aspects of offspring phenotype as much as or more than the offspring's own genotype or its direct interaction with the environment (Mousseau and Fox, 1998b). Given the importance of trans-generational connections in affecting offspring fitness under changing environmental conditions (Badyaev, 2009; Badyaev and Uller, 2009; Marshall and Uller, 2007; Solemdal, 1997), maternal effects carry potentially powerful evolutionary implications, as they may ultimately affect the rate and direction of evolutionary responses to selection (e.g. Kirkpatrick and Lande, 1989; Wade, 1998), and influence dispersal and, consequently, the dynamics of range expansion and population dynamics (Benton et al., 2001; Donohue, 1999; Duckworth, 2009; Ginzburg, 1998; Plaistow and Benton, 2009).

Maternal thermal habitat, in particular, has been shown to contribute to multiple offspring phenotypic responses, such as diapause in insects or dormancy in plants (e.g. Huestis and Marshall, 2006; Mousseau and Dingle, 1991a; Mousseau and Dingle, 1991b; Mousseau and Fox, 1998b), offspring size and growth (e.g. Bacigalupe et al., 2007; Bownds et al., 2010; Chambers and Leggett, 1996; Fischer et al., 2003a; Fischer et al., 2003b; Fox et al., 1999; Kaplan and Phillips, 2006; Salinas and Munch, 2012), dispersal ability (e.g. Burgess and Marshall, 2011; Marshall, 2008) and developmental plasticity (e.g. Janhunen et al., 2010; Kurdíková et al., 2011; Magiafoglou and Hoffmann, 2003). Ectothermic species have been a recurrent target for these studies as several aspects of their physiology are directly dependent on environmental temperature, and, consequently, are particularly challenged by environmental thermal variations (Angilletta et al., 2004; Huey and Berrigan, 2001; Huey and Stevenson, 1979).

Notwithstanding the breadth of empirical support for maternal effects on a wide range of traits, a comparatively smaller number of

studies have explored the interplay between maternal thermal habitat and offspring physiological performance (e.g. Bacigalupe et al., 2007; Donelson et al., 2012; Jenkins and Hoffmann, 1994). This is quite surprising given the importance of physiological thermal tolerance in determining species' ability to cope with temperature changes (Bozinovic et al., 2011; Deutsch et al., 2008). Thermal tolerance limits, in particular, are useful proxies for measuring the ability of an individual to perform its physiological functions under different temperature conditions, and link individual thermal physiology and sensitivity to environmental changes with species ecology (Calosi et al., 2010; Peck et al., 2009; Ribeiro et al., 2012; Sunday et al., 2012).

With this study, we investigated how variation in maternal thermal habitat contributes to offspring physiological thermal tolerance, measured as lower and upper thermal tolerance limits, in the marine worm *Ophryotrocha labronica* (La Greca and Bacci, 1962) (Polychaeta, Dorvilleidae). Our aim was to gain further insight into the strategies evolved by species to cope with the thermal heterogeneity of the environment, as maternal effects constitute an important source of phenotypic variation that may favour populations facing changing environments, and drive adaptation to novel environmental challenges over short time scales (Räsänen and Kruuk, 2007; Rossiter, 1991; Rossiter, 1996). In addition, we assessed whether maternal pre-reproductive experiences may influence offspring responses differently according to the stages of offspring pre-zygotic development at which an external cue was experienced. The transmission of environmental information between maternal and offspring cells at the molecular level should in fact display a gradient of efficacy that depends on a window of maternal sensitivity to environmental cues (Mousseau and Dingle, 1991a). Thus, we expected maternal effects to progress in a way that changes according to the stage of oocyte development at which an environmental stimulus is provided to the mother.

To accomplish these tasks, we applied a factorial experimental design where both maternal and offspring environments were manipulated. In particular, we measured lower and upper thermal tolerance limits in adult offspring acclimated to 18 or 30°C (offspring acclimation temperature, T_O), produced by mothers previously reared for generations at 24°C and then exposed to 18 or 30°C (maternal temperature, T_M) at an early (early exposure treatment) and late (late exposure treatment) stage of oocyte development. For each mother–offspring temperature combination (called T_M–T_O: 18–18°C, 18–30°C, 30–30°C, 30–18°C), we determined chill coma temperatures as a proxy for cold tolerance, and loss of control over activities, onset of spasms and lethal temperature as indicators of tolerance to heat.

RESULTS

Lower thermal tolerance limits: chill coma

The interaction between maternal temperature and offspring acclimation temperature was found to be significant and dependent on the exposure treatment provided ($T_M \times T_O \times$exposure: $F_{1,129}$=137.14; P<0.001) (Fig. 1, Table 1A).

Within each offspring acclimation temperature (18 or 30°C) of the late exposure treatment, cold tolerance measured as chill coma was reached later when offspring and maternal temperatures matched (T_M–T_O: 18–18°C and 30–30°C; chill coma observed at −1.84±0.74 and 2.01±0.46°C, respectively), compared with when they did not match (T_M–T_O: 30–18°C and 18–30°C; chill coma measured at −0.78±0.47 and 3.19±0.54°C, respectively) (Fig. 1A). In contrast, within each offspring temperature of the early exposure treatment,
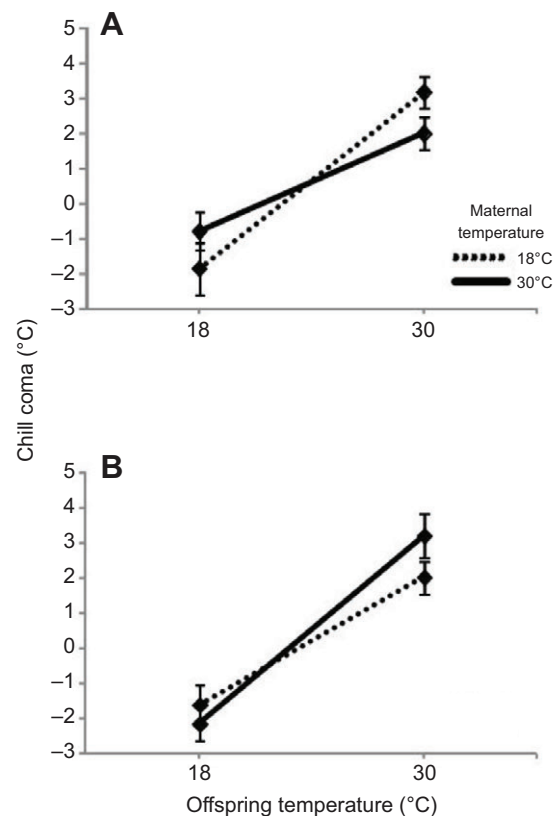
Fig. 1. Effects of *Ophryotrocha labronica* maternal temperature and offspring acclimation temperature on chill coma of offspring. Data are means ± s.d. from the late (A) and early (B) exposure treatment.

a significant decrease in chill coma temperature was observed when maternal and offspring temperatures did not match (−2.15±0.48 and 2.02±0.50°C for the 30–18°C and 18–30°C T_M–T_O combination, respectively), with respect to the situation in which mothers had been exposed to the same temperature as their offspring (T_M–T_O: 18–18°C or 30–30°C, chill coma measured at −1.60±0.57 and 2.15±0.65°C, respectively) (Fig. 1B).

Pair-wise comparisons within each exposure treatment, performed between the mean chill coma values of each offspring temperature, indicated that 18°C-acclimated offspring had significantly lower chill coma values than 30°C-acclimated offspring, in both the late and early exposure treatment (maximum W_{80}=2420; P<0.002) (Fig. 1A,B).

Preliminary analyses revealed significant differences between male and female responses in two mother–offspring temperature combinations of the late exposure treatment (T_M–T_O: 18–18°C and 30–18°C) and in one combination of the early exposure treatment (T_M–T_O: 18–18°C). In all these cases, females appeared to be more tolerant to low temperatures than males (maximum U_{18}=15.50; P<0.03) (see supplementary material Table S1). As these differences were not prevalent among the experimental combinations and did not affect the results, analyses were performed pooling male and female datasets within each T_M–T_O combination. Supplementary material Table S2 shows the results of pair-wise comparisons performed between offspring responses at 18 and 30°C within each exposure treatment. Supplementary material Table S3 reports the mean values for each lower and upper thermal tolerance limit measured separately for male and female offspring.

Table 1. ANOVA testing for the effects of maternal temperature (T_M), offspring acclimation temperature (T_O) and exposure treatment on lower and upper thermal limits of *Ophryotrocha labronica* offspring

Source	A Chill coma				B Loss of control				C Onset of spasms				D Lethal temperature			
	d.f.	MS	F	P	d.f.	MS	F	P	d.f.	MS	F	P	d.f.	MS	F	P
Within groups																
Late exposure treatment																
Body size					1	0.27	0.30	0.59	1	1.34	2.71	0.11	1	0.84	1.53	0.22
T_M					1	0.69	0.75	0.39	1	1.24	2.51	0.12	1	3.15	5.74	0.02
T_O					1	368.79	400.65	<0.001	1	9.11	18.46	<0.001	1	5.19	9.47	0.003
$T_M \times T_O$					1	1.82	1.97	0.17	1	0.68	1.38	0.25	1	1.38	2.52	0.12
Error					58	0.92			50	0.49			58	0.55		
Early exposure treatment																
Body size									1	0.001	0.001	0.98	1	0.01	0.02	0.90
T_M									1	16.27	16.26	<0.001	1	0.19	0.26	0.61
T_O									1	90.74	90.70	<0.001	1	1.23	1.68	0.20
$T_M \times T_O$									1	3.04	3.04	0.09	1	1.58	2.16	0.15
Error									75	1.00			75	0.73		
Among groups																
Body size	1	7.66	28.82	<0.001	1	0.33	0.46	0.50	1	0.54	0.68	0.41	1	0.43	0.67	0.42
T_M	1	0.18	0.67	0.41	1	14.99	20.70	<0.001	1	0.12	0.15	0.70	1	5.70	8.78	0.004
T_O	1	531.15	1999.02	<0.001	1	3.35	4.63	0.03	1	11.71	14.68	<0.001	1	1.11	1.71	0.19
Exposure	1	3.75	14.12	<0.001	1	785.12	1084.04	<0.001	1	72.19	90.48	<0.001	1	1.35	2.09	0.15
$T_M \times$exposure	1	0.59	2.21	0.14	1	0.40	0.55	0.46	1	3.66	4.58	0.03	1	2.33	3.59	0.06
$T_O \times$exposure	1	5.46	20.55	<0.001	1	3.92	5.42	0.021	1	11.26	14.11	<0.001	1	6.74	10.39	0.002
$T_M \times T_O$	1	0.97	3.65	0.06	1	19.58	27.03	<0.001	1	3.25	4.07	0.05	1	2.80	4.31	0.04
$T_M \times T_O \times$exposure	1	36.44	137.14	<0.001	1	5.55	7.66	0.006	1	0.17	0.22	0.64	1	0.003	0.004	0.95
Error	129	0.27			134	0.72			126	0.80			134	0.65		

(A) Chill coma; (B) loss of control over activities; (C) onset of spasms; and (D) lethal temperature. When the main interaction ($T_M \times T_O \times$exposure) was not significant, the interaction between maternal temperature and offspring acclimation temperature ($T_M \times T_O$) was considered within each exposure treatment. Within-group ANOVA was also performed for loss of control over activities to test for the absence of any maternal effect in the late exposure treatment. Body size was used as covariate. For each thermal limit, the source, degrees of freedom, mean squares (MS), F-ratio and P-values are reported.

Upper thermal tolerance limits: loss of control over activities, onset of spasms and lethal temperature

Maternal and offspring acclimation temperature, together with the exposure treatment, were major determinants of offspring heat tolerance when measured as loss of control over activities in the early exposure treatment ($T_M \times T_O \times$early exposure: $F_{1,134}$=7.66; P=0.006) (Table 1B). Here, in both offspring acclimation temperatures, the temperature at which a loss of control over activities was observed was higher when thermal conditions did not persist across generations (T_M–T_O: 18–30°C and 30–18°C, loss of control measured at 37.50±0.46 and 32.10±0.79°C, respectively), compared with when maternal and offspring temperatures matched (T_M–T_O: 30–30°C and 18–18°C; loss of control observed at 36.94±1.58 and 31.93±0.81°C, respectively) (Fig. 2B).

Conversely, when heat tolerance was measured as loss of control over activities in the late exposure treatment (Fig. 2A), and as onset of spasms (Fig. 2C,D) and lethal temperature (Fig. 2E,F) for both treatments, the interaction between the three main factors lost its significance (maximum $T_M \times T_O \times$exposure: $F_{1,126}$=1.97; P=0.17) (Table 1B–D). In the above-mentioned cases, no maternal effects on offspring heat tolerance were found when analyses were performed within each exposure treatment (maximum $T_M \times T_O$: $F_{1,75}$=3.04; P=0.09) (Table 1B–D).

Within each exposure treatment, the average heat tolerance of 18°C-acclimated offspring was lower than that observed for offspring acclimated to 30°C (maximum W_{80}=2420; P<0.001). The dissimilarity of responses between 18°C- and 30°C-acclimated offspring gradually decreased as the upper thermal tolerance limits were approached, being, for the late and early exposure treatments, 5.21 and 4.50°C, respectively, for loss of control over activities (Fig. 2C,D), and 0.97 and 2.13°C, respectively, for onset of spasms (Fig. 2E,F). Offspring acclimated to 18°C died somewhat earlier than 30°C-acclimated individuals in the late exposure treatment, while lethal temperatures were not significantly different in the early exposure treatment (t_{78}=−1.30; P=0.20).
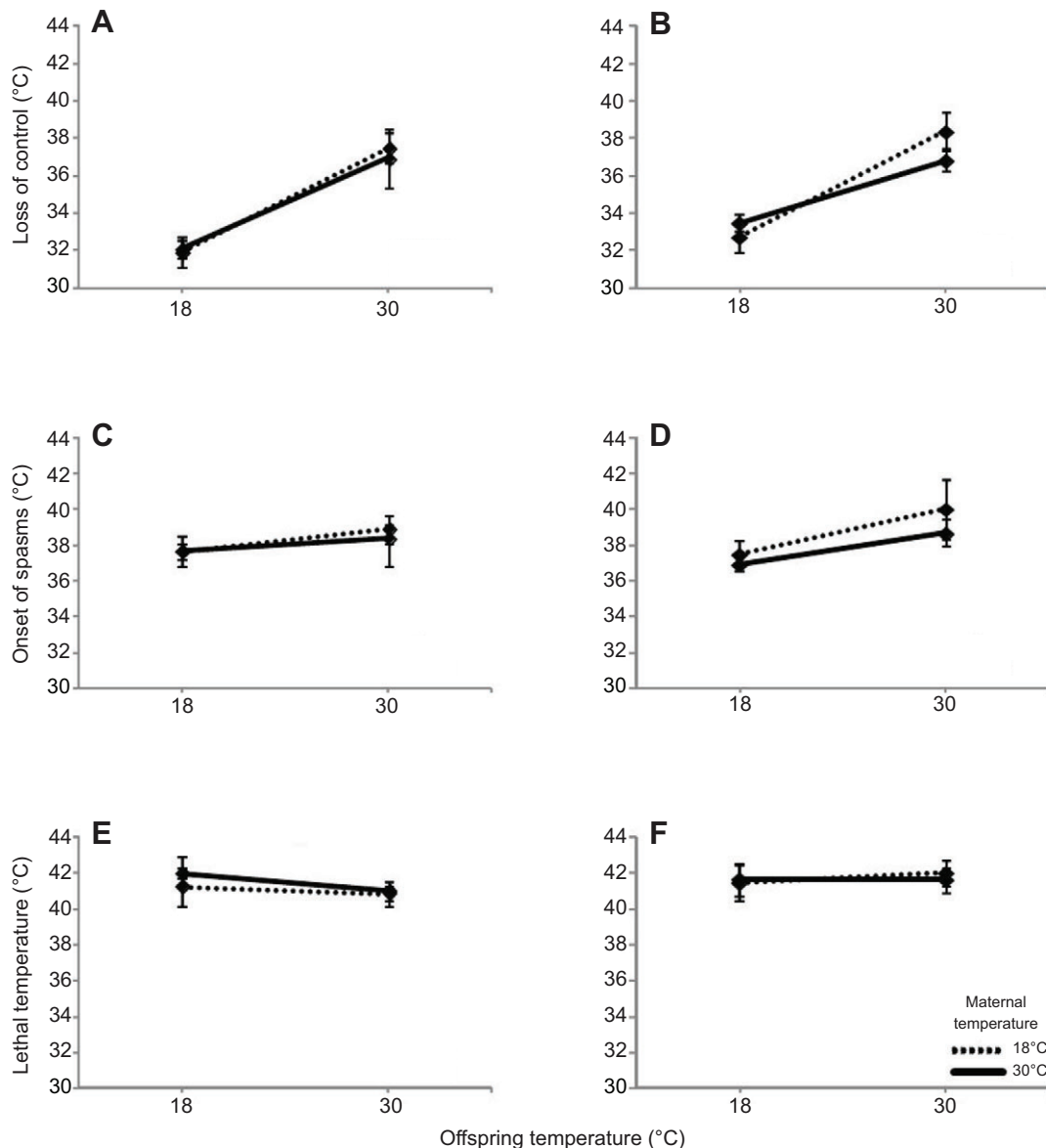

Fig. 2. Effects of *O. labronica* maternal temperature and offspring acclimation temperature on upper thermal limits of offspring. Data are means ± s.d. from the late (A,C,E) and early (B,D,F) exposure treatment. (A,B) Loss of control over activities; (C,D) onset of spasms; (E,F) lethal temperature.

DISCUSSION

The present study shows that maternal thermal habitat influences offspring responses to short-term decreases and increases in water temperature, and that this effect is modulated by maternal pre-reproductive environment. In the early exposure treatment (i.e. when mothers experience a temperature change early during oogenesis), offspring more tolerant to cold and heat are produced whenever maternal and offspring thermal conditions do not match, compared with when they match (T_M–T_O: 18–18°C<18–30°C and 30–30°C<30–18°C). In contrast, in the late exposure treatment (i.e. when mothers experience a temperature change during the late stages of oocyte development), offspring performance increases when temperature persists across generations, while descendant ability to endure acute thermal stresses is reduced whenever a trans-generational difference in temperature conditions takes place (T_M–T_O: 18–18°C>18–30°C and 30–30°C>30–18°C).

Our results demonstrate that variations in environmental temperature are transmitted to the next generation through a modification of offspring physiological responses to thermal changes, providing evidence for a trans-generational effect of temperature on physiological thermal tolerance to heat and cold. Thermal tolerance limits represent indirect measures of fitness, but are essential in setting the thermal performance curve of organismal functions more strictly related to individual fitness, such as survival, growth and reproduction (Pörtner et al., 2006). Organisms, in fact, maximise their fitness within an 'optimal' environmental range, with upper and lower critical values, beyond which performance quickly declines to zero (Denny and Dowd, 2012; Huey and Kingsolver, 1989; Spicer and Gaston, 1999). Demonstrating that physiological thermal tolerance comprises a non-genetically heritable component is thus important for understanding how organisms respond to variations in temperature conditions, and predicting the capacity of species to keep pace with a rapidly changing environment.

Furthermore, our findings show that the pathway by which maternal effects span the generations is modulated by the temperature experienced by mothers before reproduction, generating two different scenarios. In fact, the role of oocyte developmental stage in determining the observed patterns can only be supposed, owing to differences in the duration of maternal exposure to the experimental temperatures provided in the two exposure treatments. Mothers were actually kept at 18 or 30°C for a longer time in the early exposure than in the late exposure treatment (20 days versus 13 days at 18°C; 5 days versus 3 days at 30°C), which introduces a confounding factor for the interpretation of the results. The role of the duration of maternal exposure at the two exposures is discussed below.

In the first scenario, mothers go on to produce more tolerant offspring when temperatures change across generations, suggesting the presence of an adaptive response triggered by the variation in maternal culturing temperature (from 24°C to 18 or 30°C). When abiotic or biotic conditions change, for example along with seasonal fluctuations, maternal effects are known to exert an important influence on offspring phenotype (Bernardo, 1996; Bondurianski et al., 2012; Marshall and Uller, 2007; Wade, 1998). In particular, if an external stimulus constitutes a predictive cue of the impending change or degradation of offspring conditions ['adaptive matching' between maternal and offspring environments (Uller et al., 2013)], mothers may be able to buffer the likely negative impact of environmental variation on offspring performance by contributing to the interaction between offspring environment and phenotype. In most studies, the evolution of adaptive trans-generational plasticity

has been documented when similar environmental conditions persist across generations, as scenarios where offspring were more likely to encounter the same environment as their mothers were usually considered (for example, early stages of offspring development) (Galloway and Etterson, 2007; Monaghan, 2008; Mousseau and Fox, 1998b; Sultan et al., 2009; Uller et al., 2013). However, in our study, we measured offspring responses in adult individuals, which can take up to 1 month to reach adulthood from the spawning of the eggs (Massamba-N'Siala et al., 2011). Given the marked temporal heterogeneity of thermal conditions characterising temperate latitudes, *O. labronica* individuals are likely to encounter different temperature conditions from those of their parents, especially during the seasons of transition (during autumn, seawater temperatures in La Spezia harbour can drop from a mean daily temperature of 20°C to 13°C in 1 month).

Our finding that the environment experienced by parents retains an influence late into offspring ontogeny goes against the general expectations, which see the strength of the effect of non-Mendelian information transmitted by mothers being greater during the embryonic or first stages of post-embryonic development (Hunt and Simmons, 2002; Mousseau and Dingle, 1991a; Mousseau and Fox, 1998b). The persistence of maternal effects throughout a sufficient amount of time during which environmental temperatures may vary widely, supports the gaining of fitness benefits via maternal effects when different environments across generations are involved. Evidence for an 'anticipatory' role of maternal effect on offspring phenotype has been found in temporally and/or spatially variable environments where maternal environment is a good predictor of offspring environment (e.g. Agrawal, 2001; Agrawal, 2002; Fox et al., 1997; Fox et al., 1999; Galloway and Etterson, 2007; Gustafsson et al., 2005), despite the fact that the occurrence of this form of adaptive trans-generational plasticity may be rare or difficult to recognise in natural systems (see Uller et al., 2013).

The role of the duration of maternal exposure in defining the patterns observed in the first scenario appears marginal. We would expect that longer maternal exposure to 18 or 30°C would enhance offspring performance when maternal–offspring conditions match rather than when they do not match. The maintenance of lower or higher temperatures for a greater amount of time, in fact, should be predictive of the preservation of those conditions in the next generation. In some insect species, for example, only a sufficiently high number of days of exposure to low temperatures leads to the production (or modulates the production) of overwintering offspring, while shorter exposures do not induce (or modulate) any diapause response (Fox and Mousseau, 1998; Mousseau and Dingle, 1991b; Tauber et al., 1986).

In the second scenario, offspring at a higher advantage are produced when thermal conditions persist across generations. We hypothesise that both the thermal change (with respect to culturing conditions) and the different duration of exposure to 18 and 30°C experienced by mothers triggered a maternally induced response in the offspring. The epigenetic mechanisms underpinning the transmission of these two environmental signals could have displayed different pathways, whose efficacy is influenced by the stage of oocyte maturation at which the cues are provided. On the one hand, when the cue of temperature variation is provided in the last stages of oogenesis, limitations in information transfer may be responsible for the lack of correlation between maternal experiences and offspring performance when mother–offspring environments do not match. The ability of mothers to condition the phenotype of their offspring, in fact, depends on a window of maternal sensitivity to environmental signals within which the production and transfer of

maternally derived factors through the oocytes (or egg) is possible (Mousseau and Dingle, 1991a). On the other hand, offspring may be able to benefit from maternal influence because of the effect of maternal exposure to 18 or 30°C. Or, alternatively, the production of offspring with a wider thermal tolerance window when mother–offspring temperature conditions match could be the result of the simple passing of the maternal experiences through the generations (Marshall and Uller, 2007).

Maternal experiences are not the only determinants of offspring responses: 18°C- and 30°C-acclimated offspring exhibit higher tolerance to cold and heat, respectively, independent of the maternal treatment, showing evidence for a beneficial effect of offspring acclimation temperature (Massamba-N'Siala et al., 2012). Hence, current (offspring) and past (maternal) environments interact to define offspring phenotype and its plasticity, influencing the individual's ability to cope with environmental changes. This interaction, however, ceases to have an effect when temperatures approach the upper sub-lethal and lethal limits. This trend confirms the fact that onset of spasms and lethal temperature are less plastic traits with respect to the other thermal tolerance limits measured in our study (see also Alford et al., 2012; Massamba-N'Siala et al., 2012; Terblanche et al., 2006). Accordingly, in *O. labronica*, the potential for physiological adjustments in response to increasing temperatures via maternal effects reduces towards the upper edge of the individual's thermal tolerance window, posing limits to the evolution of trans-generational plasticity of physiological performance.

Our findings support the high context dependency of maternal effects, whose relative strength and direction depend on multiple factors, such as the nature of the environmental signals, their timing and intensity, and are the result of a balance between the costs and benefits connected with the production of more resistant phenotypes (Badyaev and Uller, 2009; Marshall and Uller, 2007; Marshall, 2008; Plaistow and Benton, 2009). This is particularly true for environments characterised by high local heterogeneity and seasonal regimes, where species able to reproduce many times during their life, such as *O. labronica*, may encounter different thermal conditions along their reproductive window. The correlation between biological responses and environmental context across two consecutive generations, and the resulting maintenance or re-establishment of the best organism–environment interplay, bear important evolutionary implications for understanding the ecological role of trait variation. Cross-generational relationships and their effects on offspring phenotypic variations, in fact, may accelerate adaptive processes, produce lags in the evolutionary response of a trait under selection, or even cause evolutionary outcomes opposite to those favoured by natural selection (Badyaev and Uller, 2009; Bernardo, 1996; Lande and Kirkpatrick, 1990).

To comprehensively assess the adaptive (or maladaptive) nature of the trans-generational responses observed in our study, further investigations are needed. Maternal advantages (or disadvantages) in affecting offspring phenotype, for example, should also be considered (Marshall and Uller, 2007), and the level of prediction between maternal and offspring environments should be measured (Burgess and Marshall, 2011; Raubenheimer et al., 2012; Uller et al., 2013).

Since the time when maternal effects were mainly treated as a source of environmental noise to be controlled or eliminated, a growing amount of studies has supported their ubiquity in nature and importance for life in heterogeneous environments (Bernardo, 1996; Mousseau and Fox, 1998b; Rossiter, 1996), recognising their central role in determining the ability of populations and species to face and surmount the challenges raised by climate change (Bonduriansky et al., 2012; Parker et al., 2012; Vehmaa et al., 2012).

The increase in the frequency and intensity of extreme temperature events expected with climate change, for example, may disrupt the link between the thermal cues predictive of the forthcoming alteration of environmental conditions, and offspring environment. Under such a scenario, the chance to adjust offspring phenotype to suit prevailing conditions via adaptive maternal effects could decrease (Schaper et al., 2012). At the same time, maternally induced responses, thanks to their context dependency, may be among the solutions to these environmental challenges (Donelson et al., 2012; Salinas and Munch, 2012; Vehmaa et al., 2012).

MATERIALS AND METHODS
Study species
Ophryotrocha labronica is a globally distributed marine benthic polychaete occurring in a variety of temporally and spatially fluctuating coastal habitats such as harbours and lagoons (Massamba-N'Siala et al., 2011; Prevedelli and Simonini, 2003; Simonini et al., 2009; Simonini et al., 2010; Thornhill et al., 2009). *Ophryotrocha labronica* is a gonochoric iteroparous species with semi-continuous reproduction and direct development: females reproduce many times over an extended breeding period, laying their eggs in tubular masses at each spawning event (Paxton and Åkesson, 2007). Eggs are externally fertilised by males and parental care is provided until they hatch (Paxton and Åkesson, 2007).

Animal maintenance and experimental methods
The animals used in this study originated from a population of *O. labronica* collected in 2010 in the harbour of La Spezia (Italy: 44°06′29″N; 9°49′44″E). Field-collected animals were transferred into a temperature-controlled room set at the temperature measured in the field (14°C). After 1 day, we gradually acclimated the individuals to 24°C by increasing the temperature at a rate of $1°C\,h^{-1}$ (Massamba-N'Siala et al., 2012). This temperature was higher than that measured in the field, but within the thermal range (18–28°C) experienced by this species during the period of highest density (June to October), when faster reproduction and growth occur compared with the colder months of the year (Massamba-N'Siala et al., 2012; Prevedelli et al., 2005). The animals were divided into reproductive pairs formed by a sexually mature male and female, with each pair isolated in a 20 ml glass bowl and fed *ad libitum* with chopped spinach. Forty pairs were then formed with individuals of the F_1 generation by crossing sexually mature males and females belonging to different broods in order to avoid inbreeding effects. The same procedure was followed for seven generations to reduce the effect of field temperature on individual phenotypic responses.

To test for trans-generational plasticity of thermal tolerance, and assess whether maternal thermal habitat affects offspring responses differently depending on the stage of oocyte maturation at which a temperature cue is provided, we applied a factorial experimental design where both maternal and offspring environments were manipulated, specifically changing maternal temperature at a late and an early stage of oocyte development, as explained below.

First, we paired sexually mature males and females from the F_7 generation (the parental generation) and isolated each pair in a 20 ml glass bowl (a total of 160 pairs). Females were easily distinguished from males by the presence of mature oocytes, which were easily visible through the body wall, i.e. when oogenesis was in its last stages (Paxton and Åkesson, 2007). At this stage of oocyte development (late exposure treatment), 80 reproductive pairs were randomly and uniformly assigned to one of two maternal temperature treatments (T_M): 18 and 30°C. As soon as females reproduced for the first time, their egg masses were divided into two equal groups, one assigned to 18°C and the other to 30°C (offspring acclimation temperature, T_O), and maintained at that temperature until the hatchlings reached adulthood. Because, in *O. labronica*, parental care is required for hatching of the eggs, the entire glass bowl containing both the parents and the egg mass was exposed to the T_O, and the parents were removed after hatching.

To assess whether offspring responded differently when changes in maternal temperature took place at an early stage of oocyte maturation, the

remaining 80 pairs of the parental generation was exposed to the T_M after the females had laid their first egg mass (which was discharged), specifically before mature oocytes were again visible in the coelomatic cavity. This group of females experienced the T_M during the whole duration of oogenesis (early exposure treatment), and the second egg masses produced were then exposed to the T_O following the procedure described above.

For all treatments, temperature was increased at a rate of 1°C h^{-1}, and photoperiod (12 h:12 h light:dark) and salinity (35‰) were kept constant throughout the experiment. Individuals were fed *ad libitum* with chopped spinach.

The use of the first and second broods for the late and early exposure treatments, respectively, could confound the attribution of effects related to the stage of oocyte development. Thus, in supplementary material Table S4, we have provided data from a previous experiment (G.M.-N'S., unpublished) demonstrating the absence of differences in thermal tolerance performance between first and second broods in laboratory individuals of *O. labronica* (strain originally collected in Porto Palo di Capo Passero, Italy, 36°41′1″N; 15°08′1″E).

Thermal tolerance analysis

For each exposure treatment, thermal tolerance limits of 20 adult individuals (10 females and 10 males) were measured for each mother–offspring temperature combination (T_M–T_O) using dynamic thermal limit analysis (Lutterschmidt and Hutchison, 1997a; Lutterschmidt and Hutchison, 1997b). Chill coma, defined as a reversible state where motionless individuals did not respond to prodding, was used as a measure of tolerance to cold. For heat tolerance, the following end points were observed: loss of control over activities, responsible for a reversible arrythmicity in locomotor activities [corresponding to the ∪-shaped end point described previously (Massamba-N'Siala et al., 2012)]; onset of spasms, where the individual displayed a spasmodic contraction of the entire body; and lethal temperature, which was defined as the temperature at which no recovery was observed after cooling (Massamba-N'Siala et al., 2012). These end points were used as proxies for the gradual physiological impairment, reversible or not, caused by the exposure to sub-optimal or lethal environmental temperatures.

Each trial was carried out observing a maximum of five individuals in a glass bowl (diameter 3 cm, depth 2 cm) placed in a computer-controlled re-circulating ethylene glycol bath (I462-7028, temperature range: −40 to +200°C, 13 l, Prog. 1197P, VWR, Radnor, PA, USA), heated and cooled via a ramping program set at 1°C min^{-1}. Experiments started at the temperature to which individuals of a given treatment had been acclimated. The temperature within the glass bowl was measured using a digital thermometer (Testo 922, T/C Type K Radio, Milan, Italy) equipped with a precision fine wire thermocouple (T/C type K, Testo). Prior to starting any trial, we assessed the size of each individual by counting the number of chaetigers, i.e. the segments bearing bristles (Massamba-N'Siala et al., 2012). The number of offspring (males and females) actually measured per mother for each treatment combination ranged from 10 to 20 individuals.

Statistical analysis

We performed a 3-way covariance test (ANCOVA) to assess how offspring thermal tolerance was affected by maternal temperature (T_M; fixed, two levels: 18 and 30°C), offspring acclimation temperature (T_O; fixed, two levels: 18 and 30°C), and the oocyte developmental stage at which variation from maternal culturing temperature was provided (exposure) (fixed, two levels: late and early exposure treatment). Body size was used as covariate. When the main interaction ($T_M \times T_O \times$ exposure) was not statistically significant ($P=0.05$), we compared the effect of maternal temperature and offspring acclimation temperature, and their interaction ($T_M \times T_O$), within each exposure treatment, using body size as covariate. Prior to data analysis, we assessed the assumptions for normality and homogeneity of variance by means of Kolmogorov–Smirnov and Levene tests, respectively. A *t*-test or Wilcoxon–Mann–Whitney test (using U or W statistic test) was used to evaluate the differences between male and female responses within each treatment combination when homogeneity of variance was or was not met, and to reciprocally compare the average thermal limit values measured for each combination within and between exposure treatments. Statistical analyses were computed using the IBM SPSS software, version 19.

Supplementary material

Supplementary material available online at
http://jeb.biologists.org/lookup/suppl/doi:10.1242/jeb.094474/-/DC1

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