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Genotype-by-environment interactions during early development of the sea urchin *Evechinus chloroticus*

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Abstract The increase in seawater temperature due to anthropogenic climate change is likely to affect population persistence and changes in distributional ranges of marine species. Adaptation to warmer environmental conditions will be determined by the presence of tolerant genotypes within a population. The present study determined the genotype-by-environment (G × E) interactions during early development of the New Zealand sea urchin *Evechinus chloroticus* cultured at 18 °C (mean annual temperature), 21 °C (ambient summer temperature) and 24 °C (+3 °C above ambient summer temperature). The experiment was performed in 3 experimental blocks using gametes from 3 males and 3 females crossed in all combinations (North Carolina II cross-breeding design), resulting in 9 families per experimental block (i.e., total of 27 families). Differences between female and male identities were quantified during cleavage and gastrulation: Reaction norms (i.e., interaction plots) showed a clear G × E interaction, with some genotypes performing better than others at high temperatures. Heritability during gastrulation was 0.51, indicating that 51 % of the variability corresponds to genetic variation. Overall, the present study shows that seawater temperature has a negative effect on early development of *E. chloroticus*; however, there are resilient genotypes in the studied population that could provide the genetic potential to adapt to future ocean conditions.

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Introduction

Increasing emission of greenhouse gases and their accumulation in the atmosphere have resulted in an increase in mean global temperatures. Globally, average combined air and seawater temperature has increased to 0.85 °C over the last 132 years, while surface seawater temperature (SST) has increased by 0.11 °C per decade over the period between 1971 and 2010 (IPCC 2014). In the particular case of New Zealand, SSTs of the North and South Island have increased by 0.5–0.6 °C in the last 30 years (Schiel 2013; Schiel et al. 2016), with a further projected increase between 0.7 and 2.3 °C by the year 2090 (IPCC 2014).

The global increase in SST can have dramatic consequences on marine life due to the influence of temperature on biochemical reactions and physiological processes (Willmer 1999; Hochachka and Somero 2002). Thermal responses in a climate change scenario will depend on the species-specific temperature response, but also the individual response of animals within a population. Some animals may be more thermotolerant, which may be beneficial for the population by maintaining the more resilient genotypes through generations (Somero 2010; Hoffmann and Sgro 2011; Byrne and Przeslawski 2013). Less thermotolerant species and populations will need to have the capacity to acclimatize to the new conditions or adapt through evolutionary adaptation by genetic accommodation (West-Eberhard 2003).

Evolutionary adaptation will be possible for those species, which have a high level of genetic variability in a

population (Bell and Collins 2008). The capacity for adaptation of a species can be studied using quantitative genetics, which refers to the study of genetic variation of phenotypic traits among individuals of a population (Falconer and Mackay 1996). This can be determined by performing breeding designs such as the North Carolina II, which estimates quantitative genetic parameters by mating multiple times each member from a male group to each member from a female group (Lynch and Walsh 1998; Nduwumuremyi et al. 2013). Thus, some offspring genotypes share the same mother and some share the same father. The North Carolina II design allows the quantification of the contribution of genotypes and their interaction with the environment through the calculation of variance components to determine adaptive potential to a new environment (Lynch and Walsh 1998). In addition, the determination of variance components can be used to obtain estimated values of narrow sense heritability (h^2), hereafter called heritability, which determines the proportion of variation of a phenotypic trait that corresponds to genetic variation, using the value of additive genetic variance and total phenotypic variance (Falconer and Mackay 1996; Lynch and Walsh 1998). Additive genetic variance is considered as the variation observed among male identities as males contribute only genetic material to their progeny (Kelly et al. 2013).

Genetic variation can also be observed graphically through the use of reaction norms when artificially selecting genotypes, which show the phenotypic variation of a particular genotype (*y*-axis) across different environments (*x*-axis) (Falconer and Mackay 1996). When a genotype performs well in one environment but fails in another (i.e., different genotypes respond differently to environmental variation), there are genotype-by-environment (G × E) interactions (Eisen and Saxton 1983; Falconer and Mackay 1996; Hoffmann and Sgro 2011). Studies to date on the adaptive capacity of marine animals to climate change (e.g., warmer and acidified ocean) show G × E interactions and genetic variability in the offspring through responses in early development (Foo et al. 2012, 2014, 2016), larval size (Sunday et al. 2011; Kelly et al. 2013), thermal tolerance (Császár et al. 2010), growth rate and reproductive investment (Pistevos et al. 2011) and metabolic rate (Calosi et al. 2013).

The present study determined the capacity for adaptation of the New Zealand echinometrid *Evechinus chloroticus* (Valenciennes 1846) to higher seawater temperatures by comparing cleavage, gastrulation and normal development in different genotypes using the North Carolina II breeding design. This species is found in shallow depths (<14 m) throughout New Zealand, from the Three Kings Islands (34°10′S) to the Snares Islands (47°60′S) (Dix 1970a; Fenwick and Horning 1980; Schiel et al. 1986; Barker 2013), and shows genetic differentiation only between the North and South Islands (Nagel et al. 2015). Due to its broad latitudinal distribution, this species is naturally exposed to a wide range of seawater temperatures during the year, from 8 °C in winter to 22 °C in summer (Garner 1969; Barker 2013). However, as *E. chloroticus* reproduces once a year during the austral summer along its entire distribution (Dix 1970b; Barker 2013), embryos develop in the water column when seawater temperatures are highest, ranging from 8–15 °C in the south to 13–22 °C in the north of New Zealand (Barker 2013). Previous research has also shown that early developmental stages of *E. chloroticus* are particularly sensitive to temperature (Delorme and Sewell 2013) and salinity (Delorme and Sewell 2014). Here, we determine the adaptive capacity of early development in *E. chloroticus* to seawater temperatures representing the average annual temperature (18 °C), the maximum summer temperature in northern New Zealand (21 °C) and the maximum summer temperature of 21 °C + 3 °C (24 °C) as predicted by 2090 (IPCC 2014).

Materials and methods

Animal collection, laboratory maintenance and spawning

Adult animals were collected in December 2012 (17.5 °C) by free divers from shallow depths (2 meters) in Matheson's Bay, northeastern New Zealand (36°18′17″S; 174°47′51″E) and transported 5 km to the Leigh Marine Laboratory, University of Auckland. In the laboratory, the animals were maintained for 10 days in a 460-L tank with flowing seawater at 18 °C and fed with *Ecklonia radiata*.

The North Carolina II design was completed in three separate experimental trials (blocks) using single male–female crosses. The animals used for experimentation were an average size of 6.7 cm test diameter (±0.4, SD, $n = 18$), with no significant differences in size among blocks (ANOVA, $F_{(2,15)} = 0.593$, $P = 0.565$). Spawning was induced through a peristomal injection of 5 mL of KCl (0.55 M). Female gametes were collected in 1-µm filtered and UV-treated seawater (FSW) at 18 °C, and sperm was collected dry from the gonopore and stored in a 1.5-mL Eppendorf tube at 4 °C until use. The quality of the eggs was checked before experimentation through a preliminary fertilization success trial; eggs from all females showed a fertilization success ≥70 %. The quality of the sperm was checked through motility of the diluted sperm (20 µL of dry sperm in 60 mL of FSW), which was counted with a hemocytometer to get an appropriate concentration to ensure fertilization and avoid polyspermy (50,000–100,000 sperm mL^{-1}, Franke 2005). The average sperm concentration over the three experimental blocks was 80,741 ± 2796 sperm mL^{-1} (±SD, $n = 3$).

Breeding design

Each experimental block was run over a 2-day period, with 3 males and 3 females crossed in all combinations, resulting in 9 full-sibling families per block. Each family was exposed to 3 different temperatures (18, 21 and 24 °C). The experimental system consisted of a temperature-controlled 14-L water bath with flowing seawater at each treatment temperature. Twenty-seven plastic containers (35 mL) were placed inside the tank and held by a polystyrene rack. Each container was filled with FSW and left for an hour to reach the desired temperature; ca. 500 eggs were then placed in each beaker for 30-min acclimation, and then, diluted sperm was added with a transfer pipette at an appropriate concentration as described above.

Each block had 81 containers (3 males × 3 females × 3 temperatures × 3 replicates), with a total of 27 families being analyzed in the complete North Carolina II design. Three additional containers with FSW only were also placed at each temperature as a control to measure temperature, dissolved oxygen and pH. Seawater temperature was measured with a submersible thermometer twice a day in each experimental block (four times in total). Dissolved oxygen and pH were measured at 24 h after fertilization in experimental (with embryos) and control containers (FSW only) using a HACH IntelliCAL™ LDO101 probe and a pH tester with spear electrode, respectively.

Each container was sampled for embryos (100–500 µL aliquot) at 2 h post-fertilization (hpf) and 24 hpf and was preserved with formalin (5 %) in 1.5-mL Eppendorf tubes for later scoring. Each sample was observed under a compound microscope (Leica) using a Sedgewick–Rafter cell, with the first 50–100 embryos observed in a random transect (Sewell and Young 1999) and scored according to their cleavage stage at 2 hpf and developmental stage of embryo (blastula, gastrula and late gastrula) and presence of abnormal development (arrested embryos, abnormal blastulae or gastrulae) at 24 hpf. Percent of normal gastrulae and late gastrulae were combined for the analysis of gastrulation.

Statistical analyses

Percent data were arcsine transformed for statistical analyses. The data were analyzed with a nested ANOVA test run in the PERMANOVA routine of Primer V6, using temperature (*T*) as a fixed factor, block (B) as a random factor, and male (M) and female (F) as random factors nested within blocks. Significance of the *F*-ratios was calculated using 9999 permutations. Heritability (h^2) was calculated across all temperature treatments as follows (Lynch and Walsh 1998):

$$h^2 = \frac{\sigma_A}{\sigma_P}$$

where σ_A correspond to the additive genetic variance and σ_P correspond to the total phenotypic variance. The proportion of phenotypic variance that corresponds to additive genetic is 4× the among-male variance component (Lynch and Walsh 1998). Estimates of variance components for each data set were used for the calculation of heritability and calculated for random factors using restricted error maximum likelihood (REML) included in the statistical software SPSS (IBM Corp.). σ_P was calculated from the sum of the remaining variance components (i.e., male, female, male × female, temperature × male, temperature × female, temperature × male × female and residual variance components) (Falconer and Mackay 1996); experimental block was excluded from the total phenotypic variance (Sunday et al. 2011). Heritability was only calculated for gastrulation as at this time variation is an offspring trait, whereas variation during cleavage can be influenced by the embryo genome and fertilization efficiency (Foo et al. 2012). Additional statistical analyses for adult size data, oxygen concentration and pH in the vials during experimentation were performed in Sigma Plot 12.5. (SYSTAT Software, Inc.).

Results

Seawater temperature across experimental blocks ranged from 18.2 ± 0.1 to 18.4 ± 0.2, 21.0 ± 0.1 to 21.4 ± 0.2 and 23.7 ± 0.1 to 24.1 ± 0.2 °C (±SD $n = 4$), with a maximum variation between blocks of 0.4 °C in the 21 and 24 °C treatments. Overall mean temperature per treatment between experimental blocks was: 18.3 ± 0.1, 21.2 ± 0.2, 23.9 ± 0.2 °C (±SD, $n = 3$), with all temperature treatments being significantly different from each other (ANOVA: $F_{(2,6)} = 646.301$, $P < 0.001$). Oxygen saturation and pH in the containers were >95 % and ca. 8.1 pH units, respectively, with no significant differences between experimental and control containers at all temperatures (oxygen saturation: $F_{(1,4)} = 1.243$, $P = 0.327$, $F_{(1,4)} = 4.043$, $P = 0.115$, and $F_{(1,4)} = 0.223$, $P = 0.662$ for 18, 21, and 24 °C, respectively; pH: $F_{(1,4)} = 0.327$, $P = 0.598$, $F_{(1,4)} = 3.571$, $P = 0.132$, and $F_{(1,4)} = 0.658$, $P = 0.463$ for 18, 21, and 24 °C, respectively).

There was no significant effect of temperature (Table 1) on cleavage success in *E. chloroticus*; however, there was a trend to decreased cleavage success with increasing seawater temperature for male and female identities (Fig. 1a, b) with a high variability in development at 24 °C. Both female and male identities were significant during cleavage (Table 1), although explaining a low percent of the variation: female identity = 8 %; male = 5 % (Table 1). Cleavage success was significantly affected by all the interaction effects (Table 1), with the largest contributions being the

Table 1 Result of nested ANOVA performed on arcsine-transformed percent data of cleavage, gastrulation and normal development of *Evechinus chloroticus* cultured at different temperatures

		Cleavage					Gastrulation					Normal development				
	df	MS	F	P	VC	%	MS	F	P	VC	%	MS	F	P	VC	%
Temperature (*T*)	2	5657.2	4.6	0.061	–	–	13,188.0	4.8	0.079	–	–	20785.0	9.6	**0.031**	–	–
Block (B)	2	1547.2	1.6	0.203	<0.001	0	938.5	1.3	0.307	<0.001	0	259.7	0.5	0.827	<0.001	0
Male (M)	6	378.2	3.1	**0.045**	5.732	5	427.8	4.8	**0.011**	12.118	8	91.9	3.2	**0.040**	<0.001	0
Female (F)	6	653.1	5.3	**0.009**	10.060	8	356.3	4.0	**0.019**	<0.001	0	468.8	16.2	**<0.001**	<0.001	0
T × B	4	1225.2	2.6	**0.019**	28.361	22	2736.3	4.3	**0.001**	61.318	39	2152.5	3.5	**<0.001**	35.933	30
T × M (B)	12	173.8	2.3	**0.034**	10.982	9	82.1	0.9	0.530	<0.001	0	158.9	2.0	0.067	8.245	8
T × F (B)	12	329.0	4.4	**0.001**	28.236	22	570.1	6.4	**<0.001**	45.708	29	477.8	6.0	**<0.001**	45.827	46
M (B) × F (B)	12	122.2	5.7	**<0.001**	5.254	4	89.6	6.8	**<0.001**	0.028	0	28.9	1.9	**0.034**	<0.001	0
T × M (B) × F (B)	24	75.0	3.5	**<0.001**	17.913	14	88.5	6.7	**<0.001**	24.657	16	79.1	5.3	**<0.001**	15.747	16
Residuals	162	21.6			21.562	17	13.2			13.187	8	15.1			15.064	15

Temperature (*T*) was used as a fixed factor, block (B) as a random factor, and male (M) and female (F) identities as random factors nested within blocks. Significant *P* values are shown in bold. In addition, estimates of variance components (VC) and percent of total variance (%) determined from restricted error maximum likelihood (REML) analysis for random factors are also shown

interactions between temperature × block and temperature × female (22 %, Table 1).

Gastrulation (the percent of gastrula and late gastrula) also tended to decrease with increasing seawater temperature for both male and female identities (Fig. 2a, b); again, however, no statistically significant effect was observed (Table 1). The number of gastrula and late gastrula showed an increase at 21 °C compared to 18 °C; however, this is the direct result of a slow development rate at 18 °C (Figs. 4, 5). Both male and female identities were significant in the percent of gastrulation (Table 1), with male identity being the major contributor to the variation (8 %, Table 1). Significant interaction effects were observed in all but the temperature × male interaction (Table 1). The interactions that contributed the highest percent of variation were temperature × block (39 %), temperature × female (29 %) and temperature × male × female (16 %) (Table 1). Heritability (h^2) for gastrulation across temperatures was 0.51, meaning that 51 % of the observed variation corresponds to genetic variation.

At 24 °C, the offspring's genotypes that had a percent of cleavage <75 % were genotypes from males 1, 2, 3, 5, 6 and 9 and from females 2, 3 and 6 (Fig. 1a, b). During gastrulation, the offspring's genotypes that had a percent of gastrulation <75 % were genotypes from males 1, 2, 3 and 4, and females 2, 3 and 6 (Fig. 2a, b).

Normal development was significantly lowered by increasing seawater temperature for both male and female identities (Fig. 3a, b; Table 1). Male and female identities showed different development rates with some offspring developing more slowly than others (Figs. 4, 5). Abnormal embryos increased with temperature, but some genotypes were more sensitive than others (Figs. 4, 5). Abnormal embryos among female identities ranged from 16 to 82 % (Fig. 4), whereas abnormal embryos among male identities ranged from 14 to 57 % (Fig. 5). Both male and female identities were significant for normal development (Table 1). A significant interaction was observed in all but the temperature × male interaction (Table 1). The interactions that contributed with the highest percent of variation were temperature × female (46 %), temperature × block (30 %) and temperature × male × female (16 %) (Table 1).

Discussion

Early developmental success in *E. chloroticus* was mainly determined by the parental identity (offspring genotype), and the interaction of genotype and environmental temperature, with no significant effect of temperature alone during cleavage and gastrulation. The nonsignificant temperature effect may be the result of high variability between genotypes at 18 °C due to slower rates of development (i.e., no cleavage at 2 hpf or pre-gastrula stage at 24 hpf). High variability is also evident between genotypes at 24 °C, where 6 paternal and 3 maternal crosses showed a percent of cleavage lower than 75 % and 4 paternal and 3 maternal crosses for gastrulation. The male and female identities that performed worst at higher temperature during cleavage also performed poorly during gastrulation, indicating a connection of performance across early developmental stages in *E. chloroticus*. This connection in performance across developmental stages has also been shown in other echinoid species (Foo et al. 2012, 2016); however, lack of connection has also been observed when genotypes that perform worst

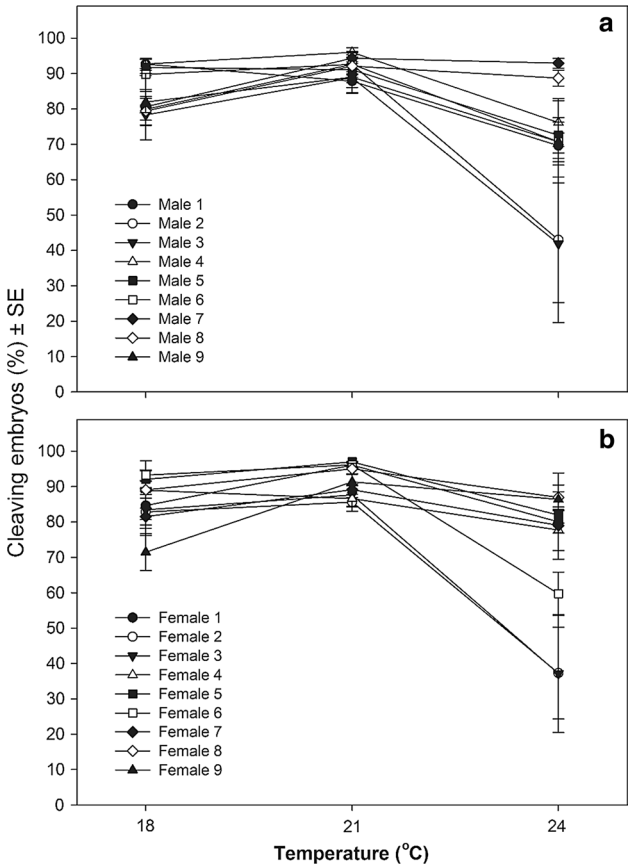

Fig. 1 Reaction norms showing the % cleavage of embryos (at 2 h post-fertilization) of 9 males (**a**) and 9 females (**b**) *Evechinus chloroticus* identities to different seawater temperatures (±SE, $n = 3$). Animals *1–3* were evaluated in the first block, animals *4–6* were evaluated in the second block, and animals *7–9* were evaluated in the third block. Animals from each block were crossed in all combinations, with reaction norms showing the performance of offspring grouped by those that share the same father (**a**) and those that share the same mother (**b**)

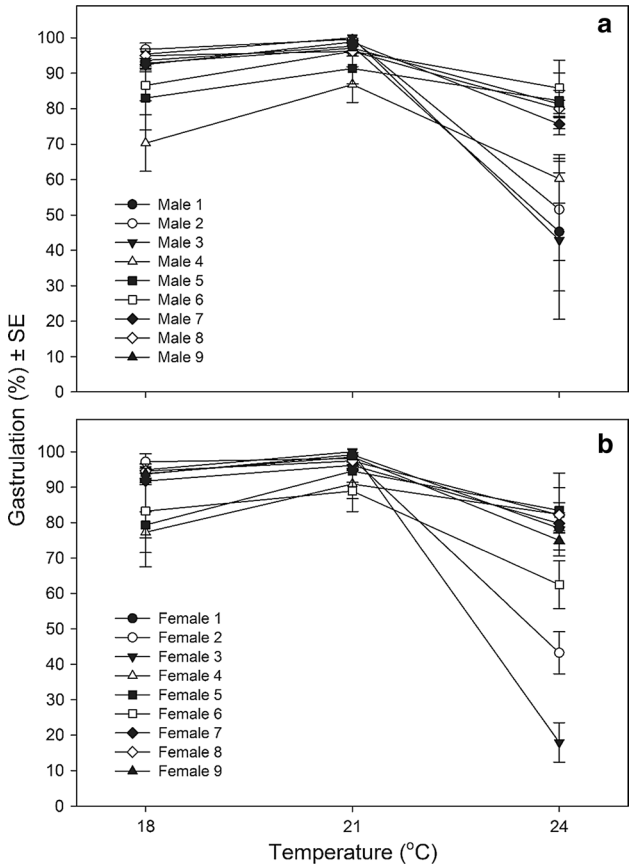

Fig. 2 Reaction norms showing the % gastrulation (gastrula and late gastrula at 24 h post-fertilization) of 9 males (**a**) and 9 females (**b**) *Evechinus chloroticus* identities to different seawater temperatures (±SE, $n = 3$). Animals *1–3* were evaluated in the first experimental block, animals *4–6* were evaluated in the second block, and animals *7–9* were evaluated in the third block. Animals from each block were crossed in all combinations, with reaction norms showing the performance of offspring grouped by those that share the same father (**a**) and those that share the same mother (**b**)

during fertilization are not the same genotypes that perform poorly during gastrulation (Foo et al. 2014).

Male and female identities showed strong interactions with temperature, which indicates that the success of a population is not only defined by an environmental component but also defined by genetic factors (Falconer and Mackay 1996; Lynch and Walsh 1998). The maternal effect (female identity) is known to influence metazoan development as females can load eggs with cellular protective factors (e.g., mRNAs and proteins) during gametogenesis to assist development under stressful environmental conditions (Evans and Marshall 2005; Evans et al. 2007; Hamdoun and Epel 2007; Tadros and Lipshitz 2009; Sunday et al. 2011; Kelly et al. 2013). In this study, maternal effects were larger, based on the variance components obtained for cleavage in *E. chloroticus*; however, the paternal effect was larger for the percent of gastrulation.

The paternal effect (male identity) is less related to influence development since males only contribute genetic material to the zygote (Foo et al. 2012; Kelly et al. 2013). However, the fact that male identity had a larger contribution than female identity during *E. chloroticus* gastrulation suggests that both sexes can influence development and performance of the offspring. Determining paternal variance is considered useful to identify the adaptive potential of species since adaptation depends on the presence of additive genetic variance within a population (Foo and Byrne 2016). Paternal effects have previously been reported in marine invertebrate and vertebrate broadcast-spawning species raised in different environments such as parental density and male quality (Crean and Marshall 2008; Green 2008; Crean et al. 2013). In addition, this paternal effect can differ with the ontogenetic stages of the individuals in fish (Heath et al. 1999; Hutchings et al. 1999; Butts and

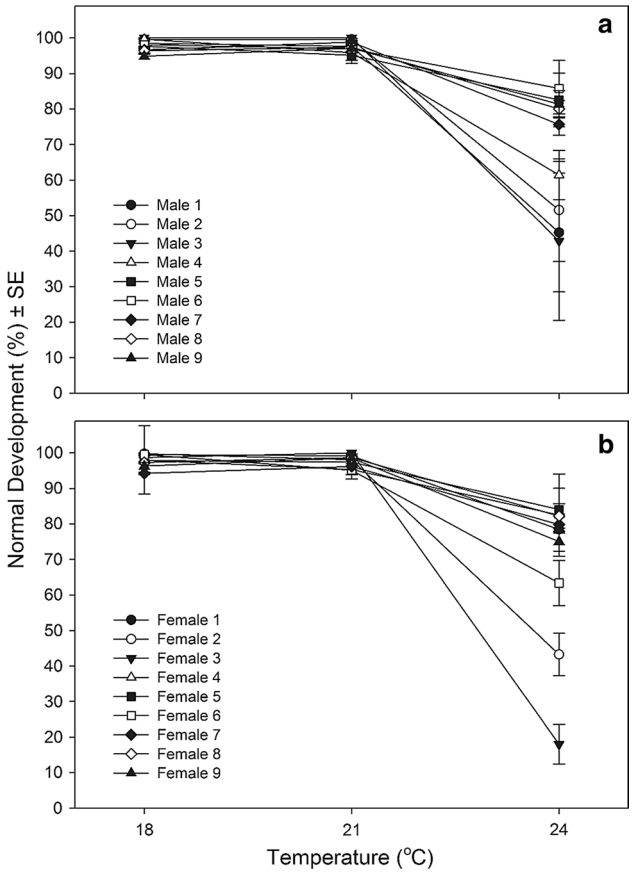

Fig. 3 Reaction norms showing % of normal development at 24 h post-fertilization of 9 males (**a**) and 9 females (**b**) *Evechinus chloroticus* identities to different seawater temperatures (±SE, $n = 3$). Animals *1–3* were evaluated in the first experimental block, animals *4–6* were evaluated in the second block, and animals *7–9* were evaluated in the third block. Animals from each block were crossed in all combinations, with reaction norms showing the performance of offspring grouped by those that share the same father (**a**) and those that share the same mother (**b**)

Litvak 2007; Green 2008). For example, in winter flounder and Atlantic cod, the fathers have a greater effect on fertilization success (Hutchings et al. 1999; Butts and Litvak 2007). In Chinook salmon, the mother identity has shown to have larger effect on offspring size before hatching of the larvae, while the father identity has shown to have a larger effect on offspring size after hatching (Heath et al. 1999). In the present study, the maternal effect of *E. chloroticus* was greater on cleavage success, while the paternal effect was larger on the gastrulation success, suggesting that male and female identities are both important for development of *E. chloroticus*, but their contribution differs depending on the developmental stage.

Evechinus chloroticus showed a genotype-by-environment (G × E) interaction, with some genotypes performing better than others at higher temperatures, indicating the potential for adaptation to warmer conditions (Falconer and Mackay 1996; Foo et al. 2012; Foo and Byrne 2016). G × E interactions have been observed and reported for a variety of marine species (Foo and Byrne 2016) such as bryozoans (Pistevos et al. 2011), corals (Meyer et al. 2009; Császár et al. 2010), molluscs (Kvingedal et al. 2010; Sunday et al. 2011) and echinoderms (Sunday et al. 2011; Foo et al. 2012; Kelly et al. 2013; Zhang et al. 2013; Foo et al. 2014, 2016). However, despite the fact that a certain population shows G × E interactions, it is important to know how much of the observed phenotypic variance is due to additive genetic effects (Falconer and Mackay 1996). In the present study, the heritability estimate for the percent of gastrulation in *E. chloroticus* shows that 51 % of the observed phenotypic variance corresponds to additive genetic factors. This value is in the upper range of estimates of heritability for other sea urchin species, which show an additive genetic effect of 1–50 % for larval growth (Sunday et al. 2011; Kelly et al. 2013) and 2–50 % for adult growth (Liu et al. 2004, 2005; Chang et al. 2012), but is higher compared to estimations made for early development of the tropical sea urchin *Pseudoboletia indiana* (2–30 %, Foo et al. 2014). In the present study, the fact that 51 % of the observed variation in gastrulation is genetic means that half of the observed variation in temperature response of *E. chloroticus* offspring is caused by variation in genotypes of the studied population (Visscher et al. 2008).

Adaptation to a changing environment is determined by the degree of genetic variability within a population (Bell and Collins 2008; Munday et al. 2013). Normal development in *E. chloroticus* was very variable at high temperature, with abnormalities ranging between 0 and 81 % at 2hpf and 4 and 89 % at 24 hpf among the 27 families studied. Previous studies using pooled gametes from multiple parents have shown that increasing seawater temperature has a negative effect during early development of *E. chloroticus* with 20–50 % of abnormal embryos observed after 24 hpf at 24 °C (Delorme and Sewell 2013). The present study shows a wider range of abnormal development compared to previous studies that have used multiple male–female crosses (Delorme and Sewell 2013). This may be due to the fact that in multiple male–female crosses, success can be attributed to the high performance of the tolerant eggs and sperm in the mix of pooled gametes and to differences in gamete compatibility (Evans and Marshall 2005; Evans et al. 2007; Foo et al. 2012).

Quantitative genetics studies are useful to determine genetic variability of particular traits and the evolutionary potential of species and to identify species at risk under future conditions (Hoffmann and Sgro 2011; Munday et al. 2013). However, the adaptive capacity of a species will depend not only on genetic factors, but also on the non-genetic phenotypic plasticity associated with the parent's environment (Salinas et al. 2013) and the degree of

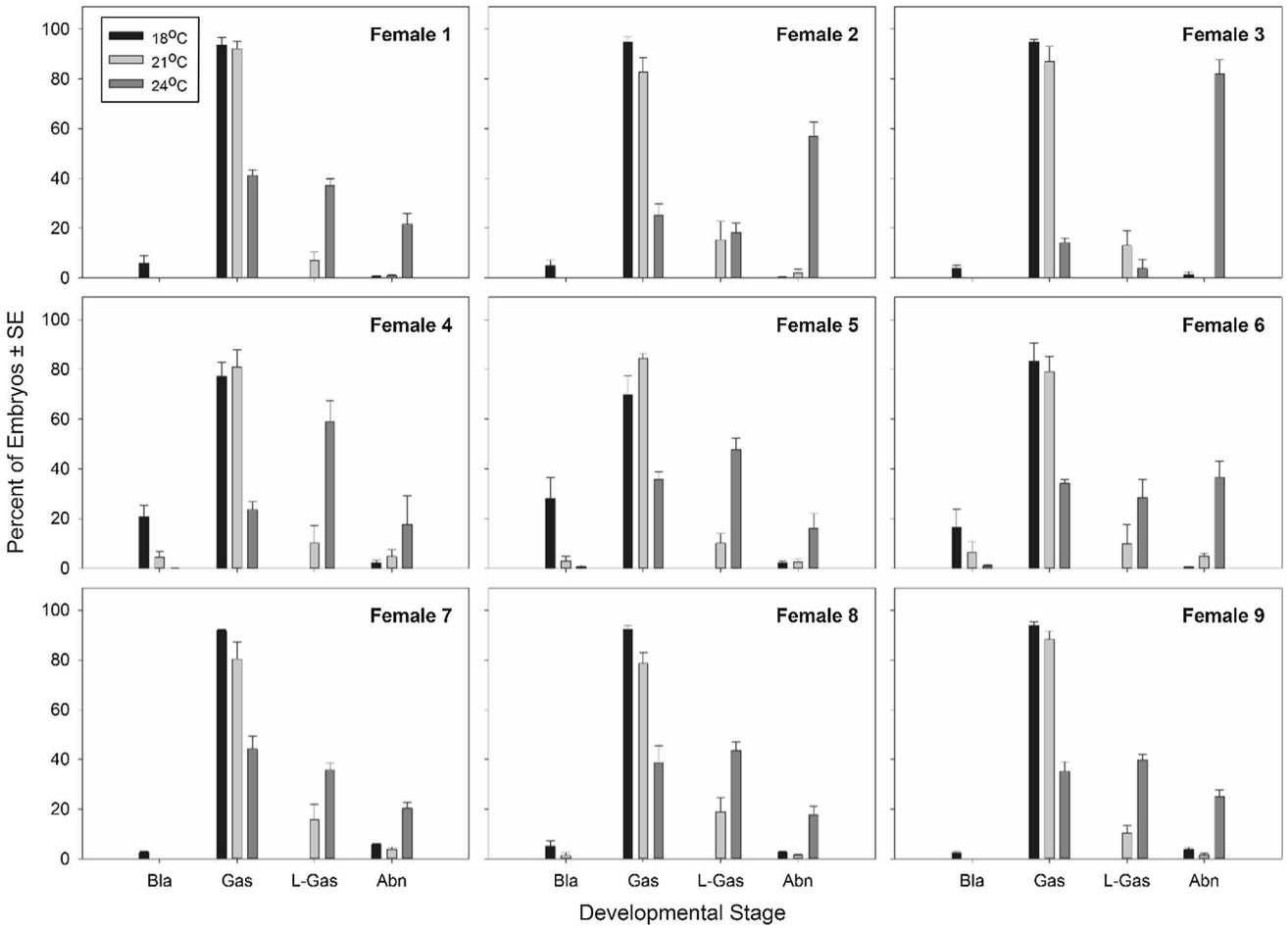

Fig. 4 Effect of temperature on development of *Evechinus chloroticus* at 24 h post-fertilization for 9 different female identities. Data represent the mean developmental stage ± standard error (SE, $n = 3$) for each female identity. *Bla* blastula, *Gas* gastrula, *L-Gas* late gastrula, *Abn* abnormal embryos

local adaptation within the population. Epigenetics and/or changes in gene expression due to exposure to external or environmental factors can also play a fundamental role in adaptation to future climate conditions (Franks and Hoffmann 2012). Consequently, phenotypic plasticity and epigenetics, together with genetic adaptation, are key factors to consider when studying species risk to climate change (Munday et al. 2013).

Evechinus chloroticus has the potential to be an important study species for the effects of temperature change on temperate reef invertebrates. Previous research on the same *E. chloroticus* population from northeastern New Zealand has shown an optimum temperature for development between 16 and 21 °C and that mean gastrulation success is less than 50 % at 24 °C (Delorme and Sewell 2013). Here, we have shown further that this population of *E. chloroticus* has genetic variability, which might allow genetic adaptation to climate change. However, it is not yet known whether this adaptation can occur during what it can be considered a rapid period of ocean warming in this area (0.6 °C warming over the last 30 years, Schiel 2013). Experimental acclimation experiments (90 days) during the period of gonad growth in adult *E. chloroticus* have also shown the complete loss of reproductive output and negative growth at 24 °C (Delorme and Sewell 2016), which might constrain the potential for adaptation in this population if warm summer temperatures associated with La Niña conditions become more prevalent or there is an increasing influence of the tropically derived East Auckland Current (Schiel 2013). Future research needs to determine whether other populations of *E. chloroticus* around New Zealand, particularly the genetically differentiated populations of the South Island (Nagel et al. 2015), show the same genetic variance to warmer temperatures and to a combination of climate change stressors, not only during early development but also in larvae, juveniles and adults.

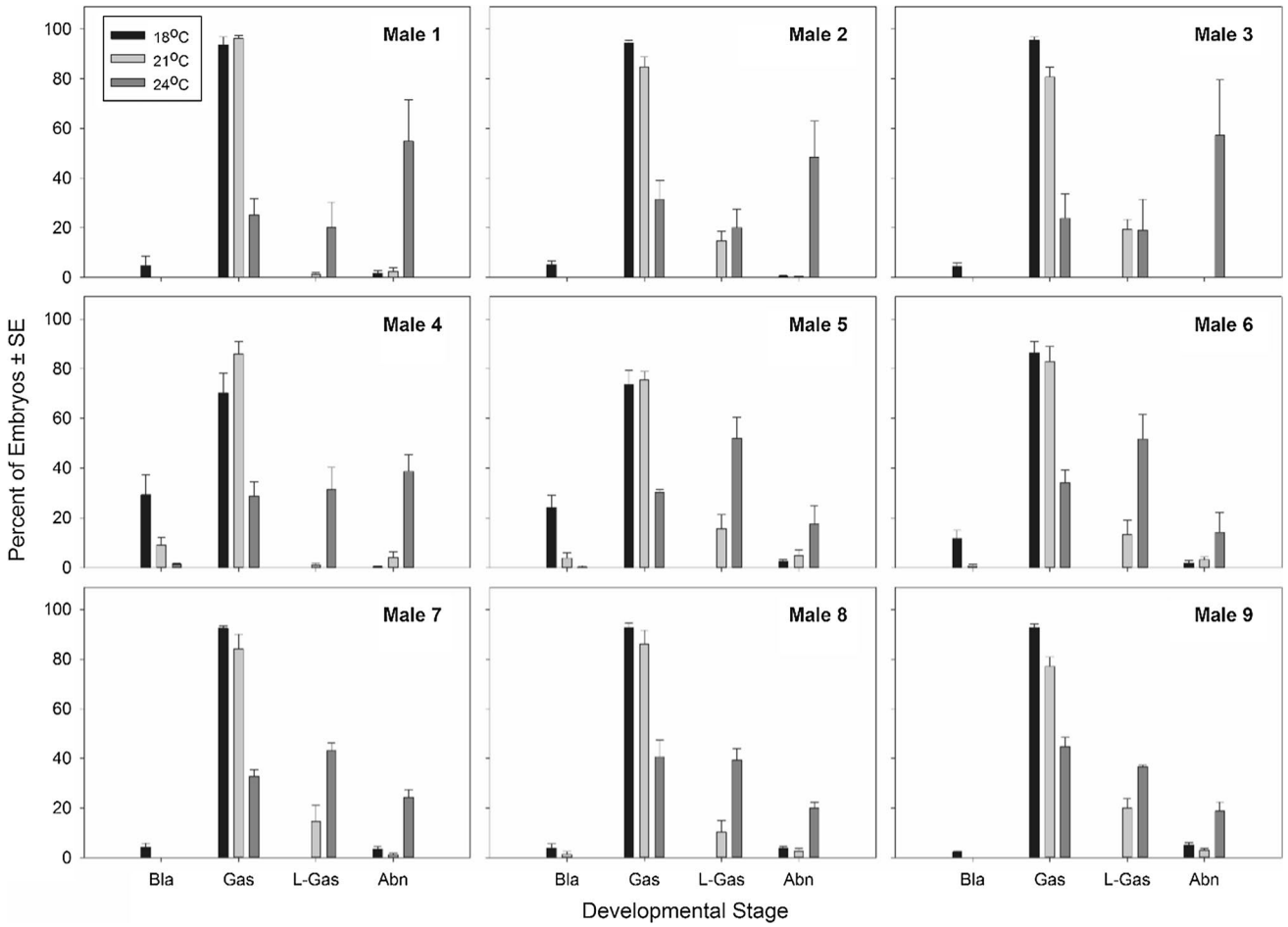

Fig. 5 Effect of temperature on development of *Evechinus chloroticus* at 24 h post-fertilization for 9 different male identities. Data represent the mean developmental stage ± standard error (SE, $n = 3$) for each female identity. *Bla* blastula, *Gas* gastrula, *L-Gas* late gastrula, *Abn* abnormal embryos

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Compliance with ethical standards

Conflict of interest All authors declare that they have no conflict of interest.

Ethical approval All applicable international, national and/or institutional guidelines for the care and use of the animals were followed.

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