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Local adaptation, intrinsic coadaptation and the effects of environmental stress on interpopulation hybrids in the copepod *Tigriopus californicus*

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Abstract

Hybridization between divergent populations may cause a reduction in fitness due either to disruption in local adaptation or disruption in intrinsic coadaptation. We tested for both effects in the tidepool copepod *Tigriopus californicus*. Fitness surrogates were measured in pure populations and interpopulation hybrids, with broods split between three environmental treatments: (1) Standard: 15 °C/100% seawater; (2) High temperature: 25 °C/100% seawater; and (3) Low salinity: 15 °C/50% seawater. Effects of these treatments were independent of population, providing no evidence for local adaptation. Comparison of mean fitness in pure populations, F_1 hybrids and F_2 hybrids showed that hybridization caused beneficial interactions between alleles at the same locus and detrimental interactions between loci (i.e., disruption of intrinsic coadaptation). The effects of hybridization were environmentally dependent as exposure to the most stressful treatment (high temperature) resulted in the maintenance of F_1 heterosis and a substantial reduction in F_2 breakdown.

Keywords: Copepod; Fitness; Hybridization; Local adaptation; Salinity; Temperature

1. Introduction

When divergent populations are hybridized, the offspring may show reduced fitness due to disruptions in local adaptation, disruptions in intrinsic coadaptation, or a combination of both mechanisms. Understanding the mechanisms underlying hybrid fitness is important for managing both natural marine populations and aquaculture stocks,

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since mixing between previously isolated groups is becoming increasingly common due to accidental translocation/introgression as well as intentional efforts to combat the effects of inbreeding (e.g., Johnson, 2000; Utter and Epifanio, 2002).

Local adaptation involves beneficial interactions between genotype and environment and should be strongest when the environment is heterogeneous and dispersal is limited. Despite the relatively mild barriers to gene flow in the ocean, numerous examples of local adaptation in marine species have been reported (e.g., Conover, 1998; Parsons, 1998; Pearson et al., 2000; Grosholz, 2001). Hybridization can disrupt local adaptation by creating intermediate phenotypes that do poorly in both parental niches (Rice and Hostert, 1993; Rundle and Whitlock, 2001). Examples of environment-dependent hybrid inferiority include sticklebacks (Hatfield and Schluter, 1999; Rundle, 2002) and aphids (Via et al., 2000).

Intrinsic coadaptation involves gene interactions that are largely independent of the external environment. Intrinsic coadaptation can be disrupted in first-generation (F_1) hybrids due to underdominant interactions within loci or epistatic interactions between loci (e.g., Lynch, 1991; Orr, 1995; Turelli and Orr, 2000). However, breakdown is often not apparent until the second generation of hybridization (F_2) when meiosis and recombination expose incompatibilities between recessive alleles. Examples of F_2 breakdown have been found in a variety of organisms including *Drosophila* (Dobzhansky, 1948) and salmon (Gharrett et al., 1999). Distinguishing between extrinsic adaptation and intrinsic coadaptation is not only important for understanding speciation mechanisms (Rice and Hostert, 1993; Orr, 1995; Rundle and Whitlock, 2001), but also has conservation implications because the efficiency with which selection can "purge" outbreeding depression depends on the underlying mechanism (Templeton, 1986; Edmands and Timmerman, 2003).

The tidepool copepod *Tigriopus californicus* is one species that appears to show intrinsic coadaptation, but has not been explicitly tested for local adaptation. The species ranges from southeast Alaska to central Baja California, Mexico (Dethier, 1980; Ganz and Burton, 1995), and is restricted to supralittoral pools due to predation at lower levels (Dethier, 1980). While both adults and larvae are free-swimming and have seemingly high potential for dispersal, genetic data show extensive divergence between populations as little as a few kilometers apart (Burton et al., 1979; Burton and Lee, 1994; Edmands, 2001). Interpopulation hybridization under common garden conditions produces a pattern consistent with disruption of intrinsic coadaptation F_1 hybrids are typically similar to or more fit than their parents, while F_2 hybrids are less fit than either parent (Burton, 1986, 1990a,b; Edmands, 1999). Furthermore, deviations from expected Mendelian segregation patterns in hybrids provide evidence for both nuclear–nuclear (Burton, 1987) and nuclear–cytoplasmic (Willett and Burton, 2001) coadaptation.

While *T. californicus* populations show clear intrinsic coadaptation, it is not as clear whether or not they exhibit local adaptation. On the one hand, we might expect local adaptation since the species is highly subdivided and spans a range of over 3500 km and nearly 30 latitudinal degrees, thereby experiencing considerable variation in factors such as temperature, precipitation and wave exposure. On the other hand, local adaptation may be thwarted by the hugely variable physical conditions in the high intertidal. The supralittoral pools that these animals inhabit are subject to extensive fluctuations in salinity and temperature (Egloff, 1967; Vittor, 1971; Dethier, 1980) and sometimes evaporate completely (Dybdahl, 1994; Burton, 1997).

These physically harsh and variable conditions result in broad environmental tolerances. Live *T. californicus* are found in tidepools with temperatures ranging from at least 4 °C (Vittor, 1971) to 35 °C (S. Edmands, personal observation). Osmotic tolerance is even more striking, with activity observed at salinities as low as 6 ppt (Burton et al., 1979) and as high as 102 ppt (Egloff, 1967). Inactive animals exposed to salinities up to 334 ppt can even be revived following transfer to normal seawater (Egloff, 1967). Their ability to survive complete desiccation is more controversial. Powlik and Lewis (1996) found that rehydration of copepods within dried samples of algae and sediment resulted in recovery of ~ 11% of individuals. In contrast, Vittor (1971) never observed recovery in adults or larvae subjected to prolonged desiccation. Egloff (1967) reported an intermediate result, with all life stages surviving up to 30 min of exposure to air at 100% humidity. If *T. californicus* can indeed survive complete desiccation, this would enhance the potential for local adaptation in sites subjected to frequent evaporation.

Despite a fair amount of work on environmental tolerance in *T. californicus*, there are few data on population differences in environmental tolerance. Vittor (1971) found some evidence for differential salinity and temperature tolerance among samples taken from different locations, but also found substantial differences between colonies taken from the same location. Studies of an allozyme locus involved in osmoregulation also showed patterns suggesting local adaptation, but the relationship between allele frequency and salinity regime was not significant (Burton and Feldman, 1983; Burton, 1986). Finally, Dybdahl (1995) found higher osmotic and salinity stress at wave exposed sites, suggesting the potential for localized selection, but did not actually test for local adaptation.

The ideal test for local adaptation would involve reciprocal transplants between locations (e.g., Rundle and Whitlock, 2001). However, in *T. californicus* where genetic divergence occurs over very small geographic distances, such an exercise could irrevocably alter the genetic structure of natural populations. Instead, we measured fitness under controlled laboratory conditions in three pure populations and in first- and second-generation interpopulation hybrids. Fitness was measured in three environmental conditions: Standard, High temperature (which might be expected to most stressful for the northernmost population from the coldest climate) and Low salinity (which might be expected to be most stressful for the southernmost population from the hottest, driest climate). Extrinsic adaptation would be expected to result in fitness interaction effects between population and environment, while intrinsic coadaptation would be expected to result in fitness changes between hybrid generations within the same environment. Lastly, environmental modulation of gene interactions would be expected to cause hybridity effects to differ between environments.

2. Methods

2.1. Study animal

T. californicus is an obligately sexual, harpacticoid copepod whose reproductive biology has been well-studied (Egloff, 1967; Burton, 1985). Mature males use their first antennae to clasp immature females for up to 7 days until the female undergoes her final

molt. The female is then inseminated and released. Whereas males mate multiply, females mate only once in their lifetime and use stored sperm to fertilize multiple broods of eggs. Females that are not fertilized may still produce egg sacs, but the eggs invariably fail to develop. The mating system of *T. californicus* facilitates collection of virgin females: Males and immature females that have formed clasped pairs are simply dissected apart using a fine probe. At 15 °C, fertilized females typically develop an egg sac within 2–4 days. New egg sacs are green to black in color and become orange or red as they mature, with hatching occurring after 3–6 days.

2.2. Population sampling and culture maintenance

Copepods were collected from supralittoral pools at three locations (Fig. 1): (A) Strawberry Hill Wayside, OR, USA (44°15′ N, 124°07′ W; collection dates 1/23/99 and 2/13/99); (B) Santa Cruz, CA, USA (36°57′ N, 122°03′ W; collection date 1/24/99); and (C) San Diego, CA, USA (32°45′ N, 117°15′ W; collection dates 1/19/99 and 2/15/99).

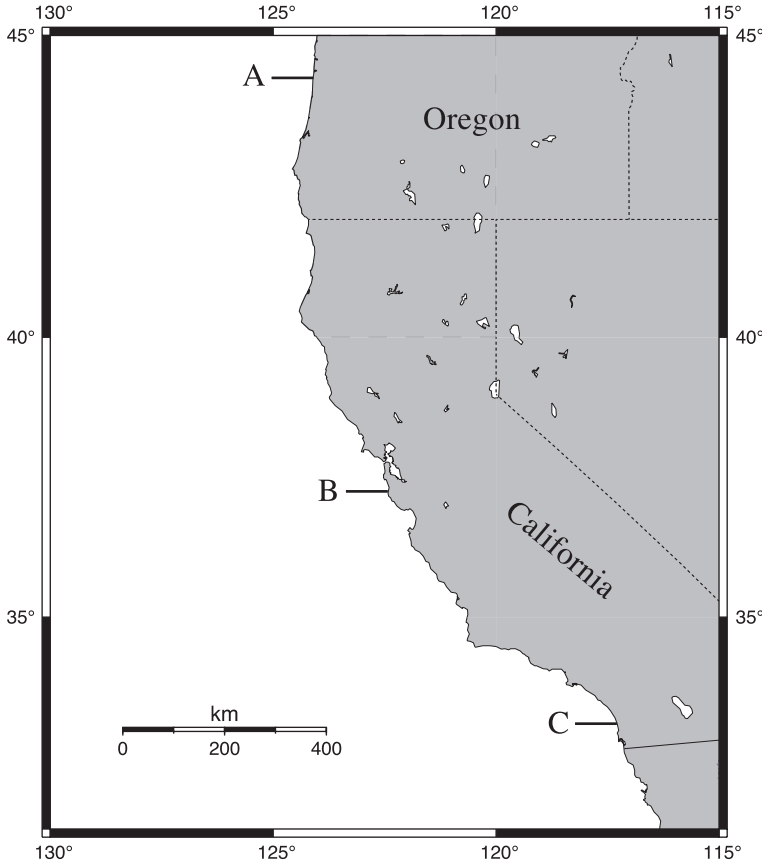

Fig. 1. Location of collecting sites.

Because previous work shows high gene flow among tidepools within a contiguous rock outcrop (Burton and Swisher, 1984), samples from pools within outcrops were combined. All samples were shipped within 3 days of collection. Cultures were kept in natural seawater in 400-ml beakers with the addition of small amounts of commercial flake-type fish food to promote an algal bloom. All cultures were maintained at 15 °C with a 12 h light/12 h dark cycle.

2.3. Tests of desiccation resistance

Previous tests of the ability of *T. californicus* to recover from desiccation produced very different results. Vittor (1971) reported 0% recovery after rehydration for copepods from Cape Arago, OR (USA), while Powlik and Lewis (1996) reported ~ 11% recovery for copepods from Barkley Sound, British Columbia (Canada). We therefore conducted a pilot study of desiccation resistance in the three populations used for the current study. One hundred nauplii (larvae), 100 adult males and 100 adult females from each population were transferred to 60 × 15 mm Petri dishes (one animal per dish) and seawater was siphoned off using a pasteur pipet. Animals were left uncovered at 15 °C overnight. Fifteen milliliters of seawater was then added to each dish. Using a dissecting microscope, each animal was monitored for movement after 1 h of rehydration and again after 24 h.

2.4. Experimental crosses and fitness assays

Crosses were performed under standard conditions, and offspring were subsequently split into one of three environmental conditions: (1) Standard: 15 °C/100% seawater; (2) High temperature: 25 °C/100% seawater; and (3) Low salinity: 15 °C/50% seawater. The three populations studied might be expected to be differentially adapted to these three regimes. The high temperature treatment was predicted to be most stressful for the northernmost population (population A) where temperatures are lowest. *T. californicus* tidepool temperatures average approximately 1.6 °C higher than mean air temperatures (Egloff, 1967). For the year in which copepods were sampled, mean monthly minimum and maximum air temperatures were 3.8 and 18.4 °C for Newport, OR (closest weather station to population A), 4.6 and 22.6 °C for Santa Cruz, CA (Population B) and 8.8 °C and 25.4 °C for San Diego, CA (population C) (National Climatic Data Center, http://www.ncdc.noaa.gov). In contrast, the low salinity treatment was predicted to be most stressful for the southernmost population (population C) where temperatures are highest and precipitation is lowest. Natural seawater has a salinity of ~ 35 ppt but live *T. californicus* have been observed in pools with salinities as high as 102 ppt (Egloff, 1967) due to evaporation at high temperatures, or as low as 6 ppt (Burton et al., 1979) due to precipitation. Total precipitation for the year in which copepods were sampled was 220.5 cm for Newport, OR (near Population A), 76.7 cm for Santa Cruz, CA (Population B) and 13.8 cm for San Diego, CA (Population C) (National Climatic Data Center, http://www.ncdc.noaa.gov).

Seven crosses were performed, with broods split between the three environments, for a total of 21 treatments. The crosses (male × female) were: (1) A × A; (2) B × B; (3)

C × C; (4) F_1: A × C; (5) reverse F_1: C × A; (6) F_2: [A × C F_1] × [A × C F_1]; and (7) temporal control: [C × C generation 1] × [C × C generation 1]. Animals used for experimental crosses were kept in natural seawater filtered twice through Whatmann no. 1 filter paper, with the addition of 0.04 g nutritional yeast per 100 ml seawater. As with the stock cultures, experimental crosses were maintained on a cycle of 12 h light/12 h dark.

Crosses were initiated by using a fine probe to dissect apart clasped pairs of males and females and then randomly distributing the single copepods into appropriate crosses. For each of the five first-generation crosses, six replicates of 10 females × 10 males were established (A × A 1–6, B × B 1–6, etc.). Each replicate was housed in a 150 × 15 mm plastic Petri dish containing 35 ml of seawater plus yeast. Dishes were monitored using a dissecting microscope three times per week (Tuesdays, Thursdays and Saturdays). When females formed egg sacs they were transferred to a new 60 × 15 mm Petri dish containing 15 ml seawater plus yeast (one female per dish). When the first clutch of eggs hatched, larvae were transferred to one of three treatment dishes: Standard, High temperature or Low salinity. A maximum of 10 larvae was placed in each dish (if less than 30 larvae were found they were distributed evenly between the three treatments). Fourteen days after the larvae were transferred, the number of live copepodids (juvenile copepods) in each dish was counted to determine the metamorphosis proportion (number copepodids/original number larvae) and the numbers of live nauplii (larvae) and live copepodids were summed to determine the survivorship proportion (number larvae + copepodids/original number larvae).

For crosses continuing into the second generation (C × C and A × C), females were transferred to new Petri dishes after the birth of the first clutch, and subsequent clutches were used to found the next generation. Dishes were monitored three times per week. On each observation day, each female was transferred to a new Petri dish, and the contents of the old dish were transferred to a 250-ml beaker for either "odd" (e.g., A × C 1, A × C 3) or "even" (e.g., A × C 2, A × C 4) crosses (Fig. 2). Dishes were combined into beakers until the water level reached 200 ml. Beakers were monitored three times per week for the formation of clasped pairs (potentially including full siblings). Pairs were dissected apart and then recombined in new mating dishes ("even" female × "odd" male or "odd"

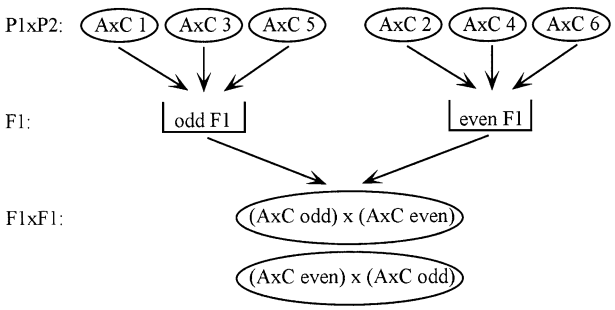

Fig. 2. Mating design to prevent inbreeding in the second generation. Crosses are listed as male × female.

female × "even" male) to avoid inbreeding. The remainder of the protocol was as described for the first generation.

2.5. Data analysis

Data for the F_2 cross [(A × C F_1) × (A × C F_1)] in each environmental treatment were first corrected for possible time effects by subtracting from each F_2 value the difference between the means of cross 7 (C × C generation 2) and cross 3 (C × C generation 1). This method assumes that population C and the F_2 cross respond to any time effects in the same way. However, because population C fitness tended to decrease between generations in all environmental treatments, this method was conservative for detecting F_2 hybrid breakdown. Treatment effects (High temperature vs. Standard and Low salinity vs. Standard) were tested for each cohort by paired, two-tailed *t* tests. Gene × environment interactions (i.e., local adaptation) were assessed by testing for population × environment interaction in an ANOVA.

The most appropriate model of gene action for crosses in each environment was assessed using joint scaling tests (Mather and Jinks, 1982) as described in Hard et al. (1992) and modified in Armbruster et al. (1997) for four experimental generations (two parents, pooled F_1 and F_2). These tests use the mean and experimental variance for fitness measures in each generation to derive estimates of composite additive and dominance effects. With purely additive gene action, fitness in F_1 and F_2 hybrids would equal the midparent value (the average of the two parents). With dominance, F_1 fitness would exceed the midparent due to increased heterozygosity, and F_2 fitness would be midway between F_1 and midparent due to the loss of heterozygosity caused by independent assortment. With beneficial epistasis in the parental populations, F_2 fitness would drop below the average of midparent and F_1 values due to the disruptive effect of recombination on gene interactions (Lynch and Walsh, 1998).

Generation means were first tested for conformance to an additive model using a chi square test (Hayman, 1958) with 2 degrees of freedom. If the additive model was rejected ($P < 0.05$), the data were then tested for conformance to an additive-dominance model with 1 degree of freedom. Rejection of this model indicates the presence of significant epistasis.

Values for dominance and epistasis were obtained by using the same genetic model for crosses in each environment. Phenotypic means (represented by z) for midparents (P), F_1 and F_2 were used to estimate dominance (δ_{1x}) and additive × additive epistasis (α_{2x}) according to the following equations (Lynch, 1991):

$$\delta_{1x} = z(\mathrm{F}_1) - z(\mathrm{F}_2)$$

$$\alpha_{2x} = z(\mathrm{F}_1) - 2z(\mathrm{F}_2) + z(\mathrm{P}).$$

3. Results

Overnight desiccation followed by rehydration resulted in 100% mortality (100 adult males, 100 adult females and 100 larvae from each of the three populations).

Table 1
The proportion of individuals that survived or metamorphosed after 14 days under conditions of high temperature or low salinity, relative to results under standard conditions (e.g., high temperature survival − standard condition survival)/standard condition survival)

Cross	High temperature		Low salinity	
	Relative survival	Relative metamorphosis	Relative survival	Relative metamorphosis
A × A	*− 0.193 (0.0032)*	*− 0.183 (0.0050)*	*+ 0.117 (0.0234)*	*+ 0.120 (0.0234)*
B × B	*− 0.258 (0.0024)*	*− 0.272 (0.0016)*	+ 0.075 (0.2621)	+ 0.075 (0.2621)
C × C	*− 0.267 (0.0001)*	*− 0.211 (0.0017)*	− 0.066 (0.2194)	− 0.038 (0.5355)
A × C	*− 0.244 (0.0003)*	*− 0.257 (0.0001)*	+ 0.038 (0.4987)	+ 0.035 (0.5485)
C × A	*− 0.137 (0.0342)*	− 0.087 (0.1980)	+ 0.106 (0.0562)	*+ 0.130 (0.0254)*
(A × C) × (A × C)	*− 0.107 (0.0222)*	− 0.025 (0.5390)	+ 0.021 (0.6949)	+ 0.034 (0.4792)

Crosses are listed as male × female. Deviation from standard conditions was tested by paired, two tailed *t* tests. *P* values are shown in parenthesis and significant tests are shown in italic.

Sample sizes for the experimental crosses ranged from 40 to 42 broods per cross (mean 40.3) with the number of larvae per brood ranging from 3 to 30 (mean 23.8). Increasing the temperature from 15 to 25 °C tended to reduce survival and metamorphosis in both intra- and interpopulation crosses, with significant reductions in 10 out of 12 cases (Table 1). Decreasing salinity from ~ 35 to ~ 17.5 ppt tended to increase both survival and metamorphosis in all but the southernmost population (C), although these changes were significant in only 3 out of 12 cases (Table 1). Notably, two of the three significant tests showed higher fitness in the northernmost (high rainfall) population. No significant differences were found between reciprocal F_1s in any of the three environmental treatments (unpaired, two-tailed *t* tests).

Analysis of variance (Table 2) for the three intra-population crosses (A, B and C) showed highly significant variation among environmental treatments, but no significant variation among populations. The interaction between population and environment was also non-significant, providing no evidence for local adaptation.

Generation means (Fig. 3) show F_1 heterosis for survival and metamorphosis in all three environmental treatments. Measures of F_2 fitness were below the midparent in the standard and low salinity treatments, and equivalent to the midparent in the high

Table 2
Two-way ANOVA for the effects of population (A, B and C) and environment (Standard, High temperature and Low salinity) on fitness (proportion survival and proportion metamorphosis)

Source	*df*	Survival		Metamorphosis	
		MS	*F* test	MS	*F* test
Population	2	0.347	2.927	0.206	1.668
Environment	2	2.762	23.308***	2.547	20.640***
Population × Environment	4	0.106	0.892	0.112	0.910
Error	351	0.118		0.123	

df = degrees of freedom, MS = mean square.
*** $P < 0.001$.

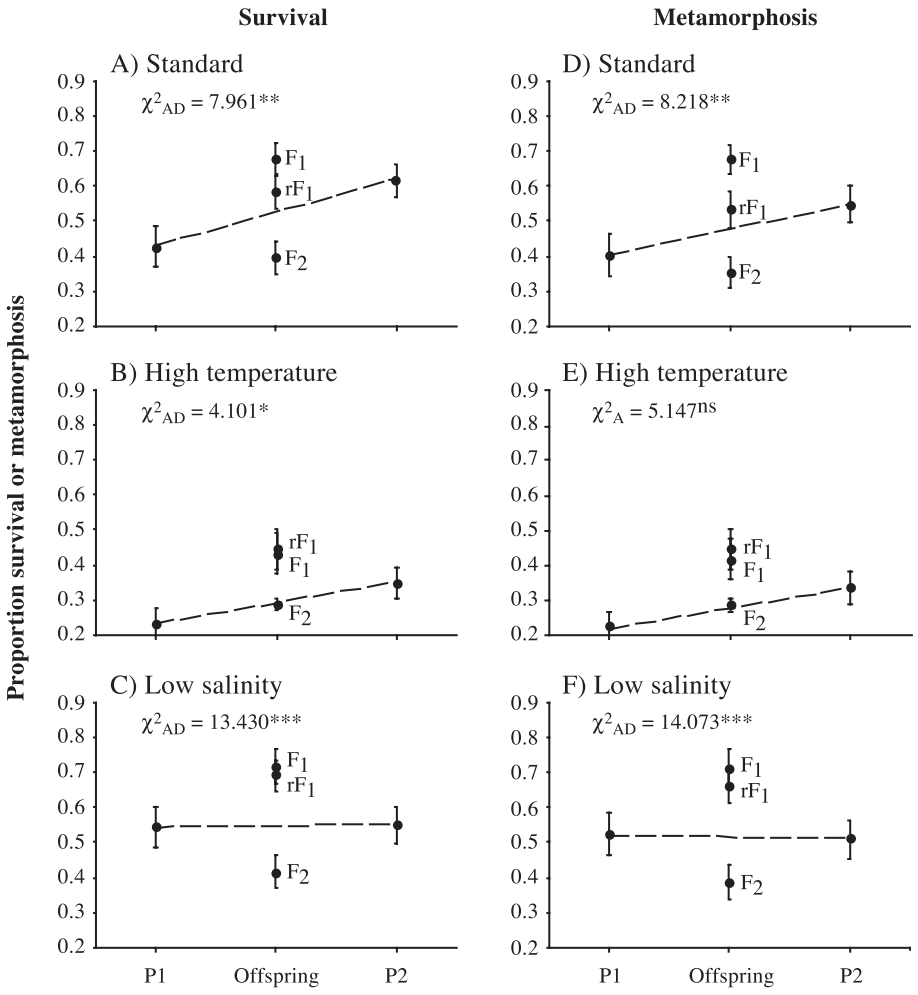

Fig. 3. Mean and standard error for survival and metamorphosis in parental population A (P1), parental population C (P2), F_1 hybrids (male A × female C), reverse F_1 (rF_1) hybrids (male C × female A) and F_2 hybrids ($F_1 \times F_1$).

temperature treatments. Joint scaling tests rejected the additive-dominance model (indicating significant epistasis) in all but one case. In this one case, metamorphosis at high temperature, the additive model was accepted.

Estimates of gene action (Table 3) obtained by comparing mean fitness in midparent, F_1 and F_2 showed positive dominance (effects δ_{1x}) in all cases, indicating beneficial effects of heterozygosity. In contrast, estimates of epistatic effects ($-\alpha_{2x}$) were negative in all cases, indicating detrimental effects of disrupting interactions between loci. Values were generally similar in the Standard and Low salinity treatments. However, in the stressful

Table 3
Estimated dominance and additive × additive epistatic effects calculated from mean values for midparents, F_1 and F_2 as described in the text

Treatment	Dominance effects (δ_{1x})		Epistatic effects ($-\alpha_{2x}$)	
	Survival	Metamorphosis	Survival	Metamorphosis
Standard	0.715	0.904	− 1.036	− 1.248
High temperature	0.505	0.450	− 0.519	− 0.420
Low salinity	0.719	0.832	− 1.033	− 1.167

Data were standardized to have F_2 means equal to 1.

High temperature treatment, there was a reduction in both the beneficial dominance effects and the detrimental epistatic effects.

4. Discussion

No population differences in desiccation resistance were found, as overnight desiccation resulted in 100% mortality for all three populations. This contrasts with the results of Powlik and Lewis (1996) who found that rehydration of completely evaporated tidepools resulted in partial recovery of all life stages. Because Powlik and Lewis' samples came from a colder, wetter location (Barkley Sound, Canada), it seems unlikely that they had higher desiccation resistance. A more likely explanation may be that our samples were subjected to complete desiccation, whereas Powlik and Lewis' samples may have retained trace amounts of moisture (copepods were encased within natural deposits of algae and sediment in evaporated tidepools that were "dry to the touch"). The inability to survive complete desiccation means that populations will be limited in their ability to adapt to local conditions where complete evaporation is a frequent occurrence. It is also very important for interpreting laboratory-based breeding studies—if a completely dried cyst on a beaker or Petri dish could be revived, then this would greatly amplify the danger of contamination between genetically differentiated lines.

Increasing temperature from 15 to 25 °C proved stressful for all three populations. This was not surprising. While 25 °C is within the range of temperatures experienced by *T. californicus*, it is well above the mean air temperature for these particular locations (11–19 °C, National Climatic Data Center, http://www.ncdc.noaa.gov). More surprising were the sometimes beneficial effects of reducing salinity from 100% to 50% seawater. Previous work by Vittor (1971) found no significant variation for five out of seven fitness traits among constant salinity treatments of 50%, 100% and 150% seawater. However, Burton and Feldman (1983) found increased mortality when larvae hatched in 50% seawater were transferred to 100% seawater. In contrast, we did the opposite experiment (larvae transferred from 100% to 50% seawater) and found a trend toward increased fitness in 10 of 12 cases, with significant increases in three of these cases. Because experiments were done in coarsely filtered seawater, these effects may be attributable to differential growth of microbes or phytoplankton between treatments, rather than to salinity itself.

Results showed little evidence for local adaptation. Overall, environmental effects were independent of population, as shown by the non-significant interaction terms in the

analysis of variance. The finding of significant beneficial effects of low salinity only in the northernmost (high precipitation) population does provide some hint of local adaptation. Effects of low salinity in the remaining two populations were not significant, but follow a trend consistent with local adaptation in that both relative fitness measures were lowest in the southernmost population and intermediate in the central population. However, effects of high temperature are exactly the opposite of predicted patterns, with the northernmost population suffering the smallest reduction in fitness. The lack of substantial adaptive differences between populations may be attributed to the extreme environmental fluctuations found within and among tidepools within a single outcrop. This is consistent with recent work on *T. californicus* showing that the level of population subdivision for quantitative traits (Q_{ST}) was lower than that for presumably neutral molecular markers (F_{ST}, Edmands and Harrison, 2003). This is the opposite of patterns found in most taxa (e.g., McKay and Latta, 2002) and suggests that stabilizing or fluctuating selection is limiting adaptive differentiation among *T. californicus* populations.

It must be noted that test for local adaptation under laboratory conditions require certain caveats. The chosen environmental treatments (Standard, Low salinity and High temperature) may not adequately reflect the historical selective regimes that have driven local differentiation in natural populations. Different conditions or combinations of conditions (hypersalinity, temperature fluctuation, etc.) may expose greater population differences. Also, greater differences might be found between populations at the extreme endpoints of the species range, or from locations differing greatly in other factors such as wave exposure.

The lack of obvious local adaptation contrasts with substantial evidence for intrinsic coadaptation. Like previous studies (e.g., Burton, 1986, 1990a,b; Edmands, 1999), interpopulation hybridization caused an increase in fitness in the F_1 followed by a drop in the F_2. Application of a genetic model (Lynch, 1991) interprets this pattern as revealing two opposing types of non-additive gene action: beneficial interactions between alleles within loci (dominance) and detrimental interactions between loci (epistasis).

This genetic architecture is dependent on environmental conditions. In the most stressful treatment, High temperature, beneficial dominance effects were reduced but F_1 fitness was still significantly above the midparent. Deleterious epistatic interactions were also reduced and F_2 fitness was equivalent to the midparent, instead of substantially below as was seen in the other two treatments. While studies of the effects of environmental stress on hybrid fitness are few (reviewed in Hoffman and Parsons, 1991) the most common stress-induced pattern is an increase in heterosis (e.g., Pederson, 1968; Barlow, 1981; Armbruster et al., 1997). Explanations for this pattern include masking of inbreeding depression aggravated by stress (Hoffman and Parsons, 1991) and higher buffering capacity in heterozygotes (e.g., ‘‘developmental homeostasis’’; Lerner, 1954), which becomes more important at environmental extremes. Our results show a somewhat different pattern, with hybrid resistance to stress coming not from an increase in beneficial dominance effects but from a decrease in detrimental epistatic effects.

There has been considerable recent interest in the extent to which inbreeding effects are environmentally dependent (Pray et al., 1994; Keller et al., 2002), but much less work on how environmental conditions alter the effects of crossbreeding. Both are important to conservation biology because translocation between divergent populations is increasingly

being proposed as a means of rescuing populations suffering from inbreeding depression (Storfer, 1999; Johnson, 2000; Allendorf et al., 2001). Similarly, many stocks used for aquaculture are inbred and/or crossbred (e.g., Cruz and Ibarra, 1997; Rahman et al., 1995; Bayne et al., 1999; Utter and Epifanio, 2002). Effective management of such populations and stocks will require knowledge of non-additive gene action and its interaction with local environments.

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