

Contemporary climate change hinders hybrid performance of ecologically dominant marine invertebrates

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Abstract

Human activities alter patterns of biodiversity, particularly through species extinctions and range shifts. Two of these activities are human mediated transfer of species and contemporary climate change, and both allow previously isolated genotypes to come into contact and hybridize, potentially altering speciation rates. Hybrids have been shown to survive environmental conditions not tolerated by either parent, suggesting that, under some circumstances, hybrids may be able to expand their ranges and perform well under rapidly changing conditions. However, studies assessing how hybridization influences contemporary range shifts are scarce. We performed crosses on *Pyura herdmani* and *Pyura stolonifera* (Chordata, Tunicata), two closely related marine invertebrate species that are ecologically dominant and can hybridize. These sister species live in sympatry along the coasts of southern Africa, but one has a disjunct distribution that includes northern hemisphere sites. We experimentally assessed the performance of hybrid and parental crosses using different temperature regimes, including temperatures predicted under future climate change scenarios. We found that hybrids showed lower performance than parental crosses at the experimental temperatures, suggesting that hybrids are unlikely to expand their ranges to new environments. In turn, we found that the more widespread species performed better at a wide array of temperatures, indicating that this parental species may cope better with future conditions. This study illustrates how offspring fitness may provide key insights to predict range expansions and how contemporary climate change may mediate both the ability of hybrids to expand their ranges and the occurrence of speciation as a result of hybridization.

KEYWORDS

early life history stages, intertidal ecology, post-metamorph, pre-metamorph, *Pyura stolonifera* species complex, recruitment, settlement, thermal sensitivity

1 | INTRODUCTION

Changes in gene flow between genetically distinct populations or species are known to alter speciation rates. On the one hand,

increased gene flow can accelerate speciation through reinforcement (Abbott et al., 2013; Hoskin, Higgie, McDonald, & Moritz, 2005) or lead to the formation of novel genetic entities via hybrid speciation (Mallet, 2007). On the other hand, hybridization may slow speciation by allowing gene flow among diverging populations (Abbott et al., 2013). Consequently, hybridization can have a variety of effects

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on populations experiencing increased gene flow. Other effects of hybridization include an increase in genetic variation within populations, creating a larger pool of genotypes on which natural selection can act (Hegarty, 2012), or the purge of deleterious recessive alleles that have accumulated in parental populations (Keller & Waller, 2002). Hybridization can also be detrimental to parental populations, either directly, by leading to the extirpation of one or both parental populations via introgression (Arcella, Perry, Lodge, & Feder, 2014; Muhlfeld et al., 2014; Rhymer & Simberloff, 1996), or indirectly, by providing first-generation hybrids with phenotypic superiority over their parents (i.e., heterosis). Hybridization may also lead to the genesis of new phenotypes as a result of transgressive segregation, offering later generations a selective advantage (Lexer, Welch, Raymond, & Rieseberg, 2003). For example, studies on cichlid fish, sunflowers, copepods and water fleas have shown the generation of hybrid phenotypes with traits that are extreme compared to the parental phenotypes (Griebel et al., 2015; Pritchard, Knutson, Lee, Zieba, & Edmands, 2013; Rieseberg, 2003; Stelkens, Schmid, Selz, & Seehausen, 2009). Finally, hybridization can erode accumulated genetic differentiation when reproductive barriers are eventually removed (Taylor et al., 2006). Taken together, this evidence indicates that hybridization can have several genetic and phenotypic effects with outcomes that are difficult to predict, especially at a time when contemporary climate change (CCC) is extensively reshaping species distributions and abiotic conditions (Potts et al., 2014).

It is well established that range shifts allow previously isolated populations to come into contact and hybridize. Natural range expansions may arise due to changes in both biotic and abiotic factors (e.g., sudden removal of predators or gradual changes in temperatures) occurring over a wide range of temporal and/or spatial scales (Sexton, McIntyre, Angert, & Rice, 2009). For example, historic changes in climate led to the expansion of the European common frog, *Rana temporaria*, due to glacial retreat across Europe ca. 20,000 years ago (Vences et al., 2013). Another example of natural range expansions occurs when two habitats that were previously isolated because of a physical barrier come into contact, such as the formation of the Isthmus of Panama ca. 3×10^6 years ago, which led to the Great American Interchange (Marshall, 1988). Similarly, CCC greatly affects species distributions and often leads to range shifts. Indeed, warming winter temperatures associated with CCC has promoted a range expansion in the butterfly *Atalopedes campestris* across western North America (Crozier, 2004). In addition to major changes in abiotic factors, species interactions such as predation (Huang, Carrillo, Ding, & Siemann, 2012) and competition (van der Knaap et al., 2005) can also shape the nature of range shifts (Svenning et al., 2014). Range expansion of the Humboldt squid, *Dosidicus gigas*, in the eastern Pacific has been attributed in part to the removal of competing top predators, which prey on juvenile *D. gigas* (Zeidberg & Robison, 2007). Other types of range shifts are those associated with human activities, such as anthropogenic transport of species that has resulted in unprecedented increases in the speed and magnitude of species translocations (Carlton & Ruiz, 2015; Seebens, Schwartz, Schupp, & Blasius, 2016). Anthropogenic transport is particularly problematic in the marine environment, where shipping

provides an unparalleled transoceanic vector for the translocation of organisms from their native ranges to new locations, allowing the transport of large numbers of propagules to distant regions (Carlton & Geller, 1993). Range expansions as a result of anthropogenic transport may be exacerbated by CCC (Canning-Clode & Carlton, 2017; Chan et al., 2019; Hellmann, Byers, Bierwagen, & Dukes, 2008; Occhipinti-Ambrogi, 2007; Rius et al., 2014; Sorte, Williams, & Carlton, 2010), with rising temperatures enhancing settlement success (Raitsos et al., 2010) or causing phenological shifts that favour range shifting species (Chefaoui, Serebryakova, Engelen, Viard, & Serrão, 2019; Stachowicz, Terwin, Whitlatch, & Osman, 2002; Wolkovich & Cleland, 2011).

As CCC and human-mediated transport of species bring previously isolated genotypes into contact, unprecedented levels of hybridization have been reported in recent times (Canestrelli et al., 2017; Makino et al., 2018; Vallejo-Marín & Hiscock, 2016). As some hybrids have been reported to survive conditions that the parents cannot, hybridization is often associated with recent range expansions (Hegarty, 2012; Hovick, Campbell, Snow, & Whitney, 2012; Rius & Darling, 2014). Consequently, complex interactions among CCC, hybridization, anthropogenic transport of species and natural range shifts are potentially shaping speciation patterns. A clear example of this is the release of *Ambystoma tigrinum* (the barred tiger salamander), which was intentionally released from southern to western regions of North America (Riley, Shaffer, Voss, & Fitzpatrick, 2003), where it has now become invasive. Part of the range of *A. tigrinum* now overlaps with that of the native *Ambystoma californiense* (the California tiger salamander), allowing interspecific hybridization to occur. Experimental crosses have shown that temperature has a positive effect on juvenile salamander dispersal distances, suggesting that CCC may facilitate a rapid range expansion of the hybrid swarm and hence the spread of nonnative genotypes (Johnson, Johnson, & Shaffer, 2010).

Research to date has assessed how CCC affects the potential for hybridization, which can alter both pre-mating and post-mating reproductive barriers (Chunco, 2014). CCC has been shown to promote maladaptive hybrids, altering life-history traits in toads (*Bufo* spp.) (Canestrelli et al., 2017). Similarly, CCC can foster range shifts and increase the likelihood of hybridization in insects (Sánchez-Guillén, Muñoz, Rodríguez-Tapia, Arroyo, & Córdoba-Aguilar, 2013). In line with this, studies have shown alteration of spatiotemporal patterns of hybridization between the salmonids *Oncorhynchus clarkii lewisi* and *Oncorhynchus mykiss* (Muhlfeld et al., 2014). Despite all this research, little is known about how hybridization facilitates range expansions and how hybrids react to rapidly changing climatic conditions. Anthropogenic transport of species and CCC drive range shifts and species invasions, involving both hybrids or parental genotypes (Hegarty, 2012), potentially altering ecosystem structure and function across large geographic areas (Katsanevakis et al., 2014; Miehls et al., 2009). Thus, understanding how hybridization influences range expansions is an important aspect for predicting the effects of CCC on species distributions.

Here, we examined how conditions expected under CCC affect the performance of a range of ontogenetic stages of both hybrids and parental individuals of sympatric marine ascidian species, and

how hybridization shapes the probability of future range shifts and speciation. Our objectives were to: (a) Quantify the performance of hybrid and parental crosses; (b) Assess differences in performance at different temperatures between hybrid and parental crosses; (c) Find links between offspring performance and species distributions. We hypothesized first that hybrids would perform similarly to parental species under conditions matching the area where their species distributions overlap, and second, hypothesized that under extreme temperatures, hybrids would show different performance than parental crosses. To achieve this, we tested the effects of different temperature regimes across multiple life history stages, as each ontogenetic stage has the potential to act as a bottleneck for species persistence (Byrne, 2011). We predicted that later life history stages would be tolerant to a wider range of temperatures than earlier stages, in line with previous studies (Pineda et al., 2012).

2 | METHODS

2.1 | Study species

We selected two closely related bioengineer marine invertebrates [*Pyura herdmani* (Drasche, 1884) and *Pyura stolonifera* (Heller, 1878), Chordata, Tunicata, Ascidiacea] that coexist along extensive stretches of coastline in southern Africa (Rius et al., 2017). *Pyura herdmani* has also been described in north Africa (Monniot & Bitar, 1983; Lafargue & Wahl, 1986 - though identified in both references as *Pyura stolonifera*) and has recently been reported in southwestern Europe (X. Turon, personal communication). *Pyura* spp. are solitary ascidians that are broadcast spawners with a very short pelagic larval duration of <24 hr (Svane & Young, 1989). This, combined with its disjunct distribution, suggests that *P. herdmani* is either undergoing current, or has previously undergone historic, range expansion due to anthropogenic transport. In southern Africa, the two species inhabit the lower intertidal and subtidal zones, where they form dense aggregates (Rius & Teske, 2011). A phylogenetic study based on mitonuclear and nuclear loci revealed that *P. herdmani* consists of two presumably temperature-defined lineages in South Africa: a temperate lineage inhabiting the west and south coasts, and a tropical/subtropical lineage inhabiting the east coast (Teske et al., 2011). The temperate lineage of *P. herdmani* lives in sympatry with *P. stolonifera* (Figure 1), and thus, there is potential for hybridization in the field. Previous work has suggested that *P. herdmani* and *P. stolonifera* can hybridize in the laboratory (Rius & Teske, 2013), but no empirical data are available on how these hybrids perform compared to parental crosses or how they are affected by temperature.

2.2 | Field sampling

Individuals of *P. herdmani* and *P. stolonifera* were collected from natural hard substrata at spring low tides between September and November 2017 from Shark Rock Pier (only *P. stolonifera*; 33°59'28"S, 25°40'37"E) and Summerstrand Lighthouse (both *P. herdmani* and *P. stolonifera*;

33°58'47"S, 25°39'29"E; Figure 1) on the south coast of South Africa. Care was taken not to damage the inner body of the ascidians during collection, and to remove any damaged epibionts from the tunic as dead tissue leads to bacterial infection and causes causalities among the collected individuals (Monniot, 1990). Sampled ascidians were placed inside insulated cooler boxes filled with seawater and returned to the laboratory as soon as possible (within approximately 2 hr).

2.3 | Sea surface temperature data

We obtained daily sea surface temperature (SST) data for the study site from the JPL MUR MEaSUREs Project (2015) for the years between 2003 and 2017, at a 0.01 (latitude) × 0.01 (longitude) spatial resolution. From this, we calculated monthly and yearly average SST temperatures. All data extraction and analyses were performed in R version 3.3.1 (R Core Team, 2016).

2.4 | Laboratory housing of animals

Individuals were maintained in 50 L aquaria in a constant temperature room, with a 12-hr light/dark cycle. The aquaria were oxygenated using air pumps and seawater was replaced every other day using water from either the Swartkops River estuary or from Kenton-on-Sea (33°41'1.71"S, 26°41'8.52"E). Each day, the ascidians were fed 200 ml of either *Isochrysis galbana*, *Dunaliella primolecta* or a mixture of the two algae. The ascidians were checked daily for signs of bacterial infection and any individual showing signs of infection (identified by either the presence of a white bacterial mat growing on the tunic or a reduced response of the siphons to gentle physical stimuli) were immediately removed.

2.5 | Fertilization methods

Two individuals of each species were used for each cross (Figure 2). The tunics of all individuals were first removed, revealing the inner soft body. The dorsal tubercle was used to confirm the identity of each species (Rius & Teske, 2011). The strip-spawning method of Marshall, Styan, and Keough (2000) was followed to dissect out gametes. The mixture of sperm and ova was poured through a 160 µm mesh filter so the ova were retained on the mesh but the sperm were allowed to wash through to another Petri dish. The ova were then washed off the mesh using 15 ml filtered seawater (FSW) into a final Petri dish. This process was then repeated for the remaining individuals. Filtered seawater was obtained using a vacuum pump to filter the seawater collected from the field through a 0.7 µm filter. In all crosses, sperm concentration was kept as high as possible to limit the effect of sperm ageing (Marshall et al., 2000) and the time between gamete extraction and gamete mixing was kept to a minimum. The ova of each individual were then aliquoted into two Petri dishes, with the ova in one dish receiving conspecific sperm and the ova in the second dish receiving interspecific sperm

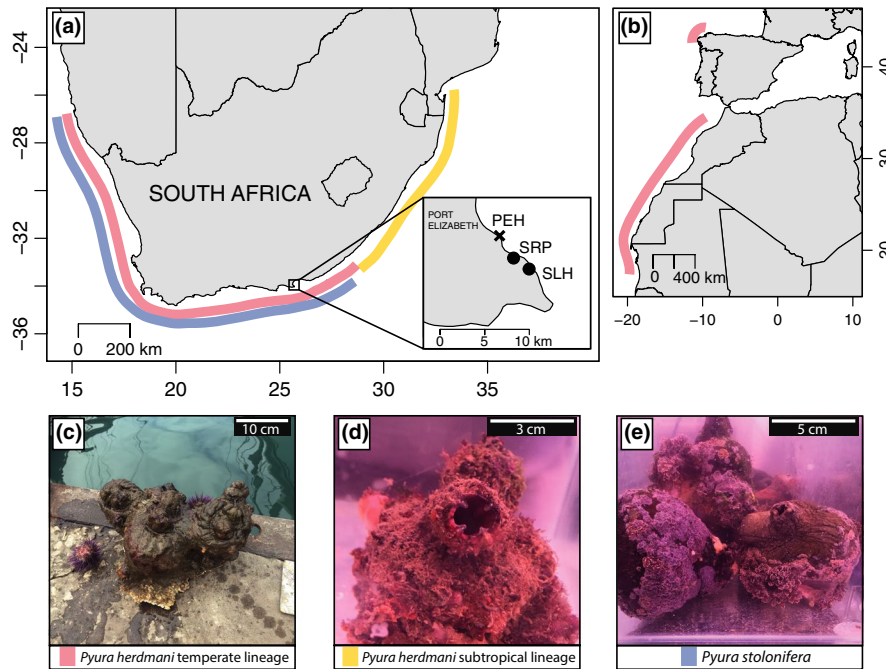


FIGURE 1 (a) The distribution of two *Pyura herdmani* lineages and *Pyura stolonifera* along the coasts of southern Africa, based on Teske et al. (2011) and Rius and Teske (2011). The two sample sites used for this study were SRP (Shark Rock Pier) and SLH (Summerstrand Lighthouse) on the south coast of South Africa. (b) *Pyura herdmani* has spread its range to include northwest Africa and southwest Europe (see details in main text). (c) Three *P. herdmani* temperate lineage individuals collected in Port Elizabeth harbour (PEH). (d) One *P. herdmani* subtropical lineage individual collected in Park Rynie (north east coast of South Africa) and housed in an aquarium at Rhodes University. (e) Three *P. stolonifera* individuals collected at SRP in an aquarium at Rhodes University

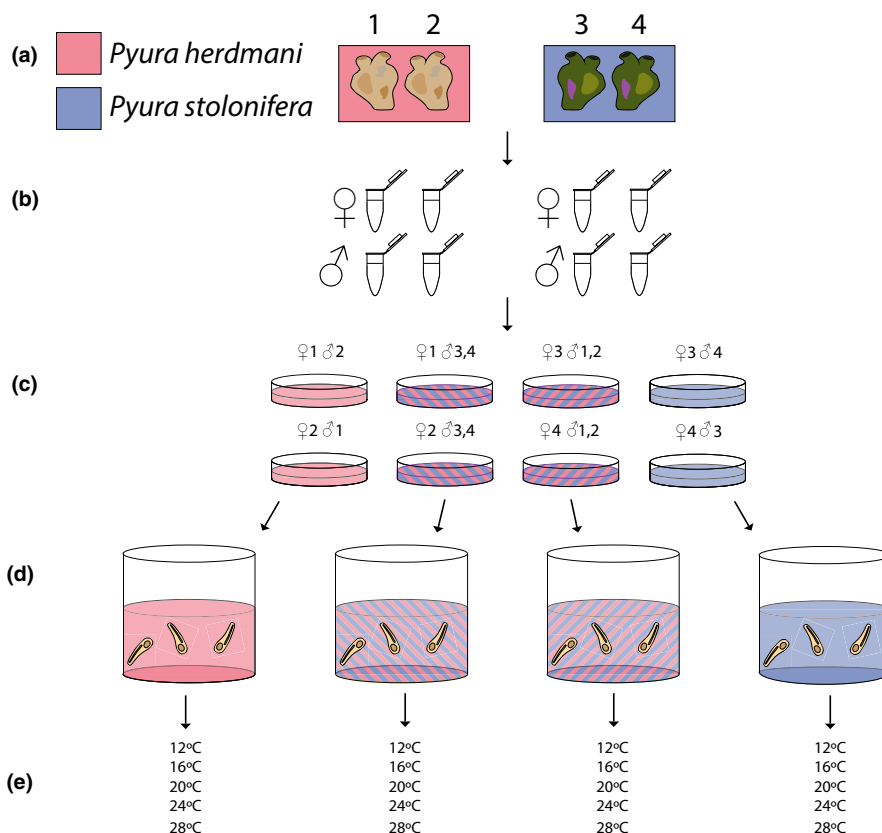


FIGURE 2 Experimental design used to test the effects of temperature on inter/intraspecific crosses. (a) Two individuals of species were used per cross. (b) Surgical collection of sperm (♂) and eggs (♀). (c) Eggs from each individual were outcrossed with sperm from either one (control cross- same species) or two (hybrid cross- different species) individuals in 5 ml of filtered seawater. The symbols above each dish represent the source individual for eggs (♀) and sperm (♂) in each dish. (d) Fertilized eggs from each dish from (c) were washed and grouped into 500 ml beakers of filtered seawater and incubated at 20°C in darkness to hatch. (e) Hatched larvae were pipetted into Petri dishes and designated a control environment room (either 12, 16, 20, 24 or 28°C), where they were assessed after 24, 72 and 120 hr. Twenty larvae were pipetted into each Petri dish, and the number of Petri dishes at each temperature for each cross is shown in Table S1

(Figure 2). A total volume of 1 ml of sperm (either from one individual for control crosses, or multiple individuals for hybrid crosses) was added to each Petri dish with ova. The sperm and eggs were kept at 20°C to allow fertilization to occur as this temperature has previously been shown to promote successful egg development in both parental species (Rius et al., 2014). Once egg cleavage was observed, one more round of filtering ensured excess sperm would be washed away, reducing the probability of polyspermy. Fertilized eggs were then grouped by cross and kept in 500 ml of aerated FSW in total darkness at 20°C (Figure 2).

Once motile larvae had hatched (after c. 12 hr), 20 randomly selected larvae from each cross were transferred into one of five pre-roughened Petri dishes with 15 ml FSW (Figure 2). The Petri dishes had been left in unfiltered seawater for a few days to promote the formation of a biofilm, which is known to facilitate larval settlement (Wieczorek & Todd, 1997). Each of the five Petri dishes was then randomly allocated to one of five temperature-controlled rooms set at 12, 16, 20, 24 or 28°C (Figure 2). Due to different numbers of hatched larvae in the various crosses, the number of replicates for testing settlement success and post-metamorph performance at each temperature varied, ranging from four to eight (Table S1).

After 24, 72 and 120 hr, the larvae in each temperature-controlled room were examined under a microscope and the stage of development of each individual was noted. These stages of development comprised floating tadpole larvae, attached tadpole larvae, attached settlers, nonattached settlers, settlers with obvious tail reabsorption, pre-metamorphs and post-metamorphs (Figure S1). As the duration of metamorphosis determines the length of time individuals are exposed to sources of mortality however (O'Connor et al., 2007), it was assumed that if individuals had not reached the post-metamorph stage within 120 hr in the laboratory, they would be unlikely to survive in the field due to the pressures of smothering and predation. Therefore, the percentage of post-metamorphs at 120 hr was used as a proxy for species performance under the different temperature treatments.

2.6 | Data analysis and statistics

Due to the proportional nature of our datasets, we analysed the data using generalized linear models (GLM) with a binomial error distribution and a logit link function. We tested for overdispersion in our data and where present we included a random factor (individual Petri dish) using the *glmer* package (Bates, Mächler, Bolker, & Walker, 2015). In order to determine whether there were any interactive effects of temperature and cross on development or not, we first investigated the effect of cross under in situ temperatures (i.e., 20°C, Figure S2), and then, assessed pre-metamorph and post-metamorph performance at 120 hr. As performance values were zero at certain temperatures, we removed 28°C from the pre-metamorph analysis at 120 hr, and similarly removed 12 and 28°C from the post-metamorph

TABLE 1 Results of generalized linear models with a binomial error distribution and a logit link function testing the effects of cross, at 20°C, on the proportion of (A) settlers after 24 hr, (B) pre-metamorphs after 72 hr, (C) post-metamorphs after 72 hr, (D) pre-metamorphs after 120 hr and (E) post-metamorphs after 120 hr

Source	Chi-square	df	p Value
(A) Proportion of settlers at 24 hr			
Cross	19.481	3	<.001
(B) Proportion of pre-metamorphs at 72 hr			
Cross	5.540	3	.063
(C) Proportion of post-metamorphs at 72 hr			
Cross	2.663	3	.264
(D) Proportion of pre-metamorphs at 120 hr			
Cross	0.348	3	.951
(E) Proportion of post-metamorphs at 120 hr			
Cross	9.857	3	.020

Note: Boldface type indicates a significant result.

analysis at 120 hr. Post hoc Tukey tests were used to determine the pairwise comparisons that drove significant differences. Repeated-measured analyses could not be performed as offspring performance through time was measured at the level of the Petri dish rather than the individual. All statistical analyses were performed in R (R Core Team, 2016).

3 | RESULTS

3.1 | Temperature results

Sea surface temperature records indicate that the average SST for Port Elizabeth waters was 19.23°C ± 0.13°C (SE) between 2003 and 2017, with average summer and winter fluctuating around 22 and 17°C, respectively (Figure S2).

3.2 | Development at in situ temperature

All reciprocal crosses at 20°C produced well-developed motile larvae (see Figure S1), with hatching occurring ~12 hr after fertilization. There were significant differences in settlement success (Table 1) between crosses under in situ temperatures (i.e., 20°C), with control *P. stolonifera* crosses being more successful than control *P. herdmani* ($p < .05$, Tukey HSD test; Table 1, Figure 3a). However, there was no significant difference in pre-metamorph success after 72 or 120 hr or in post-metamorph success after 72 hr (Table 1B–D). Despite this, we found that after 120 hr there was a significant difference between the proportion of larvae that developed into post-metamorphs from control *P. stolonifera* crosses and control *P. herdmani* crosses ($p < .05$, Tukey HSD test; Table 1E, Figure 3e).

3.3 | Development at experimental treatment temperatures

Pre-metamorphs developed under a wide range of temperatures for all crosses, only failing to develop after 120 hr at 28°C (all crosses), 12°C (hybrids crosses only) and 16°C (hybrid cross with eggs from *P. stolonifera* only; Figures 4 and 5). Post-metamorphs developed in all crosses after 120 hr, with this development only apparent at 16, 20 and 24°C.

3.4 | Effects of temperature and cross on pre-metamorphic development

There was no significant interaction between the effects of temperature and cross on pre-metamorph development after 120 hr (chi-square = 8.429, $df = 6$, $p = .208$; Table 2A), but there were significant effects of both temperature and cross individually on pre-metamorph development (temperature: chi-square = 17.433, $df = 3$, $p < .001$; cross: chi-square = 8.368, $df = 3$, $p < .05$). The percentages of control *P. herdmani* and control *P. stolonifera* pre-metamorphs after 120 hr were similar at each temperature treatment except for 24°C (Tukey post hoc test, $p < .05$, Figure 5). For all crosses, the lowest percentage of pre-metamorphs developed at 12°C (except 28°C, where no pre-metamorphs developed for any cross).

3.5 | Effects of temperature and cross on post-metamorphic development

There was a low percentage of post-metamorphs at all temperatures (mean < 30%). In contrast to pre-metamorphs, there was a statistically significant interaction between the effects of temperature and cross on post-metamorphic development after 120 hr (chi-square = 13.384, $df = 4$, $p \leq .01$; Table 2B). The highest percentage of post-metamorphs for control *P. herdmani* crosses was found at 24°C, whereas for control *P. stolonifera* this was found at 20°C (Figure 6). Interestingly, maximum values for hybrid post-metamorphs were recorded at 20°C and were intermediate between the values for the two control crosses at that temperature (Figure 6). Although some post hoc comparisons were unable to detect significant differences (Figure 6), the overall pattern showed no survival of the post-metamorph stage at the lowest and highest temperatures, with limited differences among crosses at intermediate temperatures.

4 | DISCUSSION

Our results showed that ontogenetic stages of hybrids survived a narrower range of temperatures than either parental species, suggesting that hybrids are unlikely to both expand their ranges to dissimilar environments and perform better under future conditions.

We also found that the more widespread parental species performed better at higher temperatures. Thus, our results indicate that the more tolerant parental species (*P. herdmani*) may perform better under warming conditions. Finally, our study provides insights into how CCC may inhibit both the ability of hybrids to expand their ranges and the occurrence of speciation due to hybridization.

We confirmed that reciprocal fertilization between *P. herdmani* and *P. stolonifera* produces viable offspring that can develop to the post-metamorph stage. We hypothesized that hybrids would perform differently than parental species at extreme temperatures (e.g., Welch & Rieseberg, 2002) and found that neither hybrid cross showed broader temperature tolerances than the parental crosses. In southern Africa, evidence of hybridization between *P. herdmani* and *P. stolonifera* had, until now, been anecdotal (Rius & Teske, 2013). Our study confirms that fertilization can occur between these species and provides empirical evidence of the relative success of hybrids in a laboratory setting. However, future studies are needed to study the fertility of these hybrids and their viability in the field. Even though the study species live in sympatry (Figure 1), whether hybrids occur naturally remains unclear. *Pyura stolonifera* is common along rocky shores with high wave-exposure, whereas *P. herdmani* often inhabits more sheltered regions (Rius & Teske, 2011). Consequently, opportunities for hybridization at locations, where both species are found may be fewer than initially expected. Mosaic-style hybrid zones have been reported along the European Atlantic coast, where salinity, wave exposure and tidal height explain the spatial distribution of alleles within the hybrid zones of the mussels *Mytilus edulis* and *Mytilus galloprovincialis* (Gardner, 1994). Niche segregation may, therefore, contribute to a low prevalence of hybrids, minimising or even preventing gene flow between species. Gene flow can also be reduced by spawning asynchrony, something that could occur among individuals separated by as little as 10s of metres (Marshall, 2002).

Hybrids performed generally well but in a narrower range of temperatures than either parent species. Considering the direction of predicted global SST changes, it appears unlikely that hybrids of *P. herdmani* and *P. stolonifera* will expand their range to locations with novel environmental conditions. While hybridization has been suggested to contribute to range shifts (Chown et al., 2015; Pfennig, Kelly, & Pierce, 2016), especially considering expected CCC conditions (Chunco, 2014), our results suggest that this pattern may not be as general as previously reported, as many failed hybridization events occur in the field and remain unreported.

Irrespective of parental source, all crosses showed a wider range of thermal tolerance at the pre-metamorph stage than the post-metamorph stage (Figures 4–6). This contrasts other studies using ascidians that found that later life history stages are less sensitive to environmental stress than earlier ones (Pineda et al., 2012), but is in line with studies showing that ontogenetic stages of copepods and gastropods are more tolerant to heat stress than later developmental stages (Diederich & Pechenik, 2013; Tangwancharoen & Burton, 2014). A possible explanation to this pattern is that early developmental stages of intertidal organisms experience a high variability of conditions and

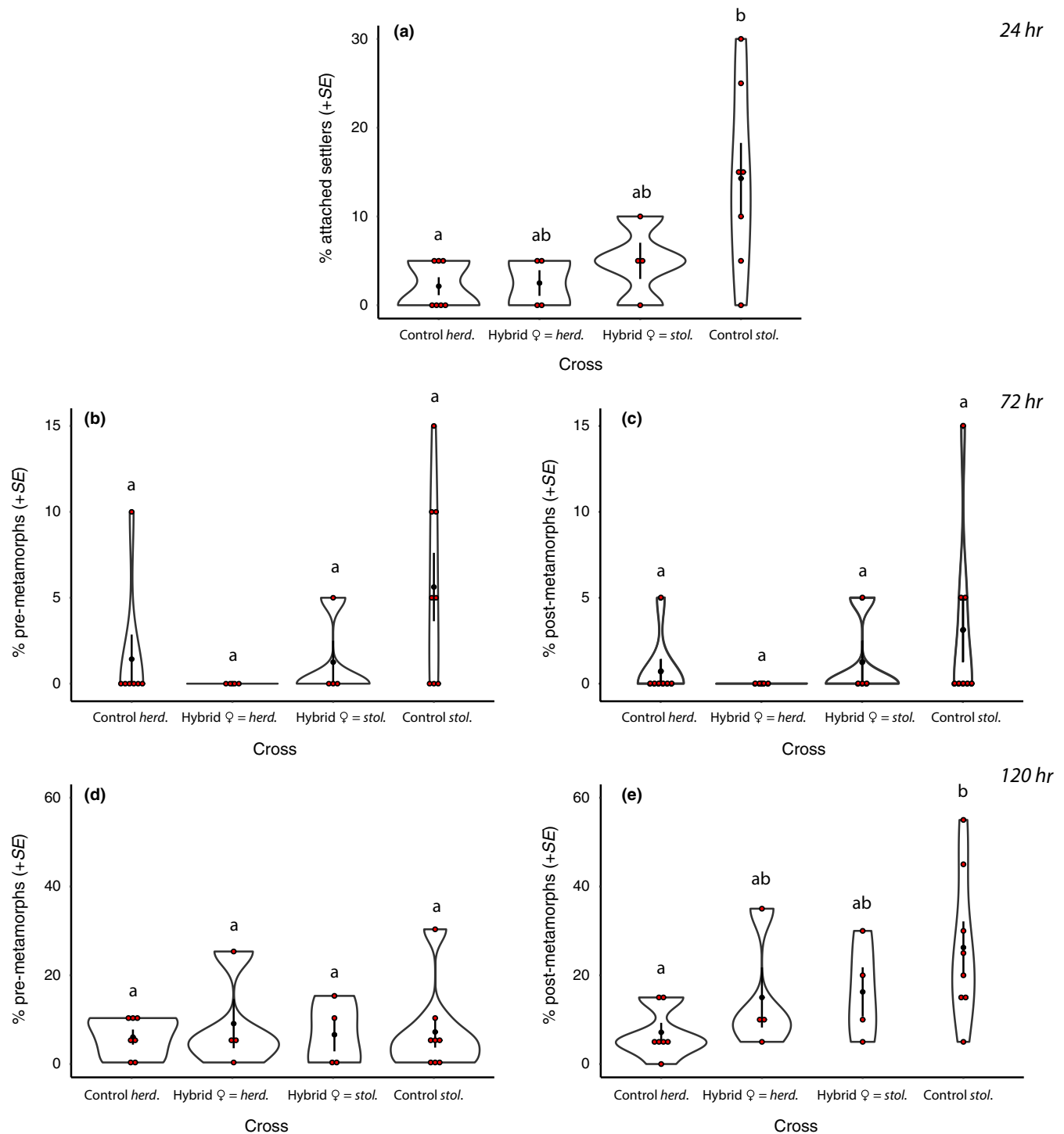


FIGURE 3 Violin plots depicting the development of control and hybrid crosses at 20°C. Percentage of (a) settlers after 24 hr, (b) pre-metamorphs after 72 hr, (c) post-metamorphs after 72 hr, (d) pre-metamorphs after 120 hr and (e) post-metamorphs after 120 hr. Percentage values are means, error bars denote standard error (SE). Dots represent raw data points. Letters indicate homogenous groups identified by post hoc Tukey tests

selection favours larvae with high thermal tolerance (Tangwacharoen & Burton, 2014). Both *P. herdmani* and *P. stolonifera* can be found in the low intertidal, where ontogenetic stages have to survive highly variable temperatures, whereas previous studies of ascidians have focussed on subtidal species (Pineda et al., 2012) that experience more stable conditions than in the intertidal zone.

While hybrid crosses did not outperform both parental crosses at any temperature (Figures 5 and 6), the percentage of post-metamorph hybrids at the temperature treatment matching in situ conditions at our sampling sites (i.e., 20°C, approximate yearly mean SST of sample sites, Figure S2) was intermediate to values for the parental crosses at this temperature (Figure 6). This is in line with previous

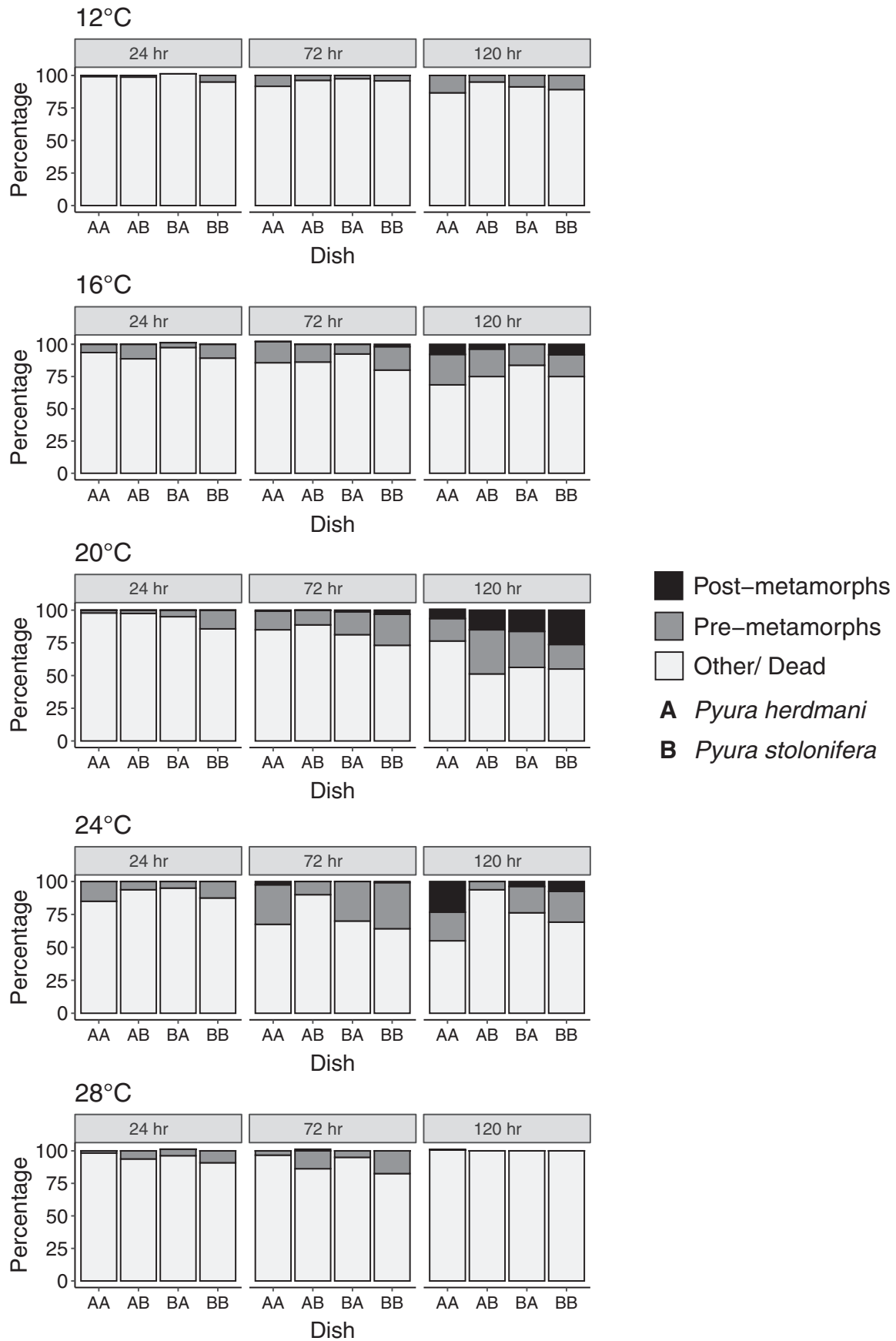
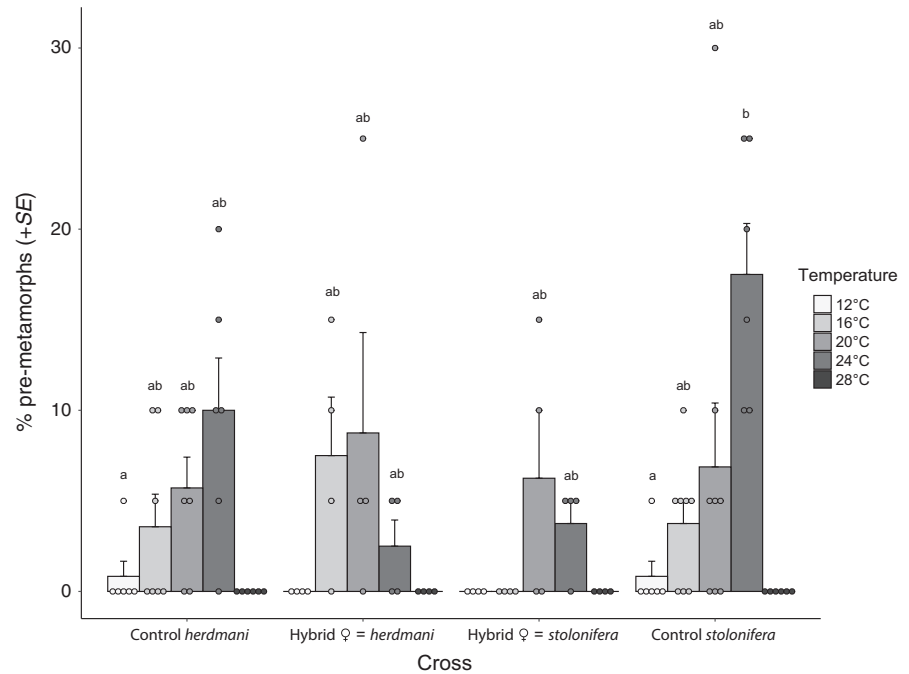


FIGURE 4 Stacked bar plots showing the percentage of post-metamorphs, pre-metamorphs and other/dead stages of larvae at different times across temperature treatments. First letter of cross abbreviation represents mother species and second letter represents father species

FIGURE 5 Effects of temperature on the pre-metamorph development after 120 hr of control and hybrid crosses. Percentage values are means, error bars denote standard error (SE). Letters indicate homogenous groups identified by post hoc Tukey tests



studies that have reported hybrids possessing similar fitness to parent species (Arnold & Hodges, 1995). This suggests that while temperature does not preclude the ability of hybrids and parental species to live in an area of sympatry, hybrids are unlikely to spread to locations with an environmental (temperature) mismatch. There are two caveats to our findings. First, we inferred in situ temperature using satellite data rather than field measurements. In situ field measurements of temperature are clearly the best way to assess the effect of temperature in the intertidal zone. However, when field and satellite SST data have been compared in the study area, studies have found an almost complete matching [see figure 4 in Smit et al. (2013)]. A second caveat is that we only used 20°C to perform fertilization, and thus, poor performance in some treatments could be a result of thermal shock from fertilization to when the petri dishes were placed at the different temperature treatments. Performing the crosses at a range of temperatures would have tackled this and

allowed testing the effects of temperature from fertilization to subsequent development stages.

The ability of species to develop successfully under conditions dissimilar to their native environment suggests the potential for future range expansions (Rius et al., 2014; Sorte et al., 2010). Although some of the differences among crosses were not significant, the highest survival of post-metamorphs at 24°C were from *P. herdmani* control crosses. Interestingly, the areas to which *P. herdmani* has supposedly expanded to (northern Africa and southern Europe) exhibit temperatures that are either similar to or cooler than those in Port Elizabeth. It has been suggested that the current disjunct range of *P. herdmani* is a relic of a historical Gondwanan distribution (Kott, 1985, 2006), but another possibility is that this distribution is due to a combination of modern anthropogenic transport and an ancient long-distance dispersal event (Rius et al., 2017; Teske et al., 2011). Given the close geographical proximity between a possible Moroccan source and the recent southern European population and the fact that our results indicate that *P. herdmani* can survive at lower temperatures, it seems likely that these regions are in gene flow contact. As seen in *P. herdmani*, the ability of *P. stolonifera* to develop to the post-metamorph stage successfully at 16, 20 and 24°C implies a wide range of temperature tolerance. Indeed, *P. stolonifera* has been recorded along an extensive stretch of the southern Africa coastline (Monniot, Monniot, Griffiths, & Schleyer, 2001), encompassing a wide range of temperature conditions (Rius et al., 2014).

Anthropogenically induced CCC is causing major alterations in the marine environment at an unprecedented rate. Mean global SST has increased at 0.07°C per decade since 1960 and at 0.11 ± 0.02°C per decade since the 1970s (Burrows et al., 2011). This upwards trend is predicted to continue, with mean global SST projected to increase by up to 2°C by 2060 (Kirtman et al., 2013). Despite this global trend of SST warming, there is increasing evidence that SST values

TABLE 2 Results of generalized linear models with binomial error distributions and a logit link function testing the effects of temperature and cross on the proportion of (A) pre-metamorphs and (B) post-metamorphs

Source	Chi-square	df	p value
(A) Proportion of pre-metamorphs			
Temp	17.433	3	<.001
Cross	8.368	3	.039
Temp × Cross	8.429	6	.208
(B) Proportion of post-metamorphs			
Temp	4.130	2	.127
Cross	4.699	3	.195
Temp × Cross	13.384	4	.010

Note: Boldface type indicates a significant result.

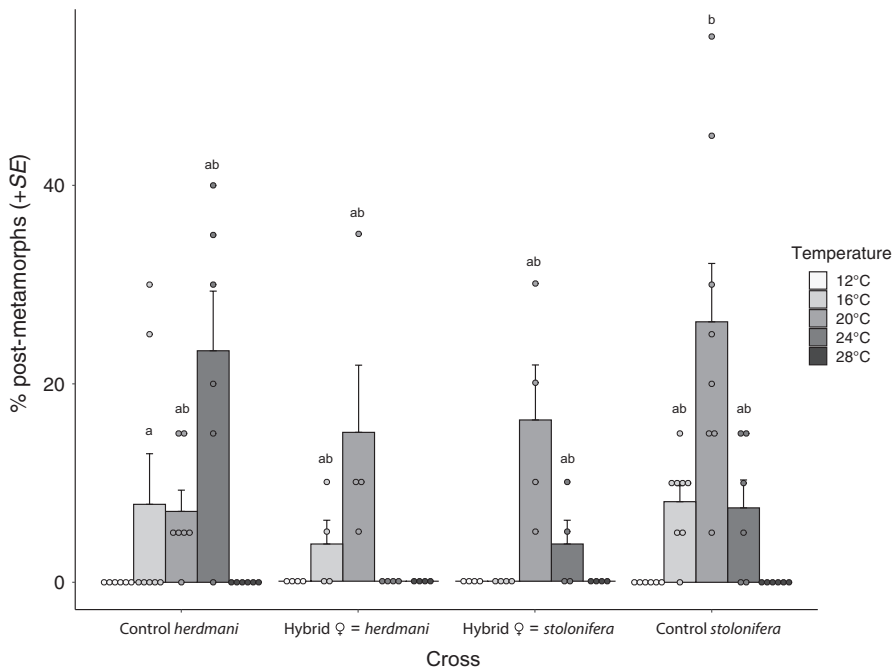


FIGURE 6 Effect of temperature on the development of different control and hybrid crosses on post-metamorphic development after 120 hr. Error bars denote standard error (SE). Letters indicate homogenous groups identified by post hoc Tukey tests. Note absence of post-metamorphs at 12 and 28°C.

are becoming more extreme in certain regions (Taboada & Anadón, 2012). Between 1960 and 2010, coastal waters around South Africa exhibited both warming and cooling of SST (Rius et al., 2014). The SST of our study area, the Port Elizabeth region, cooled between 1982 and 2009, with especially strong cooling during austral winter months, while farther east, the coast experienced strong warming of SST over the same period (Rouault, Pohl, & Penven, 2010). The sampled region of this study is ~300 km away from the documented eastern-most limit of the temperate lineage and the western limit of the subtropical lineage of *P. herdmani* (Teske et al., 2011). If the subtropical lineage had expanded southwards since the collection of the samples analysed in Teske et al. (2011), either naturally or through human-mediated transport, then, it means that this lineage is now present in Port Elizabeth. As a result, the possibility exist that subtropical individuals were collected and crosses, which may explain the highest success of *P. herdmani* post-metamorphs at 24°C.

Previous studies on marine invertebrates inhabiting the south-east coast of Africa have suggested the presence of a biogeographic break reflecting oceanographic conditions and dispersal rather than physiological tolerance (Teske et al., 2008; Zardi, Nicastro, McQuaid, Hancke, & Helmuth, 2011). For example, the invasive mussel *M. galloprovincialis* is prevented from further spread towards the east of the South African coastline by a steep transition between cool-temperate and subtropical waters along the south-eastern coast (Assis et al., 2015). Therefore, it appears unlikely that either lineage of *P. herdmani* could have spread across this biogeographic break naturally. Nevertheless, our results suggest that divergence between these divergent lineages is driven by prezygotic barriers (e.g., oceanography and dispersal) rather than thermal tolerance. It is likely that the dispersal of *P. stolonifera* to the east is similarly limited, despite the ability of its larvae to develop at the higher temperatures exhibited there (Figures 5 and 6). Extreme temperature treatments (12

and 28°C) precluded post-metamorph development in all crosses, indicating that these temperatures are outside the thermal thresholds of both species and all hybrids and that the species' ranges are unlikely to expand to cooler temperate or tropical regions (or at least regions where these temperatures coincide with spawning periods). Two points temper this interpretation. First, we sampled animals from a single area, and thus, we did not consider that individual responses may vary throughout a species range (Neuheimer, Thresher, Lyle, & Semmens, 2011), and second, future temperature change is likely to be gradual, raising the possibility of rapid adaptation helping to cope with CCC in both species.

Early ontogenetic stages are often particularly sensitive in marine invertebrates (Pineda et al., 2012; Verween, Vincx, & Degraer, 2007), and consideration of multiple life-history stages is key when exploring thermal tolerances, as these can vary considerably across the life-cycle (Rius, Turon, Dias, & Marshall, 2010). Changing SST will render some previously inhospitable environments habitable (Poloczanska et al., 2016), and this could occur in our study system. Mass mortalities of *P. stolonifera* have occurred along the southern coast of Africa in both 1991 (Hanekom, Harris, Branch, & Allen, 1999) and 2012 (Hanekom, 2013) and have been attributed to rapidly changing air and sea temperatures. The coastline where these mass mortalities took place is within the area of sympatry for *P. herdmani* and *P. stolonifera* (Figure 1). It is unknown whether the species identified as *P. stolonifera* in Hanekom et al. (1999) and Hanekom (2013) were *P. stolonifera*, *P. herdmani* or hybrids. If only *P. stolonifera* is affected by these mortalities, there may be the potential for *P. herdmani* or hybrids to quickly occupy new available substratum (Rius et al., 2017). Rates of change in SST are not consistent throughout the year in southern Africa (Rouault et al., 2010), and fluctuations in maximum and minimum SST in the study region have become more extreme in recent years

(Rius et al., 2014). Therefore, while fluctuating climatic conditions may not promote the expansion of hybrids to novel locations per se, the opening of an ecological niche may ultimately affect community composition (Sagarin, Barry, Gilman & Baxter 1999).

To conclude, we found that: (a) In situ temperature conditions did not preclude hybridization between *P. herdmani* and *P. stolonifera* and subsequent development from larvae to the post-metamorph stage; (b) Hybridization did not enhance survival under a wider range of temperatures; (c) Changes in SST as a result of CCC may enhance range expansions of the parental species but not the hybrids. Our results indicate that offspring performance at a variety of temperatures may be a good predictor of range expansions, and that ongoing CCC may inhibit, rather than promote range expansions by hybrids.

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AUTHOR CONTRIBUTIONS

M.R. conceived the study; J.H., C.D.M., M.R., designed the study; J.H. collected data; J.H., M.R. analysed data; J.H., C.D.M., M.R. wrote the manuscript.

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REFERENCES

- Abbott, R., Albach, D., Ansell, S., Arntzen, J. W., Baird, S. J. E., Bierne, N., ... Zinner, D. (2013). Hybridization and speciation. *Journal of Evolutionary Biology*, 26, 229–246.
- Arcella, T. E., Perry, W. L., Lodge, D. M., & Feder, J. L. (2014). The role of hybridization in a species invasion and extirpation of resident fauna: Hybrid vigor and breakdown in the rusty crayfish, *Orconectes rusticus*. *Journal of Crustacean Biology*, 34, 157–164.
- Arnold, M. L., & Hodges, S. A. (1995). Are natural hybrids fit or unfit relative to their parents. *Trends in Ecology & Evolution*, 10, 67–71.
- Assis, J., Zupan, M., Nicastro, K. R., Zardi, G. I., McQuaid, C. D., & Serrão, E. A. (2015). Oceanographic conditions limit the spread of a marine invader along southern African shores. *PLoS ONE*, 10, e0128124.
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48.
- Burrows, M. T., Schoeman, D. S., Buckley, L. B., Moore, P., Poloczanska, E. S., Brander, K. M., ... Richardson, A. J. (2011). The pace of shifting climate in marine and terrestrial ecosystems. *Science*, 334, 652–655.
- Byrne, M. (2011). Impact of ocean warming and ocean acidification on marine invertebrate life history stages: Vulnerabilities and potential for persistence in a changing ocean. *Oceanography and Marine Biology: An Annual Review*, 49, 1–42.
- Canestrelli, D., Bisconti, R., Chiochio, A., Maiorano, L., Zampiglia, M., & Nascetti, G. (2017). Climate change promotes hybridisation between deeply divergent species. *PeerJ*, 5, e3072.
- Canning-Clode, J., & Carlton, J. T. (2017). Refining and expanding global climate change scenarios in the sea: Poleward creep complexities, range termini, and setbacks and surges. *Diversity and Distributions*, 23, 463–473.
- Carlton, J. T., & Geller, J. B. (1993). Ecological roulette: The global transport of nonindigenous marine organisms. *Science*, 261, 78–82.
- Carlton, J. T., & Ruiz, G. M. (2015). Anthropogenic vectors of marine and estuarine invasions: An overview framework. In J. Canning-Clode (Ed.), *Biology invasions in changing ecosystems: Vectors, ecological impacts, management and predictions* (pp. 1–36). Berlin, Germany: De Gruyter Open Ltd.
- Chan, F. T., Stanislawczyk, K., Sneekes, A. C., Dvoretzky, A., Gollasch, S., Minchin, D., ... Bailey, S. A. (2019). Climate change opens new frontiers for marine species in the Arctic: Current trends and future invasion risks. *Global Change Biology*, 25, 25–38.
- Chefaoui, R. M., Serebryakova, A., Engelen, A. H., Viard, F., & Serrão, E. A. (2019). Integrating reproductive phenology in ecological niche models changed the predicted future ranges of a marine invader. *Diversity and Distributions*, 25, 688–700.
- Chown, S. L., Hodgins, K. A., Griffin, P. C., Oakeshott, J. G., Byrne, M., & Hoffmann, A. A. (2015). Biological invasions, climate change and genomics. *Evolutionary Applications*, 8, 23–46.
- Chunco, A. J. (2014). Hybridization in a warmer world. *Ecology and Evolution*, 4, 2019–2031.
- Crozier, L. (2004). Warmer winters drive butterfly range expansion by increasing survivorship. *Ecology*, 85, 231–241.
- Diederich, C. M., & Pechenik, J. A. (2013). Thermal tolerance of *Crepidula fornicata* (Gastropoda) life history stages from intertidal and subtidal subpopulations. *Marine Ecology Progress Series*, 486, 173–187.
- Gardner, J. P. A. (1994). The structure and dynamics of naturally-occurring hybrid *Mytilus edulis* Linnaeus, 1758 and *Mytilus galloprovincialis* Lamarck, 1819 (Bivalvia, Mollusca) populations- Review and interpretation. *Archiv Für Hydrobiologie*, 99, 37–71.
- Griebel, J., Giebler, S., Poxleitner, M., Faria, A. N., Yin, M., & Wolinska, J. (2015). Extreme environments facilitate hybrid superiority – The story of a successful *Daphnia galeata* × *longispina* hybrid clone. *PLoS ONE*, 10, e0140275.
- Hanekom, N. (2013). Environmental conditions during mass mortalities of the ascidian *Pyura stolonifera* (Heller) in the Tsitsikamma Marine Protected area. *African Zoology*, 48, 167–172.
- Hanekom, N., Harris, J. M., Branch, G. M., & Allen, J. C. (1999). Mass mortality and recolonization of *Pyura stolonifera* (Heller) on the south coast of South Africa. *South African Journal of Marine Science*, 21, 117–133.
- Hegarty, M. J. (2012). Invasion of the hybrids. *Molecular Ecology*, 21, 4669–4671.
- Hellmann, J. J., Byers, J. E., Bierwagen, B. G., & Dukes, J. S. (2008). Five potential consequences of climate change for invasive species. *Conservation Biology*, 22, 534–543.
- Hoskin, C. J., Higgie, M., McDonald, K. R., & Moritz, C. (2005). Reinforcement drives rapid allopatric speciation. *Nature*, 437, 1353–1356.

- Hovick, S. M., Campbell, L. G., Snow, A. A., & Whitney, K. D. (2012). Hybridization alters early life-history traits and increases plant colonization success in a novel region. *The American Naturalist*, 179, 192–203.
- Huang, W., Carrillo, J., Ding, J., & Siemann, E. (2012). Interactive effects of herbivory and competition intensity determine invasive plant performance. *Oecologia*, 170, 373–382.
- Johnson, J. R., Johnson, B. B., & Shaffer, H. B. (2010). Genotype and temperature affect locomotor performance in a tiger salamander hybrid swarm. *Functional Ecology*, 24, 1073–1080.
- JPL Mur MEaSUREs Project (2015). *JPL MUR MEaSUREs Project, GHRSSST Level 4 MUR Global Foundation Sea Surface Temperature Analysis*. Pasadena, CA: PO.DAAC.
- Katsanevakis, S., Wallentinus, I., Zenetos, A., Leppäkoski, E., Çınar, M. E., Öztürk, B., ... Cardoso, A. C. (2014). Impacts of invasive alien marine species on ecosystem services and biodiversity: A pan-European review. *Aquatic Invasions*, 9, 391–423.
- Keller, L. F., & Waller, D. M. (2002). Inbreeding effects in wild populations. *Trends in Ecology & Evolution*, 17, 230–241.
- Kirtman, B., Power, S. B., Adedoyin, A. J., Boer, G. J., Bojariu, R., Camilloni, I., ... Wang, H. J. 2013. Near-term climate change: Projections and predictability. In T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, & J. Boschung et al. (Eds). *Climate Change 2012: The physical science basis. Contribution of working group I to the fifth assessment report of the Intergovernmental Panel on Climate Change*. Cambridge, UK and New York, NY: Cambridge University Press.
- Kott, P. (1985). The Australian Ascidiacea. Part 1, Phlebobranchia and Stolidobranchia. *Memoirs of the Queensland Museum*, 23, 1–439.
- Kott, P. (2006). Observations on non-didemnid ascidians from Australian waters. *Journal of Natural History*, 40, 169–234.
- Lafargue, F., & Wahl, M. (1986). Contribution to the knowledge of littoral ascidians (Ascidiacea, Tunicata) of the Senegalese coast. *Bulletin de l'Institut Fondamental d'Afrique Noire Cheikh Anta Diop: Série A, Sciences de la vie, sciences de la terre*, 46, 385–402.
- Lexer, C., Welch, M. E., Raymond, O., & Rieseberg, L. H. (2003). The origin of ecological divergence in *Helianthus paradoxus* (Asteraceae): Selection on transgressive characters in a novel hybrid habitat. *Evolution*, 57, 1989–2000.
- Makino, W., Miura, O., Kaiser, F., Geffray, M., Katsube, T., & Urabe, J. (2018). Evidence of multiple introductions and genetic admixture of the Asian brush-clawed shore crab *Hemigrapsus takanoi* (Decapoda: Brachyura: Varunidae) along the northern European coast. *Biological Invasions*, 20, 825–842.
- Mallet, J. (2007). Hybrid speciation. *Nature*, 446, 279–283.
- Marshall, D. J. (2002). *In situ* measures of spawning synchrony and fertilization success in an intertidal, free-spawning invertebrate. *Marine Ecology Progress Series*, 236, 113–119.
- Marshall, D. J., Styan, C. A., & Keough, M. J. (2000). Intraspecific co-variation between egg and body size affects fertilisation kinetics of free-spawning marine invertebrates. *Marine Ecology Progress Series*, 195, 305–309.
- Marshall, L. G. (1988). Land mammals and the Great American Interchange. *American Scientist*, 76, 380–388.
- Miehls, A. L. J., Mason, D. M., Frank, K. A., Krause, A. E., Peacor, S. D., & Taylor, W. W. (2009). Invasive species impacts on ecosystem structure and function: A comparison of the Bay of Quinte, Canada, and Oneida Lake, USA, before and after zebra mussel invasion. *Ecological Modelling*, 220, 3182–3193.
- Monniot, C. (1990). Diseases of Urochordata. In O. Kinne (Ed.), *Diseases of marine animals* (pp. 569–636). Biologische Anstalt Helgoland: Hamburg.
- Monniot, C., & Bitar, G. (1983). Sur la présence de *Pyura stolonifera* (Tunicata, Ascidiacea) à Ras Achaccar (côte nord atlantique marocaine). Comparaison anatomique distinctive avec *Pyura praeputialis*. *Bulletin de l'Institut Scientifique Rabat*, 7, 83–91.
- Monniot, C., Monniot, F., Griffiths, C. L., & Schleyer, M. (2001). South African ascidians. *Annals of the South African Museum*, 108, 1–141.
- Muhlfeld, C. C., Kovach, R. P., Jones, L. A., Al-Chokhachy, R., Boyer, M. C., Leary, R. F., ... Allendorf, F. W. (2014). Invasive hybridization in a threatened species is accelerated by climate change. *Nature Climate Change*, 4, 620–624.
- Neuheimer, A. B., Thresher, R. E., Lyle, J. M., & Semmens, J. M. (2011). Tolerance limit for fish growth exceeded by warming waters. *Nature Climate Change*, 1, 110–113.
- O'Connor, M. I., Bruno, J. F., Gaines, S. D., Halpern, B. S., Lester, S. E., Kinlan, B. P., & Weiss, J. M. (2007). Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 1266–1271.
- Occhipinti-Ambrogi, A. (2007). Global change and marine communities: Alien species and climate change. *Marine Pollution Bulletin*, 55, 342–352.
- Pfennig, K. S., Kelly, A. L., & Pierce, A. A. (2016). Hybridization as a facilitator of species range expansion. *Proceedings of the Royal Society B: Biological Sciences*, 283, 20161329.
- Pineda, M. C., McQuaid, C. D., Turon, X., López-Legentil, S., Ordóñez, V., & Rius, M. (2012). Tough adults, frail babies: An analysis of stress sensitivity across early life-history stages of widely introduced marine invertebrates. *PLoS ONE*, 7, e46672.
- Poloczanska, E. S., Burrows, M. T., Brown, C. J., García Molinos, J., Halpern, B. S., Hoegh-Guldberg, O., ... Sydeman, W. J. (2016). Responses of marine organisms to climate change across oceans. *Frontiers in Marine Science*, 3, 1–21.
- Potts, W. M., Henriques, R., Santos, C. V., Munnik, K., Anson, I., Dufois, F., ... Shaw, P. W. (2014). Ocean warming, a rapid distributional shift, and the hybridization of a coastal fish species. *Global Change Biology*, 20, 2765–2777.
- Pritchard, V. L., Knutson, V. L., Lee, M., Zieba, J., & Edmands, S. (2013). Fitness and morphological outcomes of many generations of hybridization in the copepod *Tigriopus californicus*. *Journal of Evolutionary Biology*, 26, 416–433.
- R Core and Team (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Raitsos, D. E., Beaugrand, G., Georgopoulos, D., Zenetos, A., Pancucci-Papadopoulou, A. M., Theocharis, A., & Papathanassiou, E. (2010). Global climate change amplifies the entry of tropical species into the eastern Mediterranean Sea. *Limnology and Oceanography*, 55, 1478–1484.
- Rhymer, J. M., & Simberloff, D. (1996). Extinction by hybridization and introgression. *Annual Review of Ecology and Systematics*, 27, 83–109.
- Rieseberg, L. H., Raymond, O., Rosenthal, D. M., Lai, Z., Livingstone, K., Nakazato, T., ... Lexer, C. (2003). Major ecological transitions in wild sunflowers facilitated by hybridization. *Science*, 301, 1211–1216.
- Riley, S. P. D., Shaffer, H. B., Voss, S. R., & Fitzpatrick, B. M. (2003). Hybridization between a rare, native tiger salamander (*Ambystoma californiense*) and its introduced congener. *Ecological Applications*, 13, 1263–1275.
- Rius, M., Clusella-Trullas, S., McQuaid, C. D., Navarro, R. A., Griffiths, C. L., Matthee, C. A., ... Turon, X. (2014). Range expansions across ecoregions: Interactions of climate change, physiology and genetic diversity: Range shifts across ecoregions. *Global Ecology and Biogeography*, 23, 76–88.
- Rius, M., & Darling, J. A. (2014). How important is intraspecific genetic admixture to the success of colonising populations? *Trends in Ecology & Evolution*, 29, 233–242.
- Rius, M., & Teske, P. R. (2011). A revision of the *Pyura stolonifera* species complex (Tunicata, Ascidiacea), with a description of a new species from Australia. *Zootaxa*, 2754, 27–40.
- Rius, M., & Teske, P. R. (2013). Cryptic diversity in coastal Australasia: A morphological and mitonuclear genetic analysis of habitat-forming sibling species. *Zoological Journal of the Linnean Society*, 168, 597–611.

- Rius, M., Teske, P. R., Manríquez, P. H., Suárez-Jiménez, R., McQuaid, C. D., & Castilla, J. C. (2017). Ecological dominance along rocky shores, with a focus on intertidal ascidians. *Oceanography and Marine Biology: An Annual Review*, 55, 55–84.
- Rius, M., Turon, X., Dias, G. M., & Marshall, D. J. (2010). Propagule size effects across multiple life-history stages in a marine invertebrate. *Functional Ecology*, 24, 685–693.
- Rouault, M., Pohl, B., & Penven, P. (2010). Coastal oceanic climate change and variability from 1982 to 2009 around South Africa. *African Journal of Marine Science*, 32, 237–246.
- Sánchez-Guillén, R. A., Muñoz, J., Rodríguez-Tapia, G., Arroyo, T. P. F., & Córdoba-Aguilar, A. (2013). Climate-induced range shifts and possible hybridisation consequences in insects. *PLoS ONE*, 8, e80531.
- Sagarin, R. D., Barry, J. P., Gilman, S. E., & Baxter, C. H. (1999). Climate-related change in an intertidal community over short and long time scales. *Ecological Monographs*, 69, 465–490.
- Seebens, H., Schwartz, N., Schupp, P. J., & Blasius, B. (2016). Predicting the spread of marine species introduced by global shipping. *Proceedings of the National Academy of Sciences of the United States of America*, 113, 5646–5651.
- Sexton, J. P., McIntyre, P. J., Angert, A. L., & Rice, K. J. (2009). Evolution and ecology of species range limits. *Annual Review of Ecology, Evolution, and Systematics*, 40, 415–436.
- Smit, A. J., Roberts, M., Anderson, R. J., Dufois, F., Dudley, S. F. J., Bornman, T. G., ... Bolton, J. J. (2013). A coastal seawater temperature dataset for biogeographical studies: Large biases between *in situ* and remotely-sensed data sets around the coast of South Africa. *PLoS ONE*, 8, e81944.
- Sorte, C. J. B., Williams, S. L., & Carlton, J. T. (2010). Marine range shifts and species introductions: Comparative spread rates and community impacts. *Global Ecology and Biogeography*, 19, 303–316.
- Stachowicz, J. J., Terwin, J. R., Whitlatch, R. B., & Osman, R. W. (2002). Linking climate change and biological invasions: Ocean warming facilitates nonindigenous species invasions. *Proceedings of the National Academy of Sciences of the United States of America*, 99, 15497–15500.
- Stelkens, R. B., Schmid, C., Selz, O., & Seehausen, O. (2009). Phenotypic novelty in experimental hybrids is predicted by the genetic distance between species of cichlid fish. *BMC Evolutionary Biology*, 9, 283.
- Svane, I., & Young, C. M. (1989). The ecology and behaviour of ascidian larvae. *Oceanography and Marine Biology: An Annual Review*, 27, 45–90.
- Svenning, J.-C., Gravel, D., Holt, R. D., Schurr, F. M., Thuiller, W., Münkemüller, T., ... Normand, S. (2014). The influence of interspecific interactions on species range expansion rates. *Ecography*, 37, 1198–1209.
- Taboada, F. G., & Anadón, R. (2012). Patterns of change in sea surface temperature in the North Atlantic during the last three decades: Beyond mean trends. *Climatic Change*, 115, 419–431.
- Tangwancharoen, S., & Burton, R. S. (2014). Early life stages are not always the most sensitive: Heat stress responses in the copepod *Tigriopus californicus*. *Marine Ecology Progress Series*, 517, 75–83.
- Taylor, E. B., Boughman, J. W., Groenenboom, M., Sniatynski, M., Schluter, D., & Gow, J. L. (2006). Speciation in reverse: Morphological and genetic evidence of the collapse of a three-spined stickleback (*Gasterosteus aculeatus*) species pair. *Molecular Ecology*, 15, 343–355.
- Teske, P. R., Papadopoulos, I., Newman, B. K., Dworschak, P. C., McQuaid, C. D., & Barker, N. P. (2008). Oceanic dispersal barriers, adaptation and larval retention: An interdisciplinary assessment of potential factors maintaining a phylogeographic break between sister lineages of an African prawn. *BMC Evolutionary Biology*, 8, 341.
- Teske, P. R., Rius, M., McQuaid, C. D., Styan, C. A., Piggott, M. P., Benhissoune, S., ... Beheregaray, L. B. (2011). "Nested" cryptic diversity in a widespread marine ecosystem engineer: A challenge for detecting biological invasions. *BMC Evolutionary Biology*, 11, 176.
- Vallejo-Marín, M., & Hiscock, S. J. (2016). Hybridization and hybrid speciation under global change. *New Phytologist*, 211, 1170–1187.
- van der Knaap, W. O., van Leeuwen, J. F. N., Finsinger, W., Gobet, E., Pini, R., Schweizer, A., ... Ammann, B. (2005). Migration and population expansion of *Abies*, *Fagus*, *Picea*, and *Quercus* since 15000 years in and across the Alps, based on pollen-percentage threshold values. *Quaternary Science Reviews*, 24, 645–680.
- Vences, M., Hauswaldt, J. S., Steinfartz, S., Rupp, O., Goesmann, A., Künzel, S., ... Smirnov, N. A. (2013). Radically different phylogeographies and patterns of genetic variation in two European brown frogs, genus *Rana*. *Molecular Phylogenetics and Evolution*, 68, 657–670.
- Verween, A., Vincx, M., & Degraer, S. (2007). The effect of temperature and salinity on the survival of *Mytilopsis leucophaeata* larvae (Mollusca, Bivalvia): The search for environmental limits. *Journal of Experimental Marine Biology and Ecology*, 348, 111–120.
- Welch, M. E., & Rieseberg, L. H. (2002). Habitat divergence between a homoploid hybrid sunflower species, *Helianthus paradoxus* (Asteraceae), and its progenitors. *American Journal of Botany*, 89, 472–478.
- Wieczorek, S. K., & Todd, C. D. (1997). Inhibition and facilitation of bryozoan and ascidian settlement by natural multi-species biofilms: Effects of film age and the roles of active and passive larval attachment. *Marine Biology*, 128, 463–473.
- Wolkovich, E. M., & Cleland, E. E. (2011). The phenology of plant invasions: A community ecology perspective. *Frontiers in Ecology and the Environment*, 9, 287–294.
- Zardi, G. I., Nicastro, K. R., McQuaid, C. D., Hancke, L., & Helmuth, B. (2011). The combination of selection and dispersal helps explain genetic structure in intertidal mussels. *Oecologia*, 165, 947–958.
- Zeidberg, L. D., & Robison, B. H. (2007). Invasive range expansion by the Humboldt squid, *Dosidicus gigas*, in the eastern North Pacific. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 12948–12950.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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