

ADAPTIVE PHENOTYPIC DIFFERENTIATION ACROSS THE INTERTIDAL GRADIENT IN THE ALGA *SILVETIA COMPRESSA*

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Abstract. Populations of intertidal species span a steep environmental gradient driven by differences in emersion time. In spite of strong differential selection on traits related to this gradient, the small spatial scale over which differences occur may prevent local adaptation, and instead may favor a single intermediate phenotype, or nongenetic mechanisms of differentiation. Here I examine whether a common macroalga, *Silvetia compressa*, exhibits phenotypic differentiation across the intertidal gradient and evaluate how local adaptation, developmental plasticity, and maternal effects may interact to shape individual phenotypes. Reciprocal transplants of both adults and embryos showed a “home-height advantage” in two of the three populations tested. In laboratory trials, the progeny of upper-limit individuals survived exposure to air significantly better than lower-limit progeny from the same population. I compared the emersion tolerance of full-sib families generated from gametes produced in the field to those produced under common garden conditions. The relative advantage of upper-limit lineages was robust to maternal environment during gametogenesis; this pattern is consistent with genetic differentiation. The possible role of local adaptation has historically been ignored in studies of intertidal zonation. In *S. compressa*, phenotypic differentiation may have important consequences for vertical range, both within and among sites.

Key words: algae; environmental gradient; intertidal; local adaptation; maternal effect; phenotypic plasticity; *Silvetia compressa*.

INTRODUCTION

Organisms can respond to spatial heterogeneity in their environment with phenotypic differentiation via genetic mechanisms (i.e., local adaptation) or nongenetic ones (i.e., phenotypic plasticity). Local adaptation and phenotypic plasticity are not mutually exclusive mechanisms of differentiation; both are important components of adaptive phenotypic differentiation in most species. However, the relative contribution of plasticity vs. local adaptation to phenotypic variation at different spatial scales, and how this ultimately translates into niche breadth (defined here as the range of conditions under which the species can persist) remains unclear. Gene flow acts to homogenize genotype frequencies across space, potentially countering the effect of natural selection (e.g., Riechert 1993, Storfer and Sih 1998; see review by Lenormand 2002); thus the expectation is that plasticity in key traits should be more common than local adaptation on small spatial scales, or where the rate of environmental change over space (e.g., slope of a selective gradient, or grain size in a patchy environment) is high relative to dispersal distance (Levins 1968, West-Eberhard 1989). However, strong selection can maintain population structure in the face of gene flow, and there are examples of local adaptation occurring within

populations on very small spatial scales (e.g., Schemske 1984, Sork et al. 1993, Knight and Miller 2004), although not enough for general patterns to emerge (see review by Linhart and Grant 1996). A comparative approach is needed to address how much local adaptation we expect to evolve under different ecological conditions (Kawecki and Ebert 2004).

Rocky intertidal communities are ideal for exploring questions about adaptive differentiation because of the steep environmental gradient these habitats span. Abiotic factors correlated with tide height vary greatly over small scales in the intertidal zone, and intertidal species often display patterns of zonation that can be linked to their physiological tolerances (Menge and Branch 2001). Macroalgae are model species to study in this context because algae are sessile as adults, disperse (via gametes and/or spores) over spatial scales commensurate to that of terrestrial plants (meters to kilometers; see review by Kinlan and Gaines 2003), and unlike many invertebrates, lack obvious structural defenses against heat and desiccation associated with emersion at low tides. At the species' level, differences in algal traits related to emersion stress have often been found to sort with respect to tide height (e.g., Baker 1909). Very little is known about individual-level variation in physiological (or indeed, any) traits expressed across the intertidal gradient, or the possible role of genetic differentiation vs. plasticity in generating these differences. However, individuals high in the intertidal zone often display

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reduced growth, survival, and reproduction compared to conspecifics near the center of the distribution (but see Wright et al. 2004), supporting the idea that they experience greater physiological stress and potentially strong selection. At larger spatial scales (i.e., among sites or regions), macroalgae often show striking morphological variation that is thought to be at least partially plastic (e.g., Kubler and Dudgeon 1996, Blanchette et al. 2002, Fowler-Walker et al. 2006). However, studies have also demonstrated genetic local adaptation (e.g., Bergström and Kautsky 2005), as well as genetic variation in plastic response (e.g., Monro and Poore 2005). Studies on intertidal invertebrates have demonstrated both plasticity in traits expressed differentially across the intertidal gradient (e.g., heat-shock proteins; Somero 2001, Halpin et al. 2004) as well as habitat-related genetic clines (e.g., Schmidt et al. 2000, Johannesson and Mikhailova 2004, Grahame et al. 2006).

Here I evaluate how local genetic adaptation, developmental plasticity, and maternal effects may interact to shape the phenotypes of populations across steep environmental gradients in the common brown alga, *Silvetia compressa*. I used a reciprocal transplant/outplant approach with both adults and embryos (i.e., individuals with a developmental history in a given microhabitat and those without one) to ask if there was evidence of a "home-height advantage" in these populations, indicative of adaptive differentiation. Then I used experiments in the laboratory to investigate the magnitude and source of within-population variation in a specific trait likely to be under selection: the ability of embryos to survive emersion.

METHODS

Silvetia compressa (J. Ag) Serrao, Cho, Boo and Brawley (Fucales, Heterokontophyta) is a common seaweed found in the mid- to upper intertidal zone on the Pacific Coast of North America from northern California to Punta Baja, Mexico (Silva et al. 2004). Individuals are hermaphroditic, releasing both antheridia and oogonia in mucilage during daytime low tides (Brawley et al. 1999). After gametes are released, self-fertilization can occur. Zygotic dispersal is very low, such that most progeny settle within a meter or two of the parental alga (Johnson and Brawley 1998, Hays 2006). Long distance gene flow may arise if reproductive branches break off, disperse with the tide, and release gametes in new areas. Given that such events are typically rare (Williams and DiFiori 1996; *personal observation*), *S. compressa* can be characterized as having a relatively closed population structure. (See Appendix A for additional life history details, and methods used to culture embryos.) The experiments described next were conducted on populations from three sites <48 km north of Santa Cruz, California, USA: Pigeon Point, Greyhound Rock, and Scott's Creek (Appendix B).

Adult transplants

Transplant experiments were conducted at Scott's Creek and Pigeon Point in 2003, and at Greyhound Rock in 2004. Forty individuals were collected at 0.5-m intervals along the upper and lower edge of *S. compressa*'s intertidal distribution ($N = 80$ individuals/site); only prereproductive individuals were used, and experiments were conducted in summer (when *S. compressa* is not reproductive) to prevent accidentally altering natural patterns of gene flow. Individuals were allowed to rehydrate in the laboratory for 12 hours before maximum length and wet biomass were recorded. I transplanted algae back into the field the next day by zip-tying each thallus to a previously established anchor (a 1.27-cm stainless steel washer attached with Z-Spar marine epoxy; Kopper's, Los Angeles, California, USA) at one of four locations: the current upper limit of the species' distribution; above the upper limit by 1 m; the lower limit of the distribution; and below the lower limit by 1 m (see Plate 1). After four weeks in their new locations, transplants were reweighed/measured as described before.

Analysis.—All analyses were conducted with Systat 10.2 (Systat 2002) unless otherwise stated. Change in wet biomass and length was standardized by the initial value and log-transformed ($x + 1$). Because experiments on different populations were conducted at different times, populations were analyzed separately using crossed two-way ANOVAs (factors: source height, transplant height). A priori contrasts between upper and lower limit individuals were performed at each transplant height, and greater growth (or retention of biomass) of individuals at (or beyond) their original location was considered evidence of adaptive differentiation.

Embryo outplants

Selfed embryos of upper and lower limit parents were reciprocally outplanted into the field on plates (10 × 10 cm PVC covered with Safety-Walk; 3M, St. Paul, Minnesota, USA) attached to the bench with a central stainless steel bolt. To put zygotes from multiple lineages on the same plate, a 10 × 10 cm section of plastic grid and neoprene liner were clamped to each plate; this allowed me to pipette zygotes from different lineages into different wells formed by the grid (36 wells/plate; 150–200 embryos/well). After zygotes settled (~5 hours later), grids were removed and plates were kept in filtered seawater until outplanted, 24 hours after fertilization. The unit of replication in these experiments is the lineage, and all lineages tested in a trial were present on every plate ($N = 18 \times 2$ tide heights × 3 trials = 108 lineages/site). Eight identical plates were outplanted, four each along the upper and lower edge of *S. compressa*'s distribution. After three days, lineage survival (defined as >50 embryos alive) was scored in the field with a 10× hand lens. A subset was also evaluated in the laboratory under a compound scope, and validated accuracy of field estimates.

Analysis.—Lineage survival was averaged across the four plates at each height. Although these data are not continuous, replication was sufficiently high that they approximated a normal distribution, so I analyzed data using a crossed two-factor ANOVA for each population, with parents' height and outplant height as main factors and trial included as a blocking factor. As before with adults, a priori contrasts were conducted between upper and lower edge lineages.

Embryo emersion tolerance

Selfed zygotes from upper and lower edge parents ($N = 18$ parents \times 2 tide heights) were pipetted into glass slides (150–250 zygotes/lineage/slide). One upper edge and one lower edge lineage were randomly paired on each slide, with location (i.e., left or right side) also set randomly and scored blind with respect to parent's tide height. Each combination was replicated exactly onto three slides. After zygotes attached, slides were rinsed and placed in filtered seawater. At 18 hours (timed to mimic the first daytime low tide after a natural spawning event) two of the slides from each lineage pair were exposed to the air at $\sim 18^\circ\text{C}$ for three and six hours, respectively, before being returned to seawater; the third slide remained immersed. Slides were examined under a compound scope to score mortality (evidenced by discoloration and plasmolysis of cells); enough fields of view were examined to score >100 embryos/lineage/slide.

I assessed whether the maternal environment during gamete production influenced zygote performance by conducting this experiment with (1) gametes from the first spawn of individuals brought in from the field, and (2) gametes from those same individuals after they were kept in a common garden at Long Marine Laboratory, University of California, Santa Cruz, for five weeks (see Appendix C for details).

Analysis.—Embryo percentage survival data were arcsine square-root transformed, and analyzed using a split-plot design (whole-plot treatment, emersion time; within-plot, parent's tide height). To explicitly test for a difference in the relative performance of progeny after parents had been kept in the common garden, I calculated the difference in survival between the upper and lower limit lineage paired on each slide, and tested whether the average difference in survival changed across trials with crossed two-way ANOVAs (factors: trial, emersion time).

RESULTS

Adult transplants

Given seasonal decline in *S. compressa*, differences in size among treatment groups usually indicated an ability to retain biomass rather than growth (see Appendix D for discussion, as well as analysis of mortality/loss). Analysis of change in length and biomass gave qualitatively identical results; I report numerical results for biomass only. At Pigeon Point, *S. compressa*

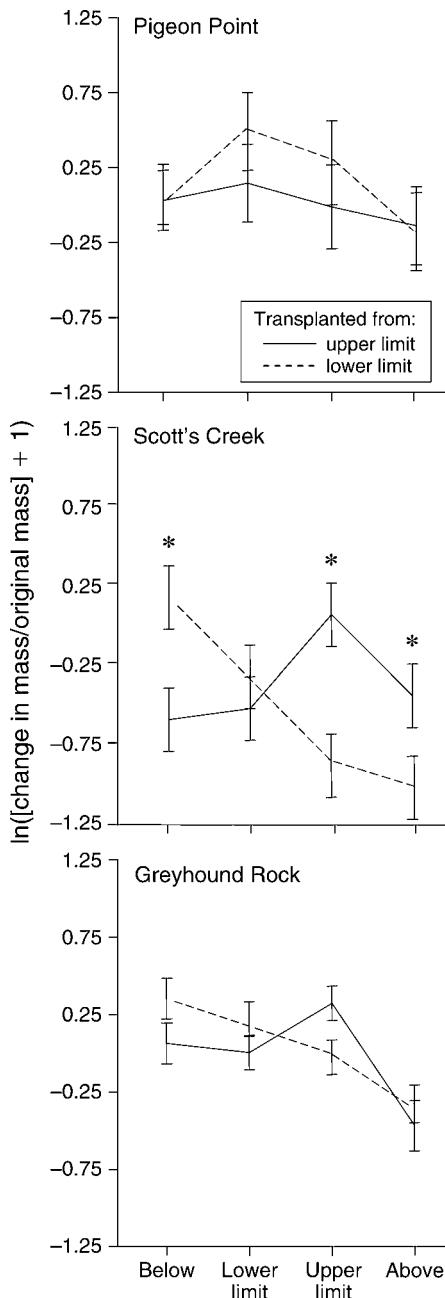


FIG. 1. Change in biomass of adult *Silvetia compressa* transplanted across and beyond the species' intertidal distribution at three sites in central California. Asterisks indicate significant ($P < 0.05$) a priori contrasts between individuals from the upper and lower limit of the distribution transplanted to a given tidal height. Values shown are means \pm SE.

displayed equivalent change in size regardless of where they were from ($F_{1,43} = 0.049$, $P = 0.83$) or where they were transplanted ($F_{3,43} = 0.785$; $P = 0.51$); there was no indication of an interaction between the two ($F_{3,43} = 0.191$, $P = 0.90$; Fig. 1). In contrast, at Scott's Creek, the effect of outplant height depended critically on original location ($F_{3,62} = 6.82$, $P = 0.0005$; Fig. 1). Individuals

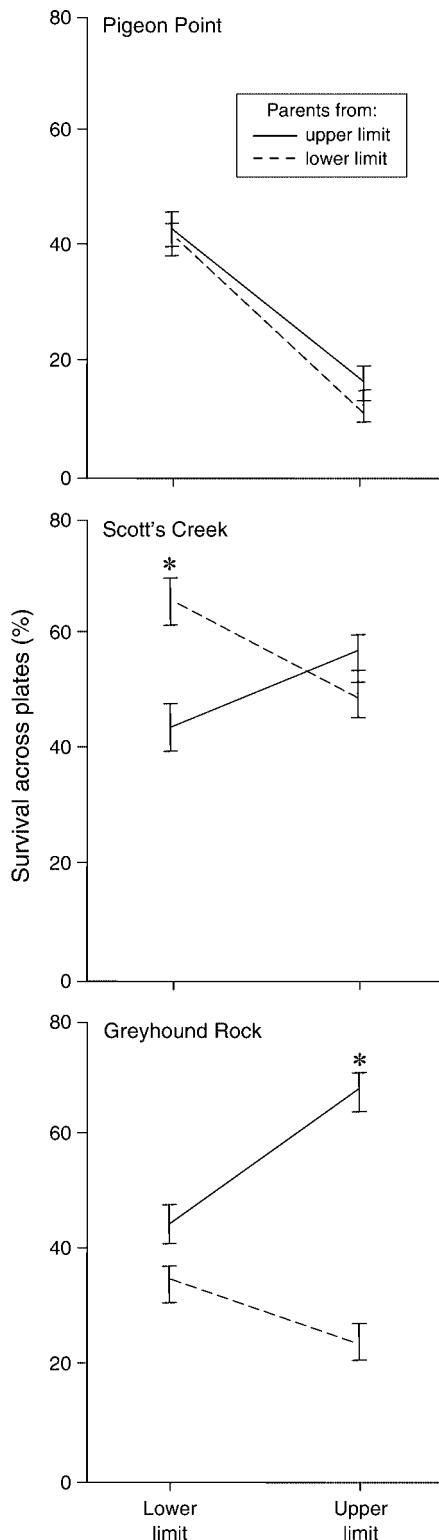


FIG. 2. Survival of embryos spawned in the laboratory and reciprocally outplanted in the field at the upper and lower edge of *S. compressa*'s distribution. Asterisks indicate significant ($P < 0.05$) a priori contrasts between upper limit and lower limit lineages. Values shown are least-square means \pm pooled SE.

from the upper edge retained significantly more biomass than individuals from the lower edge when transplanted back to the upper edge or above it (planned contrasts; $P < 0.05$), and lower limit individuals retained significantly more biomass than upper limit individuals when transplanted below the species' lower limit ($P < 0.05$). At Greyhound, the home \times outplant height interaction was not significant ($F_{3,46} = 1.90$, $P = 0.14$), but the overall trend was consistent with home-height advantage: individuals tended to retain more biomass at their original location than did their conspecifics from across the gradient (Fig. 1). Transplant height directly affected change in size ($F_{3,46} = 5.369$, $P = 0.003$), such that individuals transplanted above the current distribution lost significantly more mass than at other locations (Tukey's hsd, $P < 0.05$).

Embryo outplants

Embryos at Pigeon Point displayed greater survival at the lower limit of *S. compressa*'s distribution than the upper limit; the magnitude of this difference varied across trials ($F_{2,168} = 21.11$, $P < 0.001$). There was no detectable effect of parent's height on survival ($F_{1,2} = 6.83$, $P = 0.12$), nor any interaction between parent's height and outplant height ($F_{1,2} = 2.17$, $P = 0.28$; Fig. 2). However, at the other two sites, embryo survival at different locations along the gradient depended on parent's location (Scott's Creek, $F_{1,2} = 183.211$, $P = 0.005$; Greyhound, $F_{1,2} = 80.93$, $P < 0.012$; Appendix E shows full ANOVA). At Scott's Creek, embryos showed a home-height advantage at both edges; this was significant only at the lower limit (contrasts, $P < 0.05$; Fig. 2). At Greyhound, upper limit lineages showed higher survivorship overall, but only significantly so when plates were outplanted at the upper limit of the distribution ($P < 0.05$; Fig. 2).

Embryo emersion tolerance

In all experiments, embryo survival dropped steeply with increasing emersion time (split-plot ANOVAs, $F_{1,28} = 20.4\text{--}154.6$, $P < 0.001$), and there was a significant effect of "plot" ($F_{1,28} = 2.0\text{--}13.4$, $P = >0.001\text{--}0.034$), indicating that treatment effects varied across individual slides.

Trial one.—Parent's tide height had no detectable effect on the survival of embryos from Pigeon Point ($F_{1,28} = 0.26$, $P = 0.61$). In contrast, the progeny of upper limit parents survived exposure to air in the laboratory significantly better than progeny of lower limit parents from both Scott's Creek ($F_{1,28} = 18.32$, $P < 0.001$) and Greyhound ($F_{1,28} = 7.91$, $P = 0.009$; Fig. 3).

Trial two.—After five weeks in a common environment, there was still a significant effect of parent's original location on progeny survival (Scott's Creek, $F_{1,24} = 41.60$, $P < 0.001$; Greyhound, $F_{1,24} = 43.91$, $P < 0.001$; Fig. 3). Further, the mean difference in emersion tolerance between upper and lower limit progeny did not change significantly between trials (Scott's Creek, $F_{1,52} =$

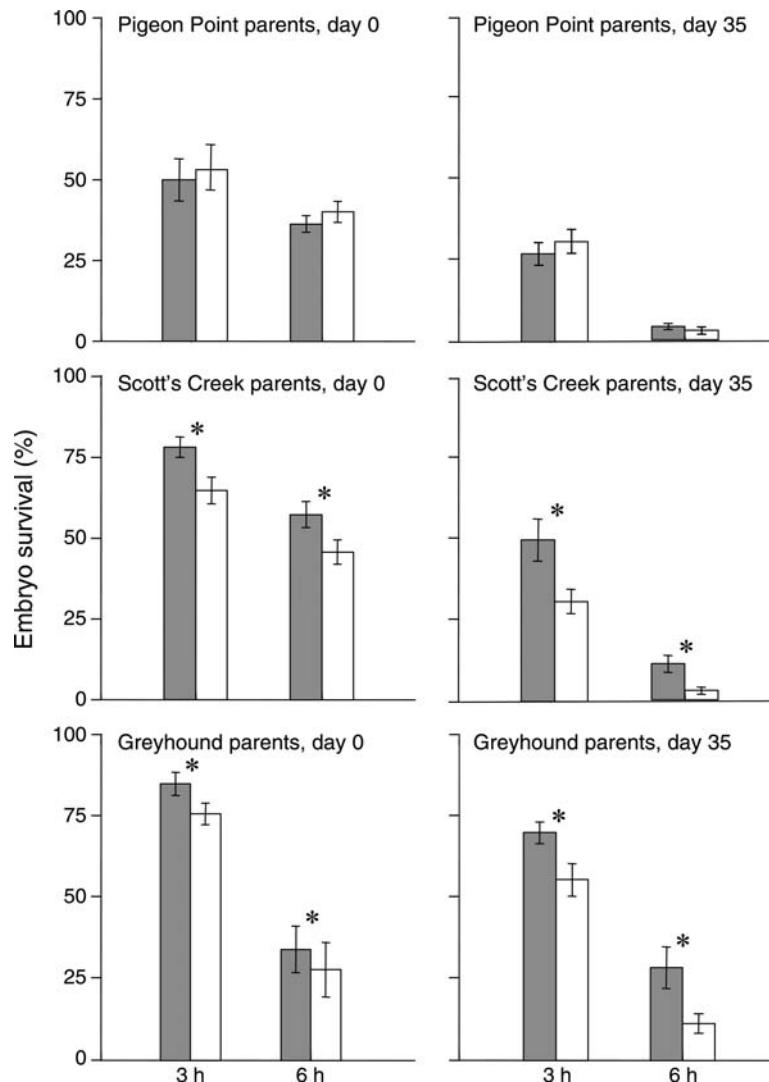


FIG. 3. Survival of embryos from lineages at the upper and lower limit of the species' distribution at each site, when exposed to air in the laboratory. The first graph of each pair shows performance of embryos generated from the first spawning event after adults were brought in from the field; the second shows performance of embryos generated from a spawning event after adults had been kept in a common garden environment in the laboratory for 35 days and induced to spawn every 2–3 days, to promote gamete turnover. Filled bars reflect upper limit progeny; open bars reflect lower limit progeny. Values shown are means \pm SE. Asterisks indicate significant differences in survival between upper and lower limit lineages (a priori contrasts, $P < 0.05$). Controls (i.e., embryos kept continually immersed) showed 100% survival for all lineages and trials, and were not plotted.

0.061, $P = 0.806$; Greyhound, $F_{1,51} = 1.69$, $P = 0.20$; Appendix F).

DISCUSSION

This study found evidence of adaptive differentiation within populations of a common intertidal alga at sites where the intertidal gradient is relatively steep, and the width of *S. compressa* zone is <5 m across. At small spatial scales, theory suggests that differentiation via phenotypic plasticity is expected to be more common than genetic adaptation. While developmental plasticity and maternal environmental effects may still have profound effects on phenotypic differentiation and

individual fitness in *S. compressa*, I found surprisingly little support for a role of these processes in creating the patterns documented here.

Phenotypic differentiation

In transplant experiments in the field, two of the three populations tested (Scott's Creek and Greyhound Rock) showed support for adaptive phenotypic differentiation across the intertidal gradient. The apparently higher fitness of adults transplanted back to their original location is consistent with genetic adaptation, but could also arise via carryover effects; by outplanting embryos spawned in the laboratory, the goal was to remove



PLATE 1. Two adult transplants at Scott's Creek. The individual anchored with the white zip-tie (left side) came from the upper limit of *S. compressa*'s intertidal distribution; the individual anchored with the black zip-tie came from the lower limit. Photo credit: C. Hays.

environmental effects incurred during development. Obviously, some of the caveats of adult transplants still apply, as maternal effects may persist across generations (review by Rossiter 1996); however, if the home-height advantage seen in adult transplants had disappeared, this would indicate acclimation. Instead, embryos displayed significantly greater survival at their parent's location along the gradient in both Greyhound and Scott's Creek, at least at one edge of the distribution.

The traits that differentiate upper and lower limit progeny at the upper edge of *S. compressa*'s distribution are likely to be linked to withstanding the physiological stress of greater emersion time (e.g., thermal stress, desiccation); this is supported by the variation in emersion tolerance detected under more controlled conditions in the laboratory. It is somewhat harder to imagine what traits may drive the difference in embryo survival at the lower edge of the distribution, but possibilities include differences among lineages in the adhesion of embryos to the substrate or in their attractiveness to herbivores. Species-level variation in these traits has been documented in intertidal algae (e.g., Bolser and Hay 1996, Taylor and Schiel 2003), as well as population- and individual-level variation in chemical defense (see review by Hay and Fenical 1988).

In the short-term laboratory experiments, there was no evidence of a physiological trade-off with emersion tolerance (all embryos that were continually immersed showed 100% survival), which presumably would have

become apparent over a longer sequence of sublethal emersion periods. Stress tolerance is assumed to carry a physiological cost that is expressed in other fitness-related traits such as competitive ability or reproductive output (Hoffman and Parsons 1991, Dethier et al. 2005), which would explain the maintenance of less-tolerant phenotypes. In the absence of continued strong selection for desiccation resistance, it should decline; a subtidal population of *Fucus vesiculosus* in the Baltic Sea, for example, shows reduced tolerance of emersion stress compared to intertidal North Sea populations (Pearson et al. 2000).

Maternal environmental effects

Mature gametes are generally thought to be metabolically inert (Gilbert 2000). However, Li and Brawley (2004) demonstrated a clear effect of conceptacle temperature on subsequent thermal tolerance of *S. compressa* embryos. To test whether such effects could be influencing the patterns documented here, I compared the performance of embryos from gametes that developed in the field to that of full siblings from gametes that developed under identical conditions in the laboratory. The significant difference between upper and lower limit progeny persisted after their parents were kept in the common garden for five weeks and regularly induced to spawn. Moreover, the mean difference in survival between upper and lower limit progeny showed no significant change between the first and 20th

spawning event in these lineages. Adaptive maternal effects reflecting mother's phenotype/genotype may still play a critical role in generating within-population variation; however, I found little evidence for a direct effect of environment during gamete production.

Local adaptation to the intertidal gradient

Decades of research on intertidal communities, including some of the most famous experiments in ecology, have characterized different biotic and abiotic factors that can influence zonation (e.g., Connell 1961, Paine 1966), providing us with a solid understanding of some of the important selective agents in these systems. In contrast, relatively little attention has been given to underlying evolutionary constraints on species' intertidal distributions, and studies of the magnitude and basis of within-site variation in traits are rare (exceptions include Sideman and Mathieson [1983], Innes [1988], and Stengel and Dring [1997]). In a population genetic study of *S. compressa* around San Diego Bay, Williams and DiFiori (1996) detected significant structure in allozyme frequencies within sites, across the intertidal zone, such that all heterozygous individuals and rare alleles were found in the upper one-third of *S. compressa*'s distribution. Estimated genetic neighborhood size was very small, so it is not possible to eliminate genetic drift as the cause of the observed within-bench differentiation; however, genetic drift seems unlikely to have produced the consistent landward distribution of rare alleles, especially given the results reported here.

In species with high dispersal, no settling behavior, and thus no correlation between parental environment and offspring environment, the presence of a genetic cline across the intertidal zone is more appropriately considered a balanced polymorphism rather than local adaptation. *S. compressa* embryos typically recruit within a few meters of their parents (Williams and DiFiori 1996, Johnson and Brawley 1998, Hays 2006), but how this dispersal distance relates to change in the selective gradient varies by site. At steep sites where *S. compressa*'s distribution is narrow (e.g., both Scott's Creek and Greyhound), it seems certain that zygotes must continually disperse across the gradient into habitats where they are unfit, and the pattern of differentiation is maintained only by continued purifying selection. However, if phenotypic differentiation is found at sites with wider horizontal distributions (e.g., Williams and DiFiori 1996), this could reflect local adaptation in the strictest sense. Gamete release in *S. compressa* is triggered by cues generated by exposure to the air during daytime low tides (Pearson et al. 1998), potentially creating asynchrony in gamete release between individuals at different tide heights and thus reducing across-gradient gene flow. Selfing rate is expected to be high in this species, which would further restrict gametic gene flow and could facilitate small-scale local adaptation (e.g., Knight and Miller 2004).

Assuming *S. compressa*'s dispersal curve is similar across sites, a simple expectation is that sites with a relatively shallow intertidal gradient should provide the greatest opportunity for genetic differentiation and local adaptation to occur. The data presented here run counter to that expectation: the site with the shallowest gradient, and greatest absolute distance between upper and lower limit individuals, is Pigeon Point (Appendix B), where *S. compressa* showed no evidence of differentiation. A major issue confounding interpretation of slope is that the extremes of *S. compressa*'s intertidal distribution are not the same across sites. In fact, populations at the two steeper sites show greater vertical tidal range, and span greater variation in environmental conditions (e.g., substrate temperature, emersion regime; *unpublished data*). This highlights a troubling circularity: is greater phenotypic variation observed in these populations because they span more variation in habitat (and presumably are under stronger selection)? Or did these populations spread into habitat further up and down the gradient because they were more variable in traits related to tide height? Obviously, populations may differ in many aspects affecting these patterns (e.g., age, disturbance history, genetic diversity). Further, there is no reason to assume that *S. compressa*'s distributions at these sites are at equilibrium. Intertidal zonation patterns often reflect an ongoing process of expansion and retraction (e.g., Readdie 2004); how phenotypic differentiation and local adaptation may play into this process remains unknown.

Compared to terrestrial systems, clear examples of local adaptation in marine species at any spatial scale are relatively rare. Given the planktonic dispersal of many species (e.g., via larvae, gametes, and/or spores), and the potential for large-scale gene flow and population connectivity that this allows, this paucity seems consistent with our expectations for how marine organisms are likely to respond to variation in their environment. However, an increasing number of examples show greater population genetic structure in marine species than predicted based on life history alone (e.g., Benzie and Williams 1997, Palumbi and Warner 2003), and suggest that local genetic adaptation may also be more common than previously thought, especially in systems characterized by strong selection (e.g., see review of invertebrate host use by Sotka [2005]). The possibility of small-scale phenotypic differentiation and adaptation has historically been understudied in intertidal species, in spite of the strong selective gradient this habitat spans. In *S. compressa*, variation in the degree of adaptive differentiation within different populations may be key to understanding variation in this species' vertical distribution across both space and time.

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APPENDIX A

A description of *S. compressa* life history and methods used to culture embryos (*Ecological Archives* E088-011-A1).

APPENDIX B

Site characteristics for the three populations (*Ecological Archives* E088-011-A2).

APPENDIX C

Common garden methodology (*Ecological Archives* E088-011-A3).

APPENDIX D

Analysis of the number of adult transplants lost over the course of the experiments, and discussion of loss of biomass (*Ecological Archives* E088-011-A4).

APPENDIX E

ANOVA designs (*Ecological Archives* E088-011-A5).

APPENDIX F

Differences among lineages in emersion tolerance before and after parents were maintained in a common garden (*Ecological Archives* E088-011-A6).