Genetic variation underlies plastic responses to global change drivers in the purple sea urchin, *Strongylocentrotus purpuratus*.

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11 Abstract

12 Phenotypic plasticity and adaptive evolution enable population persistence in response to global
13 change. However, there are few experiments that test how these processes interact within and
14 across generations, especially in marine species with broad distributions experiencing spatially
15 and temporally variable temperature and pCO_2. We employed a quantitative genetics experiment
16 with the purple sea urchin, *Strongylocentrotus purpuratus,* to decompose family-level variation
17 in transgenerational and developmental plastic responses to ecologically relevant temperature
18 and pCO_2. Adults were conditioned to controlled non-upwelling (high temperature, low pCO_2) or
19 upwelling (low temperature, high pCO_2) conditions. Embryos were reared in either the same
20 conditions as their parents or the crossed environment, and morphological aspects of larval body
21 size were quantified. We find evidence of family-level phenotypic plasticity in response to
22 different developmental environments. Among developmental environments, there was
23 substantial additive genetic variance for one body size metric when larvae developed under
24 upwelling conditions, although this differed based on parental environment. Furthermore, cross-
25 environment correlations indicate significant variance for genotype-by-environment interactive
26 effects. Therefore, genetic variation for plasticity is evident in early stages of *S. purpuratus*,
27 emphasizing the importance of adaptive evolution and phenotypic plasticity in organismal
28 responses to global change.
29

30 Keywords: additive genetic variance, parental effects, plasticity, marine invertebrates, upwelling

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34 ## 1. Introduction

35 As phenotypic distributions of populations are being shaped by rapid environmental
36 change, much attention has focused on individual species' ecological and evolutionary responses
37 to the altered environments [1]. Processes of selection and phenotypic plasticity can occur
38 simultaneously within a population, modifying demographic processes, and thereby linking
39 ecological and adaptive evolutionary phenotypic change to population persistence [1,2].
40 Phenotypic plasticity is the main mechanism by which populations can respond to environmental
41 change over the short-term [3]. Adaptive plastic responses, defined as plasticity that shifts
42 phenotypes towards trait values that maximize fitness, could occur across generations (parental
43 or carry-over effects) or within generations (intra-generational plasticity). Adaptive parental
44 effects are expected to occur when parental environments predict offspring environments, and
45 when observed, have small but significant effects on offspring traits [4–6]. Alternatively,
46 developmental plasticity is a type of intra-generational plasticity where environments
47 experienced during early development affect later stage phenotypes. Both parental effects and
48 developmental plasticity have the potential to shape population level responses to the
49 environment and pinpointing when in the life-cycle environmental change has the strongest
50 effect is key for predicting organismal responses to change.

51 While phenotypic plasticity can facilitate population persistence, it has limited
52 effectiveness during long-term environmental change. Phenotypic plasticity has developmental
53 constraints that could limit organismal responses to directional increases in environmental
54 change, such as temperature, and there may exist costs to maintaining plasticity [7,8]. Further,
55 plasticity will only be advantageous as long as the range of phenotypes produced across
56 environments by specific genotypes, or the reaction norms [9], continue to align with the

57 phenotypic optima maximizing fitness in each environment [8]. When reaction norms are no
58 longer adaptive across environments, evolutionary adaptation is the only way populations can
59 persist [1,2]. Such microevolutionary responses can occur in population mean phenotype, or in
60 the level of plasticity itself [1,10].

61 Adaptive evolutionary responses to changing or novel environments rely on the existence
62 of additive genetic variance that aligns with the direction of selection on phenotypic variation
63 [11,12]. Additive genetic variance can be environmentally dependent, thus should be estimated
64 under a variety of scenarios representing predicted environmental changes [4]. Not only is the
65 amount of adaptive variation of a trait dependent on the environment, but the relative ranking
66 among genotypes of additive genetic values can change across environments, signaling additive
67 genetic variance for plasticity [10,13]. Evolutionary responses to selection, and hence population
68 adaptation to change, relies on both environment-specific additive genetic variance in trait mean
69 as well as the additive genetic variance in plasticity. To determine how populations will respond
70 to global changes and persist, it is essential to simultaneously evaluate the separate contributions
71 of plastic and evolutionary phenotypic shifts during population responses to environmental
72 change.

73 *S. purpuratus* are widely dispersed across coastal habitats along the California Current
74 Large Marine Ecosystem. Throughout their range, extending from British Columbia in the north
75 to Baja California in the south, *S. purpuratus* experience temperature and pH variation, mostly
76 due to seasonal upwelling, which is expected to increase in frequency and intensity in the
77 Anthropocene [14–17]. High $p\mathrm{CO}_2$ alters the carbonate chemistry in seawater, reduces pH, and
78 directly impacts the ability of marine organisms to calcify, including early-stage sea urchins [18].
79 As *S. purpuratus* larvae are planktotrophs with long pelagic larval durations, body size and

80 skeletal features are critical for the ability to capture food and can influence predation rates,
81 swimming speeds, and stability in flowing water [19–21]. Phenotypic plasticity in larval
82 morphometrics has been observed before in *S. purpuratus*, both in response to high pCO_2 alone
83 [22–25] but also in upwelling conditions mirrored in this experiment [26–28]. In previous
84 experiments, larval cultures were generated from pooled gametes of multiple adults, thus
85 phenotypes represent treatment averages across multiple genotypes and lack resolution to
86 separate the contributions of parental effects, developmental plasticity, or genetic effects on
87 variation in the measured traits [28–30]. Here, we used a quantitative genetic analysis to partition
88 out the roles of the environment, genetics, and parental effects on observed variation in
89 phenotypic plasticity of larval body size morphometrics. Thus, our experimental design enabled
90 us to further extend these studies by quantifying family-level variation in plastic responses to
91 upwelling and non-upwelling conditions and compare evolvability to short-term plastic
92 responses at ecological time scales, which together extend our knowledge of how marine
93 organisms will respond to global change.
94
95 ## 2. Methods
96 *(a) Collection and adult conditioning*
97 *S. purpuratus* is an external fertilizer that spawns large numbers of gametes between January and
98 May. Adult urchins were collected by hand on SCUBA from two sites (25km apart) with similar
99 habitat quality [31], in August and September (site details in ESM1). Urchins were placed in one
100 of four 90-liter glass tanks per treatment (10 urchins per tank, 4 tanks per treatment), while
101 keeping track of site identity (details in ESM1). Adult conditioning was conducted under two
102 regimes differing in temperature and pCO_2: Non-upwelling (N) (mean values 17°C and 596μatm

103 pCO$_2$) and Upwelling (U) (mean values 12.8°C and 1,117μatm pCO$_2$), approximately four
104 months (ESM1 table S1). Throughout this conditioning, urchins were fed *Macrocystis pyrifera* in
105 excess once per week.

106 Temperature and pCO$_2$ levels were maintained throughout the conditioning period using
107 heat pumps regulated by Nema 4X digital temperature controllers and a flow-through CO_2
108 mixing system, modified from Fangue et al. [32]. Treated seawater was evenly pumped from two
109 reservoir tanks to conditioning tanks at a rate of 20L/hr and temperature, pH, salinity, total
110 alkalinity, and carbonate chemistry were monitored regularly (ESM1).

111

112 *(b) Crossing design, spawning, and larval culturing*

113 Due to the large number of crosses necessary for this project, we employed a staggered cross-
114 classified North Carolina II breeding design (figure 1). Spawning and generation of crosses
115 began on January 7, 2019. Gametes from 2 males and 2 females conditioned in the N treatment
116 were reciprocally crossed to yield 4 unique families. Each of these families was partitioned
117 among four cultures, two reared in the N treatment (NN) and two reared in the U treatment (NU).
118 The next day, the same crossing scheme was performed with parents from the U treatment, and
119 families reared in either the U treatment (UU) or the N treatment (UN). The 16 cultures
120 generated on a single day were designated as a block (1 parental treatment X 4 families X 4
121 cultures), and this block design was repeated 10 times in succession, alternating parental urchins
122 from non-upwelling and upwelling, for a total of 160 cultures across 40 total families.

123 Fertilizations were performed in ambient seawater conditions and embryos were placed
124 in rearing containers prior to the first cleavage, in either the same conditions as their parents or
125 the reciprocal condition (figure 1). Larval cultures were set up in a flow-through seawater system

126 with two reservoir tanks per treatment, as in the adult conditioning, feeding 6L nested buckets
127 (one bucket fitted with 30μM mesh nested within another standard bucket) at a flow rate of
128 3L/hr. Each pair of nested buckets formed one culture container. Temperature and pH of
129 reservoir tanks were measured daily while salinity and pH of larval cultures was measured 24
130 hours post fertilization (hpf) (ESM1). Larval cultures were maintained at a concentration of 10
131 larvae/mL until the early echinopluteus stage, prism, defined by the beginning of tripartite gut
132 differentiation, where the gut begins to form distinct sections (figure 1).
133
134 *(c) Morphometric measurements of eggs and larvae*
135 Unfertilized egg and prism samples were preserved in 2% formalin buffered with 100mM
136 $NaBO_3$ (pH 8.7) in FSW. Due to differences in temperature-dependent developmental delay,
137 prism larvae in N developmental treatments (17°C) were sampled between 45-46hpf and prism
138 larvae in U developmental treatments (13°C) were sampled between 55-56hpf (figure 1).
139 Photographs (N≥30 eggs per dam; N≥30 prism larvae per culture) were taken using a Motic
140 10MP digital camera fitted to an Olympus BX50 compound microscope and Motic Images Plus
141 software. All measurements, calibrated using a stage micrometer, were obtained using ImageJ
142 (https://imagej.nih.gov/ij/). For each unfertilized egg, three independent diameter measurements
143 were averaged per egg to account for any potential irregularity in shape. For each prism, two
144 measurements were taken, spicule length defined as the length from the tip of the body rod to the
145 branching point of the postoral rod and body length. For each culture the proportion of
146 developmental abnormality (N≥30 larvae per culture) was also scored. All measurements were
147 taken by two researchers to minimize variation and bias, which was included in the models
148 below.

149

150 *(d) Statistical Analysis*

151 Differences in egg diameter between treatments were quantified using a linear mixed model with
152 a fixed effect of parental treatment (U or N) and random effects of dam identity and block using
153 the *lme4* package (v1.1-27.1) [33]. Relationships between egg diameter and prism
154 morphometrics were assessed with a linear regression. Quantitative genetic linear mixed models
155 employing a character state approach (where the expression of a single phenotype in a given
156 environment defines a character state [10]) were used to decompose phenotypic variation in
157 larval spicule and body lengths into contributions from plasticity, adaptive potential, and parental
158 effects. We fit separate, identical model structures for spicule and body length within a Bayesian
159 framework and used a Markov chain Monte Carlo (MCMC) algorithm to sample posterior
160 distributions as implemented in the package MCMCglmm (v2.29) [34]. All MCMCglmm models
161 assumed Gaussian error distributions and response variables were multiplied by 100 before
162 analyses to improve model convergence; results are reported for the scaled values of the response
163 unless otherwise indicated.

164 For each larval trait, spicule length and body size, we modeled the interaction of each
165 distinct parental conditioning environment (N and U) with the two rearing environments of their
166 offspring (N and U). In the crossing design (figure 1), the gametes of parents were always
167 crossed with gametes from parents of the same conditioning environment, meaning the data from
168 N parents are independent of data from U parents. Thus, we modeled data from each parental
169 conditioning environment in separate models. Utilizing Bayesian inference allowed direct
170 comparison of posterior probability distributions for model parameters of interest across different
171 models [35].

172 For each larval trait and parental conditioning environment model (4 total) we fit separate
173 intercepts for each larval development environment (N and U) to estimate population mean
174 larval plasticity across the two character states [10] and a measurer identity fixed effect (two-
175 level continuous covariate with values –0.5 and 0.5) to control for an average difference between
176 measurers. Random effects of dam and sire were fitted to estimate the variances in maternal or
177 paternal effects, respectively. Random effects of block and culture identity were included to
178 account for phenotypic similarity among larvae due to shared block effects or container
179 environments, respectively. Preliminary models indicated homogeneity of variances between
180 larval environments for the dam, sire, block, and culture effects. Thus, a single, common
181 variance across environments was fit for each of these random terms. We also fit separate larval
182 environment residual variances, but the cross-environment covariance was fixed to zero as this is
183 not estimable when individuals are only measured in a single environment.

184 Additive genetic (co)variances within and across larval rearing environments were
185 estimated to evaluate the adaptive potential of larval morphological traits and to quantify
186 variation in genotype-by-environment interactions. We fit random effects of individual identity
187 and associated these with a generalized inverse of the numerator relatedness matrix [36,37] that
188 was calculated from a pedigree constructed based on the breeding design using the nadiv
189 package [38]. Cross-environment additive genetic covariances are estimable, unlike residual
190 covariances, because related individuals in the two environments provide information about the
191 cross-environment covariance of genetic effects [39,40]. To interpret our estimates of cross-
192 environment additive genetic correlations, we ranked family mean additive genetic values for
193 comparison between larval rearing environments (ESM6).

194 Models employed diffuse normal prior distributions for all fixed effects (mean=0, 195 variance=10^{10}) and univariate parameter expanded prior distributions for rearing culture, block, 196 dam, and sire variance components with a scaling factor of 1000 to give scaled non-central F- 197 distributions with one numerator and denominator degrees of freedom [34,41]. A multivariate 198 parameter expanded prior was used for the additive genetic covariance matrix that gave a 199 uniform marginal prior distribution for the correlation. A weak inverse Wishart prior was set for 200 the matrix of residual variances (model details are provided within R code at 201 https://github.com/qgevoeco/QGplasticity_S_purpuratus).

202 Models were run for an initial burn-in of 200000 (spicule length) or 130000 (body length) 203 iterations, after which every 1000th iteration was retained in the posterior distribution to yield 204 2000 sample MCMC chains for each model that had absolute autocorrelation values <0.1. We 205 report the marginal posterior mean, mode, and 95% highest posterior density credible interval 206 (95%CI) and for key parameters plot full marginal posterior distributions alongside prior 207 distributions to further facilitate interpretation (ESM4).

208 Narrow-sense heritability was calculated as additive genetic variance (V_A) divided by 209 total phenotypic variance (V_P), where $V_P = V_A + V_{dam} + V_{sire} + V_{culture} + V_{block} + V_{residual}$. 210 Evolvability ($I_A$; [42]), which is a mean standardized additive genetic variance, was calculated as 211 V_A / INT^2, where INT is the model intercept for a given developmental environment and 212 represents the phenotypic mean, marginalizing over measurer effects. Heritability gives an 213 absolute measure of expected evolutionary change, whereas evolvability expresses a proportional 214 change and is therefore more suitable for comparative purposes [42]. Note, heritability and 215 evolvability of the scaled response (i.e., spicule or body length × 100) are the same values for the 216 response on the un-transformed scale. Posterior distributions were obtained for all summary

217 statistics (e.g., heritability, I_A, and differences between V_As as well as I_As) and differences
218 between marginal posterior distributions by calculating desired values across each MCMC
219 sample.
220

221 3. Results

222 *(a) Environmental conditioning reveals plasticity of larval traits*

223 There was an effect of developmental environment on larval phenotypes: we observed a
224 reduction in spicule length in larvae developed in U conditions compared to N (figure 2).
225 However, spicule length in the U developmental environment depended on parental
226 conditioning. Larvae where both the parents and embryonic development occurred in upwelling
227 conditions (UU) had higher mean spicule length than larvae that developed in N conditions after
228 parents were conditioned in U (NU) (figure 2*a*). For example, there is a 0.953 probability that
229 UU spicule length is at least 7% larger than NU (or 6.2µm larger) as calculated across the full
230 probability distribution of differences (ESM 4). As with spicule length, embryonic development
231 in U led to decreased mean body length (figure 2*b*), with the combined effect of parental and
232 development U environments (UU) increasing mean body length from just the development U
233 treatment (NU). After controlling for random effects of dam and block, there was no significant
234 difference in egg diameter observed between the two parental treatments (p=0.511). Further, egg
235 size was not a good predictor of larval body size morphometrics (spicule length: R^2=-0.017,
236 p=0.5546, body size R^2=-0.025, p=0.876) (ESM3 figure S1). The proportion of developmental
237 abnormalities was scored amongst all crosses and was highest in larvae from parents conditioned
238 to upwelling that experienced upwelling embryonic development as well (UU) (ESM3 figure
239 S2).

240

241 *(b) Components of variation in larval traits*

242 To assess the potential evolutionary responses to abiotic conditions associated with upwelling,
243 we quantified variance components of larval body size metrics. Additive genetic variance
244 depended on developmental environment: additive genetic variances for spicule length are larger
245 in the upwelling developmental environment (ESM2 table S2; ESM5 figure S3*a-d*). The
246 marginal posterior mean (95% CI) difference between additive genetic variance when larvae
247 developed in U environments as opposed to N was 1.12 (-0.268 to 2.54) when parents were
248 conditioned in N (i.e., NU-NN) and 0.407 (-0.854 to 1.51) when parents were conditioned in U
249 (UU-UN). Though the credible intervals span zero for these differences, there is 0.945 and 0.770
250 probability that the estimates differ from one another (i.e., difference is greater than zero for the
251 NU-NN and UU-UN differences, respectively). The similarity of the U developmental
252 environment posterior means and modes as well as large differences between prior and posterior
253 probability density curves indicate high posterior probability that is informed by the data and not
254 the prior (ESM5 figure S3*b,d*). In contrast, body length shows much less additive genetic
255 variance for all treatments (ESM5 figure S6*a-d*). The posterior means for all treatments are less
256 than approximately 0.25 and the lower credible interval limits all converge to zero indicating
257 relatively high posterior probability at small values of effectively zero (ESM4).

258 To determine the extent of among-genotype variability in the family-level plastic
259 response, and hence genetic variation underlying phenotypic plasticity, we quantified cross-
260 developmental environment genetic correlations. For spicule length, the marginal posterior
261 distributions of the cross-development environment additive genetic correlations have posterior
262 means and modes close to zero and are broad (figure 3*e,f*), with credible intervals that span most

263 of the range of possible values, indicating some relative re-ranking of genotypes as they are
264 expressed in the two development environments (figure 3*a,b*). The upper limits of these credible
265 intervals are 0.81 or less (ESM2 table S2), excluding values near 1, hence indicative of
266 significant variance for genotype-by-environment interactive effects. Similarly for body size, the
267 marginal posterior distributions of the cross-developmental environment additive genetic
268 correlations are broad (figure 3*g,h*), with means and modes close to zero and credible intervals
269 that span most of the range of possible values (ESM2 table S3), indicating relative re-ranking of
270 genotypes as they are expressed in the two development environments (figure 3*c,d*). For body
271 size there are differences in cross-development environmental genetic correlations depending on
272 parental condition as there is approximately 0.63 posterior probability for a negative cross-
273 environment genetic correlation among larvae of non-upwelling parents versus 0.67 posterior
274 probability for a positive cross-environment genetic correlation among larvae of upwelling
275 parents. This suggests varying magnitudes of variance in genotype-by-environment interactions
276 (figure 3*g,h*), but uncertainty limits the importance of this conclusion.

277 For both spicule length and body size, dam, sire, block, and culture variances that capture
278 any remaining parental, non-additive genetic, or environmental effects all independently
279 contributed little to overall phenotypic variance (ESM2 tables S2 & S3, ESM5 figures S4 & S7).
280 Within each parental environment of both larval body size traits, sire and dam variances did not
281 differ between development environments, and hence were constrained to be equal in the model
282 (see Methods), indicating trans-generational parental effects did not vary based on offspring
283 development environment. Residual variances were largely similar between development
284 environments, both within and among parental treatments, and similar in magnitude to the
285 additive genetic variance (ESM2 tables S2 & S3, ESM5 figures S5 & S8).

286

287 *(c) Evolvability of larval body size and spicule length*

288 To quantify the potential for *S. purpuratus* evolutionary responses to U conditions simulated in
289 the lab*,* we assessed potential differences in heritability (h^2) and evolvability (I_A) to allow
290 comparisons across additive genetic variance estimates from different environments or even
291 different traits. Similar to additive genetic variance, we observed relatively smaller values of
292 heritability and evolvability in spicule length of larvae that developed in N environments (i.e.,
293 NN and UN; figure 4*a-d*, ESM2 table S2, ESM5 figure S3*e-h*). When larvae developed in U
294 conditions, substantial levels of heritability and moderate evolvability were observed with
295 differences in magnitude between the two larval U treatments depending on parental
296 environment (figure 4*b,d*, ESM2 table S2, ESM5 figure S3*f,h*). The marginal posterior mean
297 (95% CI) difference between evolvability when larvae developed in U environments as opposed
298 to N was 0.0161 (0.000753 to 0.0344) when parents were conditioned in N (i.e., NU-NN) and
299 0.00462 (-0.00486 to 0.0146) when parents were conditioned in U (UU-UN). Though the
300 credible interval spans zero for the difference between larval development environments when
301 parents were conditioned in U (UU-UN), there is 0.676 probability that this difference is 0.0025
302 or greater. In contrast to spicule length, the heritability and evolvability values for body length
303 were lower for both treatments when the parents were in N conditions (NN and NU) and
304 decreased further when the parents were reared in the U environment (UN and UU; figure 4*e-h*,
305 ESM2 table S3, ESM5 figure S6*e-h*).

306

307 ## 4. Discussion

308 *(a) The role of plasticity in shaping larval traits*

309 We observed phenotypic plasticity in *S. purpuratus* larvae reared in different developmental
310 environments, which has similarly been observed in other independent studies [27,28]. Both
311 spicule length and larval body size were reduced when reared in upwelling conditions even after
312 controlling for potentially confounding effects of developmental delay. We found evidence of
313 genetic variation in phenotypic plasticity, or genotype-by-environment interactions (GxE),
314 suggesting genotypes exhibit different plastic responses to an upwelling developmental
315 environment (figure 3). Rankings of additive genetic values across families become reordered
316 amongst full siblings exposed to different developmental conditions. *S. purpuratus* habitats tend
317 towards being highly heterogeneous, characterized by highly dynamic upwelling regimes that
318 vary in time and space [29,43] which will likely grow in frequency and intensity in future years
319 [15,16]. These heterogeneous environments appear to have favored plasticity and maintenance of
320 GxE in prism stage morphometrics, therefore slopes of reaction norms are not likely to be under
321 strong directional selection. While it is known that larval body size morphometrics are important
322 predictors of later stage survival and settlement, our results suggest prism stage morphometrics
323 measured here are either under relaxed selection [44], or selection that maintains variation in
324 GxE. While we measured morphometrics in early pre-feeding larvae, it is possible that later stage
325 larval feeding morphometrics could be under stronger selection pressure, potentially contributing
326 more to fitness, settlement, and survival. Ultimately, the temporal links between larval skeletal
327 morphometrics and larval survival should be further investigated in each environment to
328 discriminate between alternative explanations for the maintenance of variation in GxE.
329 Nevertheless, the variation in additive genetic value between families in response to different
330 developmental environments in our study, indicative of a genetic basis for phenotypic plasticity

331 in early stages of *S. purpuratus*, has important implications for the ability of this ecologically
332 important species to persist under future global change scenarios.

333 We investigated the role of parental effects, a form of phenotypic plasticity, on egg size
334 and larval body morphometrics. Egg size, a fitness trait associated with fertilization success and
335 postzygotic survival, is a direct result of maternal investment through provisioning of energy
336 reserves [45–48]. We observed no differences in mean egg diameter between dams conditioned
337 in the two treatments (ESM3 figure S1) when controlling for random effect of dam, similarly to
338 previous studies examining parental effects of upwelling stress [28,29]. Egg size has significant
339 influences on larval survival and recruitment success for a diversity of broadcast spawning
340 marine invertebrates; in echinoderms, egg volume and energetic content are highly correlated
341 [49], however, egg size is not always a robust predictor of energetic content in planktotrophic
342 species [46], including echinoderms ([28,29,50,51]). Our study did not find egg size to predict
343 larval size (ESM3 figure S1), although egg size was measured over a small range and energetic
344 content was not quantified. However, parental effects on prism larvae morphometrics were
345 observed (figure 2), suggesting parental conditioning induces latent effects that impact larval
346 fitness while early development from early embryo through gastrulation appear constrained and
347 unaffected by the environment, effects that are similarly observed in a previous experiment in *S.*
348 *purpuratus* [28]. This combined evidence of parental effects on larval morphometrics in *S.*
349 *purpuratus* could be explained by parental investment in mRNAs critical for development,
350 epigenetic processes, or differential investment of key nutrients in the eggs [27,52,53].
351 Transgenerational plasticity is mostly likely to occur when parental environments are predictive
352 of larval environments [54,55], which we observed: larvae developed in upwelling were larger
353 when their parents were also conditioned in upwelling conditions (figure 2). This suggests that

354 parental effects are a likely mechanism contributing to larval phenotypic change in response to
355 environmental conditions in *S. purpuratus.* Predictable high magnitude variation in
356 environmental parameters such as temperature and pH that occur throughout the life cycle of *S.*
357 *purpuratus* is likely to favor the maintenance of phenotypic plasticity. If this predictability
358 breaks down, broadcast spawning invertebrates such as *S. purpuratus* might be more likely to
359 exhibit bet-hedging type strategies to maintain populations, although this strategy lacks empirical
360 support in *S. purpuratus* populations studied to date [56].

361

362 *(b) The potential for adaptation to global change*

363 Adaptation to global change relies on sufficient natural genetic variation and genetic
364 correlations between selected traits. Larval body size is an important, often heritable, fitness trait
365 amongst diverse marine invertebrates but can vary based on differences in environmental effects
366 [25,57,58]. We observe higher additive genetic variance, heritability, and evolvability for spicule
367 length among larvae reared in upwelling conditions, compared to larvae reared in non-upwelling.
368 This indicates more potential for adaptive responses to conditions expected to occur under
369 anthropogenic change. *S. purpuratus* spawning activity occurs seasonally between December and
370 April, months characterized by upwelling episodes, which can last multiple days [29]; therefore,
371 the conditions in our experiment are relevant to what larvae are likely to experience in the wild.
372 Heritability values here are similar to previous estimates in *S. purpuratus* larval morphometric
373 traits after exposure to high pCO_2 [25]. Further, molecular experiments have shown that
374 upwelling conditions induce a stress response in *S. purpuratus* larvae [52]. This indicates that we
375 observe higher adaptive potential in larvae experiencing stressful environmental conditions,
376 despite additive genetic variance observed to be lower in unfavorable conditions in most studies

377 [59], including in sea urchins [58]. However, the majority of studies examining additive genetic
378 variance under stressful conditions employ a novel stress, whereas the conditions in our
379 experiment were chosen as end-points of temperature and pH already occurring naturally in their
380 environment.

381 Measures of evolvability allow us to quantify the relative extent to which phenotypes can
382 evolve in response to selection. In particular, evolvability is better suited than heritability for
383 comparing adaptive potential among environments, traits, or even species since evolvability
384 expresses change in proportion to the current trait mean (heritability expresses potential absolute
385 change) and heritability depends on the phenotypic variation in the population which itself can
386 be affected by the selective environment independent of the amount of additive genetic variance
387 [42]. We observe high evolvability in larvae reared under some conditions but not others,
388 suggesting a strong role of the environment in the evolvability of larval fitness traits in *S.*
389 *purpuratus*. For example, for larval spicule length, our posterior mean evolvability estimates
390 those developing in non-upwelling conditions (0.00205 and 0.00230 for parental conditioning in
391 non-upwelling and upwelling, respectively) are similar to the median evolvability of 0.001 for
392 length measures from 1,025 estimates compiled by Hansen & Pelabon [60]. However, our
393 evolvability estimates for spicule length of larvae developing in upwelling conditions (0.0182
394 and 0.00692 for parental conditioning environments non-upwelling and upwelling, respectively)
395 were well above the 75th percentile of 0.0047 from that same study. Minimal correlations among
396 larval rearing environments suggest that the highly variable environment *S. purpuratus*
397 experiences may limit the rate at which adaptation could occur. There is higher evolvability of
398 spicule length in larvae produced from adults conditioned in non-upwelling but developed in
399 upwelling (figure 4*b*, NU treatment) as opposed to those coming from parents conditioned to

400 upwelling and during embryonic development (figure 4*d*, UU treatment). This difference in
401 evolvability amounts to 0.0112 (posterior mean; 95%CI: –0.00463 to 0.0301), which represents a
402 potential evolutionary change in mean phenotype of approximately 1.1% more in the NU versus
403 UU treatments over a single generation. This observation suggests a subtle effect of parental
404 conditioning on the genetic contribution to phenotypic variance under upwelling conditions. We
405 also find effects of parental conditioning on plasticity and genetic contributions to phenotypic
406 variance. Plastic phenotypes, or those that shift in response to the environment, are biased toward
407 traits that have high additive genetic variance [61], which we observe in larval responses to
408 upwelling. These correlations can often be explained by developmental constraints that limit
409 phenotypic change in a particular direction. This is likely true in *S. purpuratus* early stages–
410 phenotypic change on spicule length appears to be less constrained, having both the potential to
411 be phenotypically plastic and able to be acted on by selection, as opposed to body size which
412 could be more constrained by development. However, spicule length plasticity is inherently
413 limited by the body size of the larvae, so further study into the genetic correlations and co-
414 variances between these two traits would be insightful as to how these traits contribute to
415 evolvability.
416
417 *(c) Trade-offs in larval fitness traits*
418 Developmental environments have been shown to shape later stage phenotypes in a
419 diversity of organisms and these changes in phenotypes can have trade-offs as well as latent
420 effects on later stages [62–64]. We found subtle effects of parental environment on larval traits;
421 of the larvae reared in the upwelling environment, having parents also conditioned to upwelling
422 (UU) led to an increase in spicule length compared to larvae whose parents were conditioned in

423 non-upwelling (NU). However, we observed a higher proportion of developmental abnormalities
424 amongst UU crosses, characterized by embryos that failed to successfully gastrulate. At the time
425 of adult collection, individuals were likely experiencing conditions more similar to non-
426 upwelling, therefore higher abnormalities could be explained by a mismatch between wild and
427 captive conditions for parental upwelling conditioned individuals. While upwelling parental
428 exposure may confer some benefit to larvae developing in upwelling conditions, there is a
429 compensatory trade-off in that many of the larvae derived from the UU crosses show higher
430 mortality as evident by early developmental abnormalities. As only properly developed larvae
431 were selected for morphometric analysis, this shows that the UU survivors were on average
432 larger than UN individuals. There is a well-established trade-off between growth and sensitivity
433 to high pCO_2 in coastal marine invertebrates, where slowed growth or reallocation of energy in
434 high pCO_2 facilitates high tolerance [64,65]. In the tropical urchin *Tripneustes gratilla*, parental
435 conditioning to high temperatures and high pCO_2 led to more resilient larvae with a trade-off of
436 reduced size [66]. While abnormality was high in UU crosses, the benefit of increased size
437 relative to UN crosses suggests a complex role of parental effects on early life-history stages.
438

439 ## 5. Conclusion

440 Climate models predict more frequent and severe incidences of upwelling in the future, which
441 will directly impact calcifying organisms within the California Large Marine Ecosystem, such as
442 *S. purpuratus* [15,16]. However, incorporating selection on larval body size into predictive
443 models show that negative effects of OA are likely overestimated, as larval body size exhibits
444 high heritability under these scenarios and *S. purpuratus* maintains large population sizes that
445 will enable adaptive responses to selection [67]. Our data builds upon this work to reveal that

446 effects are maintained in more ecologically relevant upwelling conditions (high pCO_2 and low
447 temperature). Additionally, we report the influence of parental environment on estimates of
448 adaptive genetic variation, which will alter how strong adaptation to increased upwelling may
449 impact these populations. Further, we report genetic variation in phenotypic plasticity, or
450 genotype by environment interactions, showing that phenotypic plasticity itself has potential to
451 evolve in this population. Therefore, in considering future upwelling scenarios, it is likely that
452 both phenotypic plasticity and adaptation will contribute to *S. purpuratus* population responses
453 to stressful periods of upwelling.
454

455 **Ethics:** Adult urchins were collected under the California Scientific Collecting Permit to GEH
456 (SC-1223).

457 **Data Accessibility:** Data and all R code are freely available on GitHub:
458 https://github.com/qgevoeco/QGplasticity_S_purpuratus.

459 **Author contributions:** Conceptualization MS, GH, MEW; Data curation, MS, MEW; Formal
460 analysis MS, MEW; Funding acquisition GH; Investigation MS, OS; Methodology MS, OS, GH;
461 Project administration MS, GH; Resources GH; Software; Supervision MEW, MS; Visualization
462 MEW, MS; Writing original draft MS, MEW; Writing review & editing MS, MEW, OS, GH.

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470
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472 References

473 1. Gienapp, P., Teplitsky, C., Alho, J. S., Mills, J. A. & Merilä, J. 2008 Climate change and
474 evolution: Disentangling environmental and genetic responses. *Mol. Ecol.* **17**, 167–178.
475 (doi:10.1111/j.1365-294X.2007.03413.x)
476 2. Davis, M. B., Shaw, R. G. & Etterson, J. R. 2005 Evolutionary responses to climate
477 change. *Ecology* **86**, 1704–1714.
478 3. Chevin, L. M., Collins, S. & Lefèvre, F. 2013 Phenotypic plasticity and evolutionary
479 demographic responses to climate change: Taking theory out to the field. *Funct. Ecol.* **27**,
480 967–979. (doi:10.1111/j.1365-2435.2012.02043.x)
481 4. Chirgwin, E., Marshall, D. J., Sgrò, C. M. & Monro, K. 2018 How does parental
482 environment influence the potential for adaptation to global change? *Proc. R. Soc. B Biol.*
483 *Sci.* **285**, 20181374. (doi:10.1098/rspb.2018.1374)
484 5. Uller, T., Nakagawa, S. & English, S. 2013 Weak evidence for anticipatory parental
485 effects in plants and animals. *J. Evol. Biol.* **26**, 2161–2170. (doi:10.1111/jeb.12212)
486 6. Swezey, D. S., Boles, S. E., Aquilino, K. M., Stott, H. K. & Bush, D. 2020 Evolved
487 differences in energy metabolism and growth dictate the impacts of ocean acidification on
488 abalone aquaculture. *PNAS* **117**, 1–7. (doi:10.1073/pnas.2006910117)
489 7. Murren, C. J. et al. 2015 Constraints on the evolution of phenotypic plasticity: Limits and
490 costs of phenotype and plasticity. *Heredity.* **115**, 293–301. (doi:10.1038/hdy.2015.8)

491 8. Hendry, A. P. 2016 Key questions on the role of phenotypic plasticity in eco-evolutionary
492 dynamics. *J. Hered.* **107**, 25–41. (doi:10.1093/jhered/esv060)
493 9. Schmalhausen, I. . 1949 *Factors of Evolution: The Theory of Stabilizing Selection.*
494 Philadelphia, PA.: Blakiston.
495 10. Via, S. & Lande, R. 1985 Genotype-Environment Interaction and the Evolution of
496 Phenotypic Plasticity. *Evolution.* **39**, 505–522.
497 11. Lush, J. . 1943 *Animal Breeding Plans*. Ames, Iowa: Iowa State College Press.
498 12. Lande, R. 1979 Quantitative Genetic Analysis of Multivariate Evolution , Applied to
499 Brain : Body Size Allometry. *Evolution.* **33**, 402–416.
500 13. Falconer, D. S. 1989 *Introduction to Quantitative Genetics. 3rd ed.* New York, NY: John
501 Wiley & Sons, Inc.
502 14. Feely, R. A., Sabine, C. L., Hernandez-Ayon, J. M., Ianson, D. & Hales, B. 2008
503 Evidence for upwelling of corrosive 'acidified' water onto the continental shelf. *Science*
504 *(80-.).* **320**, 1490–1492.
505 15. Sydeman, W. J., García-Reyes, M., Schoeman, D. S., Rykaczewski, R. R., Thompson, S.
506 a, Black, B. a & Bograd, S. J. 2014 Climate change. Climate change and wind
507 intensification in coastal upwelling ecosystems. *Science* **345**, 77–80.
508 (doi:10.1126/science.1251635)
509 16. Bakun, A., Black, B. A., Bograd, S. J., García-Reyes, M., Miller, A. J., Rykaczewski, R.
510 R. & Sydeman, W. J. 2015 Anticipated Effects of Climate Change on Coastal Upwelling
511 Ecosystems. *Curr. Clim. Chang. Reports* **1**, 85–93. (doi:10.1007/s40641-015-0008-4)
512 17. Bednaršek, N., Naish, K. A., Feely, R. A., Hauri, C., Kimoto, K., Hermann, A. J., Michel,
513 C., Niemi, A. & Pilcher, D. 2021 Integrated Assessment of Ocean Acidification Risks to

514 Pteropods in the Northern High Latitudes: Regional Comparison of Exposure, Sensitivity
515 and Adaptive Capacity. *Front. Mar. Sci.* **8**, 1–23. (doi:10.3389/fmars.2021.671497)
516 18. Kroeker, K. J., Kordas, R. L., Crim, R., Hendriks, I. E., Ramajo, L., Singh, G. S., Duarte,
517 C. M. & Gattuso, J.-P. 2013 Impacts of ocean acidification on marine organisms:
518 quantifying sensitivities and interaction with warming. *Glob. Chang. Biol.* **19**, 1884–96.
519 (doi:10.1111/gcb.12179)
520 19. Allen, J. D. 2008 Size-specific predation on marine invertebrate larvae. *Biol. Bull.* **214**,
521 42–49. (doi:10.2307/25066658)
522 20. Chan, K. Y. K. 2012 Biomechanics of larval morphology affect swimming: Insights from
523 the sand dollars Dendraster excentricus. *Integr. Comp. Biol.* **52**, 458–469.
524 (doi:10.1093/icb/ics092)
525 21. Strathmann, R. R. 1971 The feeding behavior of planktotrophic echinoderm larvae:
526 Mechanisms, regulation, and rates of suspensionfeeding. *J. Exp. Mar. Bio. Ecol.* **6**, 109–
527 160. (doi:10.1016/0022-0981(71)90054-2)
528 22. Hofmann, G. E., Barry, J. P., Edmunds, P. J., Gates, R. D., Hutchins, D. A., Klinger, T. &
529 Sewell, M. A. 2010 The effect of ocean acidification on calcifying organisms in marine
530 ecosystems: an organism-to-ecosystem perspective. *Annu. Rev. Ecol. Evol. Syst. Vol 41*
531 **41**, 127–147. (doi:DOI 10.1146/annurev.ecolsys.110308.120227)
532 23. Kroeker, K. J., Kordas, R. L., Crim, R. N. & Singh, G. G. 2010 Meta-analysis reveals
533 negative yet variable effects of ocean acidification on marine organisms. *Ecol. Lett.* **13**,
534 1419–34. (doi:10.1111/j.1461-0248.2010.01518.x)
535 24. Chan, K. Y. K. & Tong, C. S. D. 2020 Temporal variability modulates pH impact on
536 larval sea urchin development. *Conserv. Physiol.* **8**, 1–11. (doi:10.1093/conphys/coaa008)

537 25. Kelly, M. W., Padilla-Gamiño, J. L. & Hofmann, G. E. 2013 Natural variation and the
538 capacity to adapt to ocean acidification in the keystone sea urchin Strongylocentrotus
539 purpuratus. *Glob. Chang. Biol.* **19**, 2536–2546. (doi:10.1111/gcb.12251)
540 26. Strader, M. E., Wong, J. M. & Hofmann, G. E. 2020 Ocean acidification promotes broad
541 transcriptomic responses in marine metazoans: A literature survey. *Front. Zool.* **17**, 1–23.
542 (doi:10.1186/s12983-020-0350-9)
543 27. Wong, J. M., Johnson, K. M., Kelly, M. W. & Hofmann, G. E. 2018 Transcriptomics
544 reveal transgenerational effects in purple sea urchin embryos: Adult acclimation to
545 upwelling conditions alters the response of their progeny to differential pCO2levels. *Mol.*
546 *Ecol.* **27**, 1120–1137. (doi:10.1111/mec.14503)
547 28. Wong, J. M., Kozal, L. C., Leach, T. S., Hoshijima, U. & Hofmann, G. E. 2019
548 Transgenerational effects in an ecological context: Conditioning of adult sea urchins to
549 upwelling conditions alters maternal provisioning and progeny phenotype. *J. Exp. Mar.*
550 *Bio. Ecol.* **517**, 65–77. (doi:10.1016/j.jembe.2019.04.006)
551 29. Hoshijima, U. & Hofmann, G. E. 2019 Variability of Seawater Chemistry in a Kelp Forest
552 Environment Is Linked to in situ Transgenerational Effects in the Purple Sea Urchin ,
553 Strongylocentrotus purpuratus. *Front. Mar. Sci.* **6**, 1–18. (doi:10.3389/fmars.2019.00062)
554 30. Wong, J. M., Johnson, K. M., Kelly, M. W. & Hofmann, G. E. 2018 Transcriptomics
555 reveal transgenerational effects in purple sea urchins exposed to upwelling conditions, and
556 the response of their progeny to differential p CO $_2$ levels. *Mol. Ecol.*
557 (doi:10.1111/mec.14503)
558 31. Castorani, M. C. N., Harrer, S. L., Miller, R. J. & Reed, D. C. 2021 Disturbance structures
559 canopy and understory productivity along an environmental gradient. *Ecol. Lett.* **24**,

560 2192–2206. (doi:10.1111/ele.13849)

561 32. Fangue, N. A., O'Donnell, M. J., Sewell, M. A., Matson, P. G., MacPherson, A. C. &
562 Hofmann, G. E. 2010 A laboratory-based, experimental system for the study of ocean
563 acidification effects on marine invertebrate larvae. *Limnol. Oceanogr. Methods* **8**, 441–
564 452. (doi:10.4319/lom.2010.8.441)

565 33. Bates, D., Mächler, M., Bolker, B. M. & Walker, S. C. 2015 Fitting linear mixed-effects
566 models using lme4. *J. Stat. Softw.* **67**. (doi:10.18637/jss.v067.i01)

567 34. Hadfield, J. D. 2010 MCMC methods for multi-response generalized linear mixed models:
568 the MCMCglmm R package. *J. Stat. Softw.* **33**, 1–22. (doi:10.1002/ana.22635)

569 35. Morrissey, M. B., de Villemereuil, P., Doligez, B. & Gimenez, O. 2014 Bayesian
570 approaches to the quantitative genetic analysis of natural populations. In *Quantitative*
571 *Genetics in the Wild (eds A Charmantier, D Garant, LEB Kruuk)*, pp. 228–253. Oxford,
572 UK: Oxford University Press.

573 36. Henderson, C. R. 1973 Sire evaluation and genetic trends. *J. Anim. Sci.* , 10–41.

574 37. Kruuk, L. E. B. 2004 Estimating genetic parameters in natural populations using the
575 'animal model'. *Philos. Trans. R. Soc. B Biol. Sci.* **359**, 873–890.
576 (doi:10.1098/rstb.2003.1437)

577 38. Wolak, M. E. 2012 Nadiv: An R package to create relatedness matrices for estimating
578 non-additive genetic variances in animal models. *Methods Ecol. Evol.* **3**, 792–796.
579 (doi:10.1111/j.2041-210X.2012.00213.x)

580 39. Mrode, R. A. 2015 *Linear Models for the Prediction of Animal Breeding Values. 2nd ed.*
581 Cambridge, MA: CABI Publishing.

582 40. Wolak, M. E., Roff, D. A. & Fairbairn, D. J. 2015 Are we underestimating the genetic

583 variances of dimorphic traits? *Ecol. Evol.* **5**, 590–597. (doi:10.1002/ece3.1361)

584 41. Gelman, A. 2006 Prior distributions for variance parameters in hierarchical models
585 (Comment on Article by Browne and Draper). *Bayesian Anal.* **1**, 515–534.
586 (doi:10.1214/06-BA117A)

587 42. Houle, D. 1992 Comparing evolvability and variability. *Genetics* **130**, 195–204.

588 43. Kapsenberg, L. & Hofmann, G. E. 2016 Ocean pH time-series and drivers of variability
589 along the northern Channel Islands, California, USA. *Limnol. Oceanogr.* **61**, 953–968.
590 (doi:10.1002/lno.10264)

591 44. Lahti, D. C., Johnson, N. A., Ajie, B. C., Otto, S. P., Hendry, A. P., Blumstein, D. T.,
592 Coss, R. G., Donohue, K. & Foster, S. A. 2009 Relaxed selection in the wild. *Trends Ecol.*
593 *Evol.* **24**, 487–496. (doi:10.1016/j.tree.2009.03.010)

594 45. Villinski, J. T., Villinski, J. C., Byrne, M. & Raff, R. A. 2002 Convergent maternal
595 provisioning and life-history evolution in Echinoderms. *Evolution.* **56**, 1764–1775.

596 46. Moran, A. L. & McAlister, J. S. 2009 Egg size as a life history character of marine
597 invertebrates: is it all it's cracked up to be? *Biol. Bull.* **216**, 226–242.
598 (doi:10.2307/25548157)

599 47. Falkner, I., Sewell, M. A. & Byrne, M. 2015 Evolution of maternal provisioning in
600 ophiuroid echinoderms: Characterisation of egg composition in planktotrophic and
601 lecithotrophic developers. *Mar. Ecol. Prog. Ser.* **525**, 1–13. (doi:10.3354/meps11217)

602 48. Caballes, C. F., Pratchett, M. S., Kerr, A. M. & Rivera-Posada, J. A. 2016 The role of
603 maternal nutrition on oocyte size and quality, with respect to early larval development in
604 the coral-eating starfish, acanthaster planci. *PLoS One* **11**, 1–21.
605 (doi:10.1371/journal.pone.0158007)

606 49. Moran, A. L., McAlister, J. S. & Whitehill, E. A. G. 2013 Eggs as energy: Revisiting the
607 scaling of egg size and energetic content among echinoderms. *Biol. Bull.* **224**, 184–191.
608 (doi:10.1086/BBLv224n3p184)
609 50. McEdward, L. R. 1986 Comparative morphometrics of echinoderm larvae. I. Some
610 relationships between egg size and initial larval form in echinoids. *J. Exp. Mar. Bio. Ecol.*
611 **96**, 251–265. (doi:10.1016/0022-0981(86)90206-6)
612 51. Mcedward, L. R. & Janies, D. A. 1997 Relationships among development, ecology, and
613 morphology in the evolution of echinoderm larvae and life cycles. *Biol. J. Linn. Soc.* **60**,
614 381–400. (doi:10.1006/bijl.1996.0107)
615 52. Strader, M. E., Kozal, L. C., Leach, T. S., Wong, J. M., Chamorro, J. D., Housh, M. J. &
616 Hofmann, G. E. 2020 Examining the role of DNA methylation in transcriptomic plasticity
617 of early stage sea urchins: Developmental and maternal effects in a kelp forest herbivore.
618 *Front. Mar. Sci.* **7**. (doi:10.3389/fmars.2020.00205)
619 53. Eirin-Lopez, J. M. & Putnam, H. M. 2019 Marine Environmental Epigenetics. *Ann. Rev.*
620 *Mar. Sci.* **11**. (doi:10.1146/annurev-marine-010318-095114)
621 54. Donelan, S. C., Hellmann, J. K., Bell, A. M., Luttbeg, B., Orrock, J. L., Sheriff, M. J. &
622 Sih, A. 2020 Transgenerational Plasticity in Human-Altered Environments. *Trends Ecol.*
623 *Evol.* **35**, 115–124. (doi:10.1016/j.tree.2019.09.003)
624 55. Marshall, D. J. & Uller, T. 2007 When is a maternal effect adaptive? *Oikos* **116**, 1957–
625 1963. (doi:10.1111/j.2007.0030-1299.16203.x)
626 56. Flowers, J. M., Schroeter, S. C. & Burton, R. S. 2002 The recruitment sweepstakes has
627 many winners: Genetic evidence from the sea urchin Strongylocentrotus purpuratus.
628 *Evolution.* **56**, 1445–1453. (doi:10.1111/j.0014-3820.2002.tb01456.x)

629 57. Griffiths, J., Johnson, K., Sirovy, K., Yeats, M., Pan, F., La Peyre, J. & Kelly, M. 2021
630 Transgenerational plasticity and the capacity to adapt to low salinity in the eastern oyster,
631 Crassostrea virginica.
632 58. Sunday, J. M., Crim, R. N., Harley, C. D. G. & Hart, M. W. 2011 Quantifying rates of
633 evolutionary adaptation in response to ocean acidification. *PLoS One* **6**, 1–8.
634 (doi:10.1371/journal.pone.0022881)
635 59. Charmantier, A. & Garant, D. 2005 Environmental quality and evolutionary potential:
636 Lessons from wild populations. *Proc. R. Soc. B Biol. Sci.* **272**, 1415–1425.
637 (doi:10.1098/rspb.2005.3117)
638 60. Hansen, T. F. & Pélabon, C. 2021 Evolvability : A Quantitative-Genetics Perspective.
639 *Annu. Rev. Ecol. Evol. Syst.* **52**, 153–175.
640 61. Noble, D. W. A., Radersma, R. & Uller, T. 2019 Plastic responses to novel environments
641 are biased towards phenotype dimensions with high additive genetic variation. *Proc. Natl.*
642 *Acad. Sci. U. S. A.* **116**, 13452–13461. (doi:10.1073/pnas.1821066116)
643 62. West-Eberhard, M. J. 2003 *Developmental Plasticity and Evolution*. Oxford University
644 Press.
645 63. Sasaki, M. C. & Dam, H. G. 2020 Genetic differentiation underlies seasonal variation in
646 thermal tolerance , body size , and plasticity in a short-lived copepod. *Ecol. Evol.* , 1–11.
647 (doi:10.1002/ece3.6851)
648 64. Swezey, D. S., Boles, S. E., Aquilino, K. M., Stott, H. K. & Bush, D. 2020 Evolved
649 differences in energy metabolism and growth dictate the impacts of ocean acidification on
650 abalone aquaculture. *PNAS* , 1–7. (doi:10.1073/pnas.2006910117)
651 65. Pan, T.-C. F., Applebaum, S. L. & Manahan, D. T. 2015 Experimental ocean acidification

652 alters the allocation of metabolic energy. *Proc. Natl. Acad. Sci.* **112**, 4696–4701.
653 (doi:10.1073/pnas.1416967112)
654 66. Karelitz, S., Lamare, M. D., Mos, B., De Bari, H., Dworjanyn, S. A. & Byrne, M. 2019
655 Impact of growing up in a warmer, lower pH future on offspring performance:
656 transgenerational plasticity in a pan-tropical sea urchin. *Coral Reefs* **38**, 1085–1095.
657 (doi:10.1007/s00338-019-01855-z)
658 67. Kelly, M. W. & Hofmann, G. E. 2013 Adaptation and the physiology of ocean
659 acidification. *Funct. Ecol.* **27**, 980–990. (doi:10.1111/j.1365-2435.2012.02061.x)

660 **Figure Legends**

661

662 **Figure 1. Experimental crossing design.** Adult urchins were conditioned for four months to
663 either non-upwelling conditions (N) or upwelling conditions (U). Gametes from two males and
664 two females from each condition were crossed reciprocally, generating four distinct crosses, each
665 replicated four times. Two replicates from each cross were reared in the same condition as the
666 parents (NN, UU) or the opposite condition (NU, UN). Two by two crosses for each parental
667 condition were performed 5 times in succession for a total of 40 unique crosses. Spicule length
668 and body length were measured in prism stage larvae, pictured.

669

670 **Figure 2. *Strongylocentrotus purpuratus* larvae exhibit phenotypic plasticity.** Marginal
671 posterior means and 95% credible intervals (error bars) of parameters estimated in linear mixed
672 models for spicule (*a*) and body (*b*) length of larvae reared in either non-upwelling (N) or
673 upwelling (U) developmental environments. Parents were either conditioned in the non-
674 upwelling (circles) or upwelling (triangles) environments (black solid lines connect treatment
675 means from the same parental environment). Plotted colors and letters refer to treatment
676 combinations as detailed in figure 1.

677

678 **Figure 3. Variation in family-level genetic reaction norms and correlations.** Ranked family
679 mean additive genetic value for spicule length (*a, b*) and body length (*c, d*). Family mean
680 additive genetic values were calculated across all posterior samples to produce a posterior
681 distribution, from which the posterior mode was ranked for each larval environment. Black (top
682 10 ranked families in Non-Upwelling larval environment) and grey (bottom 10 ranked families
683 in Non-Upwelling larval environment) lines connect family mean genetic value ranks across

684 developmental environments and point colors refer to treatment combinations as detailed in
685 figure 1. Cross-developmental environment additive genetic correlation of larval spicule length
686 (*e, f*) and larval body size (*g, h*). Marginal posterior MCMC samples (histogram bars with the
687 range of samples depicted underneath by the thin black line), kernel density estimate (pink line),
688 posterior mean (red diamond) and mode (blue cross), 95% credible interval (grey bar), and prior
689 density (grey line).
690
691
692 **Figure 4. Evolvability.** *S. purpuratus* spicule (*a*-*d*) and body (*e*-*h*) length marginal posterior
693 MCMC samples (histogram bars with sample range depicted underneath by the thin black line),
694 kernel density estimate (black line), posterior mean (red diamond) and mode (blue cross), 95%
695 credible interval (grey bar), and prior density (grey line) for the evolvability (I_A). Colors refer to
696 treatment combinations as detailed in figure 1.
697