

1 **Nurtured by nature: Considering the role of environmental and parental legacies in**
2 **coral ecological performance**

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4 Hollie M. Putnam¹, Raphael Ritson-Williams², Jolly Ann Cruz³, Jennifer M. Davidson²,
5 Ruth D. Gates²

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7 ¹University of Rhode Island, Department of Biological Sciences, Kingston, RI USA

8 ²Hawai‘i Institute of Marine Biology, University of Hawai‘i, Mānoa, HI, USA

9 ³Micronesia Islands Nature Alliance, Garapan, Saipan 96950, CNMI

10 * Corresponding author: hputnam@uri.edu, 401-874-9510

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12 Keywords: trans-generational plasticity, epigenetics, hormesis, *Pocillopora damicornis*,
13 *Pocillopora acuta*

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24 **Abstract**

25 The persistence of reef building corals is threatened by human-induced environmental
26 change. Maintaining coral reefs into the future requires not only the survival of adults,
27 but also the influx of recruits to promote genetic diversity and retain cover following
28 adult mortality. Few studies examine the linkages among multiple life stages of corals,
29 despite a growing knowledge of carryover effects in other systems. We provide a novel
30 test of coral parental preconditioning to ocean acidification (OA) to better understand
31 impacts on the processes of offspring recruitment and growth. Coral planulation was
32 tracked for three months following adult exposure to high pCO₂ and offspring from the
33 second month were reciprocally exposed to ambient and high pCO₂. Offspring of parents
34 exposed to high pCO₂ had greater settlement and survivorship immediately following
35 release, retained survivorship benefits during one and six months of continued exposure,
36 and further displayed growth benefits to at least one month post release. Enhanced
37 performance of offspring from parents exposed to high conditions was maintained despite
38 the survivorship in both treatments declining in continued exposure to OA.
39 Preconditioning of the adults while they brood their larvae may provide a form of
40 hormetic conditioning, or environmental priming that elicits stimulatory effects. Defining
41 mechanisms of positive carryover effects, or positive trans-generational plasticity, is
42 critical to better understanding ecological and evolutionary dynamics of corals under
43 regimes of increasing environmental disturbance. Considering parental and
44 environmental legacies in ecological and evolutionary projections may better account for
45 coral reef response to the chronic stress regimes characteristic of climate change.

46

47 **Introduction**

48 Reef-building corals are the foundation for one of the most diverse and economically
49 important ecosystems (Bishop et al., 2011; Costanza et al., 2014). Corals are sensitive to
50 changes in their environment that destabilize the coral-algal symbiosis and disrupt reef
51 primary production and net ecosystem accretion. Even slight perturbations in temperature
52 nutrients, light, salinity, and pollution, can negatively affect coral symbiosis and
53 performance (Lesser, 2011) The steady increase in CO₂ emissions (Pachauri et al., 2014)
54 is heightening the magnitude and frequency of global scale environmental perturbations,
55 exacerbating reef decline already occurring due to local pressures.

56 The emission of CO₂ is driving elevated atmospheric levels, which is in turn
57 changing the chemistry of the oceans. Ocean acidification (OA) is occurring due to the
58 absorption of atmospheric CO₂ by the ocean and the resulting increase and decrease in
59 the concentrations of H⁺ and CO₃⁻² ion concentrations, respectively (Doney, Fabry, Feely,
60 & Kleypas, 2009). OA energetically challenges calcifying marine organisms because they
61 expend more energy for acid-base regulation to both maintain cellular homeostasis
62 (Kaniewska et al., 2012; Stumpp et al., 2012) and calcify in a medium with lower CO₃⁻²
63 ion concentrations. The physiological and ecological consequences of OA range from
64 changes in intracellular pH (Gibbin, Putnam, Davy, & Gates, 2014; Gibbin, Putnam,
65 Gates, Nitschke, & Davy, 2015), to direct reduction of calcification of coral skeletons
66 (Erez, Reynaud, Silverman, Schneider, & Allemand, 2011), to shifts in community
67 composition in low pH areas (Fabricius et al., 2011). Further, the interaction of multiple
68 stressors such as temperature and OA is likely to result in synergistic and antagonistic

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69 responses in comparison to the responses driven by individual stressors (Harvey, Gwynn-
70 Jones, & Moore, 2013; Pandolfi, Connolly, Marshall, & Cohen, 2011).

71 Given that local coral reef decline is now exacerbated by global issues, a greater
72 effort is being made to better understand the sub-lethal physiological effects of stressors
73 on critical coral reef processes such as coral reproduction and early life stages (Albright,
74 2011; Byrne & Przeslawski, 2013). Corals are long-lived organisms with complex
75 reproductive life history characteristics (Baird, Guest, & Willis, 2009). Early life history
76 research has focused heavily on the effects of anthropogenic factors (e.g., increased
77 temperature and ocean acidification) on fertilization and development, metamorphosis,
78 settlement, and survivorship in spawning corals (Albright, 2011; Chua, Leggat, Moya, &
79 Baird, 2013; Chua, Leggat, Moya, & Baird, 2013; Foster, Gilmour, Chua, Falter, &
80 McCulloch, 2015; Negri, Marshall, & Heyward, 2007; Randall & Szmant, 2009), and a
81 variety of physiological metrics in brooding corals (Cumbo, Edmunds, Wall, & Fan,
82 2013; Dufault, Cumbo, Fan, & Edmunds, 2012; Putnam, Edmunds, & Fan, 2010; Rivest
83 & Hofmann, 2014, 2015). Few studies have, however, tracked corals through multiple
84 life history stages including larval supply, settlement and post-settlement survival and
85 growth (Albright, 2011; Ritson-Williams, Arnold, & Paul, 2016; Ross, Ritson-Williams,
86 Olsen, & Paul, 2013), fewer still at the cross-generational scale (Putnam & Gates, 2015),
87 and none at the multigenerational scale. Thus the forecasts for population persistence and
88 replenishment have largely ignored the potentially substantial plasticity driven by
89 environmental and parental legacies (Donelson, Salinas, Munday, & Shama, 2017; Torda
90 et al., 2017).

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91 Phenotypic plasticity, or the generation of multiple performance outcomes within
92 an individual as a function of environment, has the potential to act as a buffer to rapid
93 environmental change and modulate evolutionary response (Chevin, Collins, & Lefèvre,
94 2013; Gibbin et al., 2017; Putnam & Gates, 2015). Multiple avenues can generate this
95 plasticity. While intra-generational studies of phenotypic plasticity are more common, the
96 study of trans-generational plasticity (TGP) is still in its relative infancy for marine
97 invertebrates (Donelson et al., 2017; Foo & Byrne, 2016; Ross, Parker, & Byrne, 2016;
98 Torda et al., 2017). TGP occurs when environmental legacies manifest through linked life
99 stages (i.e., the norms of reaction are shaped by the environmental conditions of prior
100 generations). Due to the difficulty of disentangling TGP *sensu stricto* (Donelson et al.,
101 2017; Torda et al., 2017), the plasticity exhibited between life stages can also be more
102 generically discussed as carryover effects, which encompass the potential for TGP and
103 developmental acclimation. The lack of data on these life stage linkages in corals is now
104 particularly critical in light of severe ecosystem declines and the growing
105 acknowledgement that adaptive responses are necessary for persistence under rapid
106 climate change (Gaylord et al., 2015; Munday, Warner, Monro, Pandolfi, & Marshall,
107 2013; Sunday et al., 2014; Sunday, Crim, Harley, & Hart, 2011).

108

109 The ecological and evolutionary ramifications of carryover effects from parental
110 or early life stage exposure in longer-lived, ecosystem engineering, calcifying marine
111 invertebrates in response to OA remain to be determined. To date, early life stage
112 exposure often appears to have negative carryover effects. Assessment of Olympia oyster
113 performance following exposure to high pCO₂ at the larval stage by Hettinger and

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114 coauthors revealed slower growth under high conditions. Even after the juveniles were
115 placed in ambient grow out conditions, negative carryover effects remained at 45 days
116 post exposure (Hettinger et al., 2012). Further assessment of the ecological performance
117 of *Olympia* oyster growth in ambient field conditions four months post exposure to high
118 pCO₂, revealed negative carryover effects on growth rate (Hettinger et al., 2013). Some
119 corals also appear to display negative carryover effects from stressors at the larval stage.
120 In larvae of *Orbicella faveolata*, low salinity treatments caused decreased survival and
121 growth after settlement (Vermeji et al., 2006). Similarly, in larvae of *Porites astreoides*
122 early life exposure to elevated seawater temperatures caused significantly higher
123 mortality in settled coral spat ~3 weeks post exposure in comparison to larvae raised in
124 ambient temperatures (Ross et al., 2013). While studies in both oysters and corals identify
125 carryover effects of early life stage exposure to stressors, this does not account for
126 plasticity that may be induced by parental environment (i.e., TGP).

127 Depending on the timing of exposure, environmental conditioning can set
128 organisms on different physiological and ecological trajectories (Foo & Byrne, 2016;
129 Ross et al., 2016; Torda et al., 2017). Studies considering the ontogenetic connections in
130 organisms with shorter life spans such as plankton, worms, oysters, clams, and fishes,
131 have documented substantial, and often positive TGP (Chakravarti et al., 2016; Foo &
132 Byrne, 2016; Gibbin et al., 2017; Lane, Campanati, Dupont, & Thiyagarajan, 2015;
133 Miller, Watson, Donelson, McCormick, & Munday, 2012; Parker et al., 2012, 2017;
134 Ross et al., 2016; Thor & Dupont, 2015; Zhao et al., 2018). For example, in the Sydney
135 rock oyster, parental exposure to high pCO₂ enhanced growth, development, and
136 metabolism in F1 offspring exposed to the same high pCO₂ conditions (Parker et al.,

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137 2012). Further, positive TGP was again observed in the F2 generation, in terms of
138 development, growth, and juvenile heart rate in the trans-generational exposure line,
139 relative to the control line (Parker, O'Connor, Raftos, Pörtner, & Ross, 2015). To date,
140 only one study of reef building corals has demonstrated cross-generational
141 acclimatization at the swimming planulae stage (Putnam & Gates, 2015), but the longer-
142 term implications of this plasticity across subsequent life stages are not yet known. These
143 responses demonstrate that understanding the potential carryover effects from parents
144 through ontogeny (i.e., ecological ramifications of TGP) is critical to our view of
145 organism performance on annual to decadal time scales.

146

147 The ecological implications of carryover effects have not been considered in
148 projections of coral performance in a future of climate change, yet acclimatization is
149 known to play a key role in intra-generational stress response (Brown & Cossins, 2011;
150 Brown, Dunne, Goodson, & Douglas, 2000; Coles & Brown, 2003), and our initial work
151 in corals suggests positive TGP is possible in corals (Putnam & Gates, 2015). Our
152 current study investigates the effects of adult preconditioning on offspring ecological
153 performance in response to OA conditions. Here, we tested the hypothesis that parental
154 exposure of corals to high pCO₂ during gametogenesis and/or brooding results in
155 beneficial acclimation of the offspring. Further, we tested the hypothesis that these
156 carryover effects are maintained beyond the larval stage, through settlement into the
157 juvenile stage, by assessing settlement and survivorship post release and tracking
158 survivorship and growth for six months in ambient and elevated pCO₂ treatments.

159

160 **Materials and Methods**

161 *Experimental Overview*

162 The experiment consisted of four phases (Fig. 1). First, adult coral colonies were
163 acclimated to ambient conditions in common garden tanks for 34d (Fig. 1a). Second,
164 adults were exposed to two different pCO₂ treatments that fluctuated with a diurnal
165 frequency for the period that contained gametogenesis and brooding, over 3 cycles of
166 planulation (~3 months, Fig 1b.). Third, larvae were collected from the pre-conditioned
167 adults and exposed to the two different pCO₂ conditions in a reciprocal fashion (Fig. 1c-
168 e) in acrylic and mesh chambers containing a settlement tile: Survivorship and settlement
169 of offspring during this phase were assessed after 96h. Fourth, the settled spat were
170 tracked for survivorship and growth (Fig. 1f) in continued reciprocal exposure after one
171 and six months post release.

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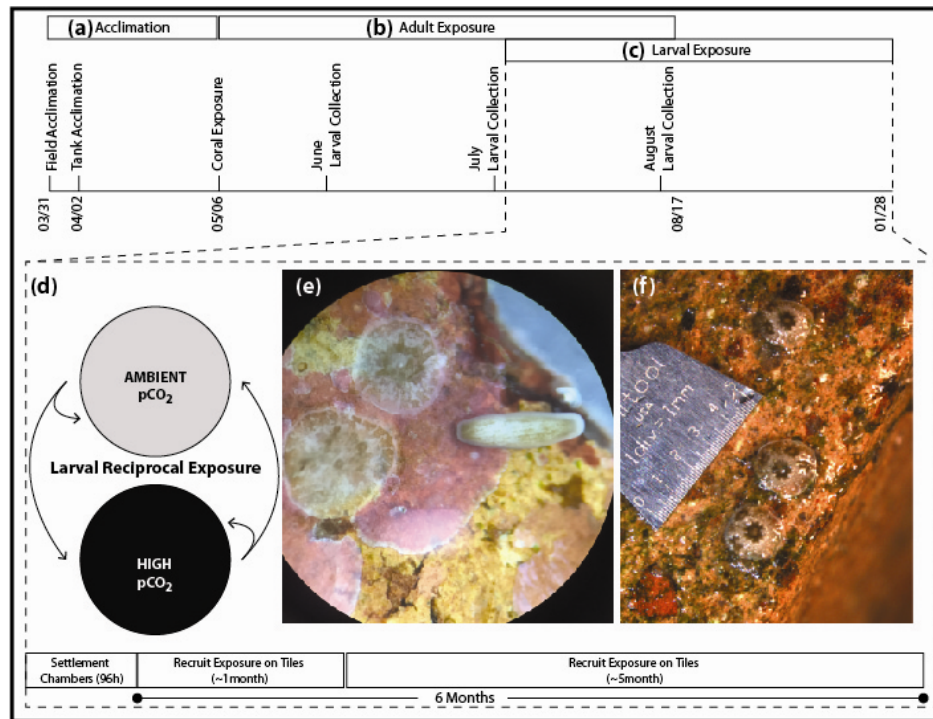


Figure 1. Experimental Design (a) Coral acclimation and (b) experimental timeline to test the effects of adult preconditioning on larval release larval performance at (c, d) ambient and high pCO₂ conditions in terms of (e) settlement, survivorship and (f) growth and survivorship were examined.

172

173 *Coral Collection and Acclimation*

174 Adult *Pocillopora damicornis* colonies (now considered *P. acuta* based on mitochondrial
175 open reading frame, mtORF, sequencing (Johnston, Forsman, & Toonen, 2018) were
176 collected from the fringing reefs of southern Kāneohe Bay, O’ahu, Hawai’i
177 (21.429845, -157.793604) under Special Activities Permit SAP2014 from Hawaii’s
178 Division of Aquatic Resources (DAR). Corals were removed from the reef at the dead
179 skeleton base to minimize direct tissue damage and were placed immediately adjacent to
180 each other in a common garden in the field for a 3-day acclimation period (e.g., Putnam,
181 Davidson, & Gates, 2016). Subsequently, corals (n=16) were moved to large, outdoor,

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182 sand-filtered, flow-through seawater, mesocosm tanks (~1,300L) at the Hawai'i Institute
183 of Marine Biology, HIMB (described in Putnam et al., 2016). Irradiance in the
184 mesocosm tanks was reduced to ~60% full irradiance using shade cloth to more closely
185 mimic collection site *in situ* light conditions, and light readings were taken every 15 min
186 with underwater loggers (Odyssey PAR loggers standardized to Li-Cor 192SA cosine
187 sensor; Long et al. 2012; Fig. S1). Seawater temperature was also recorded every 15 min
188 (Hobo Water Temp Pro v2, accuracy = 0.21°C, resolution = 0.02°C, Onset Computer
189 Corporation, Fig. S1). Light, temperature and pH fluctuated within the tanks on natural
190 cycles (Fig. S1). Corals acclimated to these tank conditions for 34d prior to initiation of
191 treatments.

192

193 *Experimental Exposure*

194 The treatment (high pCO₂) and control conditions (ambient seawater) were maintained
195 using a pH-stat CO₂ injection system (Putnam et al., 2016). Ambient pH and pCO₂
196 fluctuated daily (e.g., (Drupp, De Carlo, Mackenzie, Bienfang, & Sabine, 2011), driven
197 by ambient conditions and feedbacks from photosynthesis, calcification, and respiration
198 of the organisms on the fringing reef directly off shore of HIMB, where the seawater was
199 obtained. The high CO₂ treatment conditions retained natural diel variability while
200 decreasing the pH (Fig. S1). pH probes from the pH-stat CO₂ injection system were
201 calibrated weekly on the NBS scale and pH and temperature were logged every 15 min in
202 each tank throughout the duration of the experiment. The carbonate chemistry of the
203 seawater was assessed with discrete measurements of pH (total scale), total alkalinity,
204 temperature and salinity according to the Guide to Best Practices (Riebesell, Fabry,

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205 Hansson, Gattuso, & others, 2010). Discrete measurements were made ~daily and water
206 samples were collected ~2x per week for each adult treatment. Given the stability of the
207 total alkalinity and low biomass in the 1,300L tanks, sampling frequency was reduced in
208 the 6 months of offspring exposure to ~ every 1-2 weeks, while pH, temperature, and
209 light were tracked continuously (Fig S1). Total alkalinity samples were analyzed using
210 open cell potentiometric titrations (Dickson, Sabine, & Christian, 2007) and assessed
211 against certified reference materials (CRMs; A. Dickson Laboratory, UCSD; values on
212 average <1% different from TA CRMs); all samples were corrected for any offset from
213 the CRMs. From these measurements, the full suite of carbonate parameters was
214 calculated with the seacarb package (v3.0.11, Gattuso et al., 2016), using the average
215 corrected TA and salinity measured in each treatment tank (Table 1).

216

217 *Adult Exposure, Planulation, and Settlement*

218 Eight adult corals were exposed to each treatment beginning 06 May 2014. Two colonies
219 died very early in the high pCO₂ treatment prior to June planulation, leaving n=6 in high
220 pCO₂ and n=8 in ambient pCO₂. A common garden approach (n = 2 tanks) was chosen to
221 maximize the similarity of experimental conditions. During the 7-8 days of larval
222 collection each month, adult corals were removed from the tanks and separated into
223 individual ~4.5L bowls (one colony per bowl) with flowing treatment water (i.e., the
224 same experimental conditions as the tanks) from ~5pm to 9am to isolate the larvae
225 released from each colony (e.g., (Putnam & Gates, 2015). The flowing seawater flushed
226 the buoyant larvae into 800 ml tripour beakers with 150 µm mesh bottoms and the

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227 number of larvae released per colony were counted during the months of June, July and
228 August 2014.

229 July 2014 was the expected seasonal peak of larval release (Fig. 2), and the larvae
230 collected during this time were used for the offspring reciprocal exposure experiments
231 (Fig. 1c, d). Due to the variation in timing of gametogenesis, brooding, and the sexual or
232 asexual origin of the planulae in *Pocillopora damicornis/acuta* (Permata, Kinzie, &
233 Hidaka, 2000; Stimson, 1978; Stoddart, 1983; Stoddart & Black, 1985), it is not possible
234 to definitively state the exact timing of exposure of the offspring gametes or planulae
235 within the adults. Clarifying the timing and mechanisms of carryover effects (i.e. TGP or
236 developmental acclimation) would require, for example, exposing the adults only prior to
237 gametogenesis, only during gametogenesis, or only during brooding. Currently the
238 reproductive biology of *Pocillopora damicornis/acuta*, complicates this assessment. In
239 this case, we are testing the ecological context of TGP (e.g., (Torda et al., 2017) box 2),
240 or carryover effects.

241 Groups of 16-20 larvae were tracked from each parent colony and placed in a
242 200ml transparent acrylic chamber with 150 μ m mesh at each end. To increase replication
243 and account for variability across release date, experiments were conducted on each day
244 of larval release from 12-18 July 2014 on newly released larvae. Each chamber contained
245 a 4.5 x 4.5 x 1cm terracotta brick tile that had been preconditioned on the reef for 1-2
246 months. Conditions of pH on the fringing reef of Coconut Island in Kāneohe Bay can
247 range from ~7.6 - 8.1 (Guadayol, Silbiger, Donahue, & Thomas, 2014; Silbiger,
248 Guadayol, Thomas, & Donahue, 2014), so these tiles are not naïve to high pCO₂. Further
249 the major constituent was not crustose coralline algae and as such there should not be

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250 strong impacts of pCO₂ on the tiles themselves, thereby providing relatively equal
251 competition dynamics between the newly settled spat and tile communities. The indirect
252 effects of pCO₂ on substrate community, and therefore coral offspring settlement and
253 growth, are important considerations in experimental design for interpretation of results
254 (Albright and Langdon 2011). Chambers were placed into either ambient or high pCO₂
255 treatments and settlement and survivorship were assessed after 96h. Survivorship was
256 calculated as the total number of living larvae (both swimming and settled) in the
257 chamber divided by the initial number of larvae added. Settlement was counted as those
258 larvae that had settled and metamorphosed to the chamber walls, mesh, or tile divided by
259 the initial number of larvae added to the chamber.

260 *Spat exposure on Tiles*

261 After settlement and survivorship was assessed, new recruits were mapped on each tile
262 and the tiles with settled spat were returned to the mesocosms of their settlement
263 treatment (Figure 1, Figs. S1-S2). After both an additional month and then 6 months of
264 total exposure, tiles were re-assessed under a dissecting scope to count survivorship
265 (number of spat remaining alive relative to the initial amount added to the chamber).
266 Growth of each spat was also measured by counting the number of polyps. Growth rate
267 was calculated as: the (# of polyps - 1 primary polyp) / (# of days post settlement at
268 month 1) for the first month's growth rate, and as the (# of polyps at month 6 - # of
269 polyps at month 1) / (# of days between month 1 and month 6 measurements). Spat that
270 were fused were counted as survivors, but were not used in the growth data analysis.
271 Settlement tile was used as the level of replication to avoid non-independence of multiple
272 spat on a tile.

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273

274 *Statistical Analysis*

275 To test if the timing of larval release differed between the control and treatment
276 conditions at each sampling time-point, a two-sample Kolmogorov-Smirnov test was
277 used and release by day was treated as a continuous variable (ks.test; stats package;(R
278 Core Team, 2016). A generalized linear mixed effects model with binomial errors (lme4
279 package; R Core Team, 2016) was used to test for differences in proportional settlement
280 and survivorship between the treatment and control using a binomial distribution.
281 Settlement data were analyzed with parental (Origin) and offspring (Secondary)
282 treatments and their interaction as fixed effects and settlement tile as a random intercept.
283 Survivorship and growth data were both measured at multiple time points and, thus, were
284 modeled with the same fixed effects and interaction, but with a random intercept of
285 settlement tile nested in time point. A model selection approach was applied and the final
286 models were selected as those with the lowest delta AIC. Growth data were log
287 normalized to meet model assumptions (i.e., for normal distribution) and growth data are
288 plotted as back-transformed means and asymmetrical standard error. Full analytical
289 details are available on GitHub
290 (https://github.com/hputnam/HI_Pdam_Parental/releases/tag/Version_20180508) and
291 Dryad (doi will be added upon acceptance).

292

293 **Results**

294 *Acclimation Conditions*

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295 Corals were acclimated in tanks to fluctuating conditions (Fig. S1) similar to that on the
296 fringing reefs of Kāneohe Bay, O'ahu, Hawai'i (Putnam et al., 2016). During the
297 acclimation period, daily temperature ranged on average from 23.7 - 25.9°C (Fig. S1a).
298 Between 06:00 - 19:00, Photosynthetically Active Radiation (PAR) ranged on average
299 from 62 - 246 $\mu\text{mol s}^{-1} \text{m}^{-2}$ (Fig. S1e).

300

301 *Experimental Exposure*

302 Light and temperature varied over time within the experiment due to seasonal shifts (see
303 supplemental Figure S1 for detailed description of tank conditions). During the adult
304 pCO₂ exposure, mean temperature ranged from 26.3 - 27.9°C and 26.4 - 28.0°C in
305 ambient and treatment tanks, respectively (Fig. S1), which was on average higher than
306 the acclimation period due to seasonal warming. pH (NBS) ranged from 7.81 - 8.06 in
307 ambient conditions and 7.51 - 7.74 in high pCO₂ conditions for the adult exposures.
308 While this condition may be higher than IPCC pCO₂ predictions for open ocean
309 conditions (Pachauri et al., 2014), lower and more variable pH is common for coastal and
310 reef locations (Price, Martz, Brainard, & Smith, 2012; Rivest, Comeau, & Cornwall,
311 2017). For example, pH conditions on the fringing reefs adjacent to Coconut Island can
312 range from ~7.6 - 8.1 (Guadayol et al., 2014; Silbiger et al., 2014). Further modeling of
313 the pH change in reef locations under future scenarios results in a 2.5 fold increase in reef
314 pH variation projected with an offshore increase to 900 μatm pCO₂ (Jury, Thomas,
315 Atkinson, & Toonen, 2013). As such, our chosen pH conditions are ecologically relevant
316 in terms of fluctuation and magnitude of potential pH change in the future in this dynamic
317 reef location and do not represent extreme conditions. During the first month of larval

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318 exposure, pH ranged from 7.79 - 8.04 in ambient conditions and 7.49 - 7.74 in the high
319 pCO₂ treatment, and temperature, on average, ranged from 27.0 - 28.5°C and 27.0 -
320 28.4 °C, respectively (Fig. S1). Lastly, across the six months of juvenile exposure, pH
321 ranged from 7.77 - 8.04 in ambient conditions and 7.52 - 7.75 in high pCO₂ conditions
322 and daily temperature, on average, ranged from 25.7 - 27.1°C and 25.8 - 27.0°C,
323 respectively (Fig. S1). Discrete measurements of carbonate chemistry reveal stable TA
324 across the 10 months and strong differences in pH and pCO₂ between treatments (Table
325 1), but as these discrete measurements reflect daylight sampling only, they underestimate
326 the treatment differences in pH and temperature clearly portrayed in continuous
327 measurements described above (Fig. S1).

328 **Table 1.** Carbonate chemistry parameters for the different phases of the experiment (Figure 1). (a) Adult exposure (05 May 14 - 17
 329 August 14), (b) 1 Month of offspring exposure (12 July 14 - 19 August 14), and (c) 6 Months of offspring exposure (12 July 14 - 12
 330 January 2015). Temperature, salinity, total alkalinity, and pH were measured (N=sample size in each treatment and time point), while
 331 the remaining parameters of the carbonate system were calculated using seacarb as described in the methods.

332 *(a) Adult Exposures*

Treatment	N	Temp. °C	Salinity psu	pH Total	A _T μmol kg ⁻¹	pCO ₂ μmol kg ⁻¹	CO ₂ μmol kg ⁻¹	HCO ₃ ⁻ μmol kg ⁻¹	CO ₃ ²⁻ μmol kg ⁻¹	DIC μmol kg ⁻¹	Ω _A
Ambient	29	26.81 ± 0.12	33.9 ± 0.1	7.96 ± 0.02	2146 ± 5	482 ± 20	13 ± 1	1705 ± 14	178 ± 6	1896 ± 10	2.9 ± 0.1
High	28	26.78 ± 0.12	33.9 ± 0.1	7.71 ± 0.02	2151 ± 5	940 ± 38	26 ± 1	1878 ± 10	111 ± 4	2014 ± 7	1.8 ± 0.1

333 *(b) Offspring 1 Month*

Treatment	N	Temp. °C	Salinity psu	pH Total	A _T μmol kg ⁻¹	pCO ₂ μmol kg ⁻¹	CO ₂ μmol kg ⁻¹	HCO ₃ ⁻ μmol kg ⁻¹	CO ₃ ²⁻ μmol kg ⁻¹	DIC μmol kg ⁻¹	Ω _A
Ambient	8	27.16 ± 0.1	33.8 ± 0.2	7.9 ± 0.01	2138 ± 10	557 ± 21	15 ± 1	1747 ± 13	158 ± 4	1920 ± 12	2.6 ± 0.1
High	8	27.11 ± 0.11	33.8 ± 0.1	7.71 ± 0.03	2142 ± 12	945 ± 78	26 ± 2	1869 ± 23	111 ± 8	2005 ± 18	1.8 ± 0.1

334 *(c) Offspring 6 Months*

Treatment	N	Temp. °C	Salinity psu	pH Total	A _T μmol kg ⁻¹	pCO ₂ μmol kg ⁻¹	CO ₂ μmol kg ⁻¹	HCO ₃ ⁻ μmol kg ⁻¹	CO ₃ ²⁻ μmol kg ⁻¹	DIC μmol kg ⁻¹	Ω _A
Ambient	15	26.90 ± 0.35	33.8 ± 0.1	7.97 ± 0.04	2135 ± 7	493 ± 38	13 ± 1	1688 ± 35	180 ± 13	1882 ± 23	2.9 ± 0.2
High	15	26.92 ± 0.35	33.8 ± 0.1	7.73 ± 0.03	2135 ± 7	923 ± 70	25 ± 2	1853 ± 20	114 ± 8	1992 ± 15	1.8 ± 0.1

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335 *Planulation and Settlement*

336 Planulae release was monitored on lunar days ~16-24 for the months of June, July, and
337 August, as planulation has been reported to occur following the full moon (lunar day
338 ~15) for *P. damicornis* in Hawai'i (Jokiel, 1985; Richmond & Jokiel, 1984). A clear
339 peak in planulation was observed in July, with lowest release in August (Fig. 2). There
340 was no significant difference in the timing of planulation between treatments in either
341 June (Fig. 2a; $P > 0.05$) or August (Fig. 2c; $P > 0.05$). The general pattern suggested a
342 shift in timing of planulation between treatments (Fig. 2), with a delay in release more
343 prominent in the high pCO₂ condition in July (Fig. 2b; $D = 0.625$, $P = 0.087$).

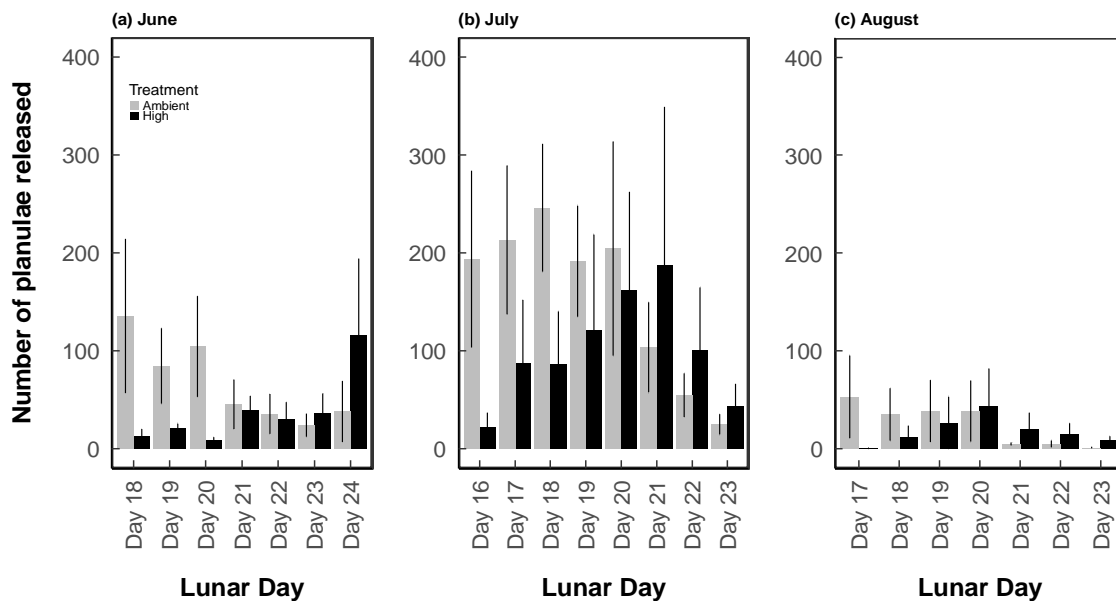


Figure 2. Average larval release per coral colony. Planulae release as a function of lunar day in (a) June, (b) July, and (c) August in from adult colonies exposed to ambient pCO₂ (n=8) and adult colonies exposed to high pCO₂ (n=6).

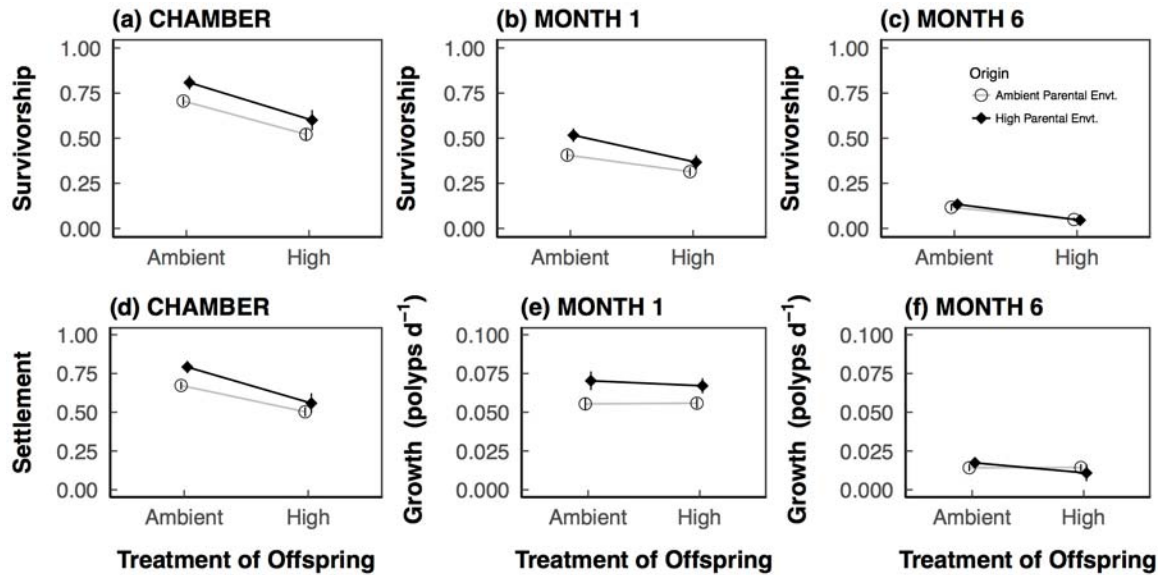
344 Offspring from high CO₂-exposed parents displayed significantly higher survivorship
345 following 96h in the settlement chambers ($P < 0.016$ Table S1a), supporting positive

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346 carryover effects. This increase in offspring survival from parents exposed to elevated
347 pCO₂ was approximately equal in both offspring treatments at time 0, with 14.5% and
348 15.1% greater survivorship in the ambient and high offspring treatments, respectively
349 (Fig. 3a). The settled spat from parents preconditioned to high pCO₂ also showed greater
350 survivorship in both offspring treatments after one month in the reciprocal exposures
351 (Table S1a), with preconditioned offspring having 27.1% greater survivorship at ambient
352 offspring exposure conditions and 16.6% at high pCO₂ exposure (Fig. 3b). After 6
353 months of reciprocal exposure, parental exposure to high pCO₂ enhanced offspring
354 survivorship by 13.6% in ambient offspring exposures, relative to spat from adults that
355 underwent ambient preconditioning. Offspring from high pCO₂ parents displayed reduced
356 survivorship (7.7%) in high offspring exposure relative to spat from adults
357 preconditioned to ambient (Fig. 3c, Table S1a). Offspring exposure to high pCO₂ also led
358 to lower survivorship regardless of parental preconditioning treatment (Table S1a).
359 Averaged across parental exposures, survivorship decreased with offspring exposure to
360 elevated pCO₂ by 26.1% at time 0, 24.5% at month 1 and 59.9% at month 6. Survivorship
361 declined significantly over time ($P < 0.001$, Table S1a), with survivorship as low as 4.6%
362 of the initial planulae by the final time point.

363 Planulae settlement was highest when parents were exposed to elevated pCO₂
364 ($P = 0.021$; Table S1b; Fig. 3d); settlement was enhanced by 17.6% and 11% for planulae
365 settling in ambient and high pCO₂ offspring treatments, respectively. Despite this overall
366 enhanced settlement of planulae from high pCO₂ parents, mean settlement was
367 significantly lower overall (26.1%) in the high pCO₂ offspring treatments ($P < 0.001$;
368 Table S1b), regardless of parental pCO₂ exposure (Fig. 3d).

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369

370 **Figure 3. Parental preconditioning to high pCO₂ enhances offspring performance.**
371 Reaction norm plots for (a) survivorship in the chambers, (b) survivorship at month 1, (c)
372 survivorship at month 6, (d) settlement at time 0, (e) growth rate at month 1, and (f)
373 growth rate at month 6. Points display data (mean±sem), while lines indicate only the
374 direction of response. Tile sample sizes for survivorship and settlement time 0, month 1
375 and month 6 and growth at month 1 ranged from 7-36 (see Table S1). Growth rates were
376 log transformed for analyses and figure displays back-transformed growth rate data.
377

378 Lastly, a trend for an Origin*Time interaction (P=0.056) was observed in spat growth,
379 where differences in growth with parental origin were apparent at month 1 (growth was
380 on average 1.3-fold higher in offspring from parents preconditioned to high pCO₂; Fig.
381 3e), but not at month 6 (Fig. 3f). Time also had a significant effect on growth, where by
382 the end of the experiment, at 6 months post release, growth rates were significantly lower
383 than at month 1 (P<0.0001, Fig. 3f).

384

385 Discussion

386 Here we present the first ecological assessment of trans-generational or carryover effects
387 in reef-building corals. In our study, the ecological and fitness-related response of coral
388 offspring was enhanced dependent on response and life-stage when their parents were

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389 exposed to a high pCO₂ environment, with carryover effects lasting into the juvenile
390 stage. Projections for future reef persistence are dire (Veron et al., 2009), but many do
391 not incorporate adaptation or acclimatization (Van Hooidonk, Maynard, & Planes, 2013),
392 likely over or under-estimating climate change effects for some stressors. When
393 adaptation and acclimatization are considered, it is clear the trajectories differ from the
394 worst-case scenarios (Ainsworth et al., 2016; Donner, Skirving, Little, Oppenheimer, &
395 Hoegh-Guldberg, 2005; Logan, Dunne, Eakin, & Donner, 2014). Our work provides
396 evidence to support the importance of the role of acclimatory processes in eco-
397 evolutionary thinking in an era of climate change and encourage the examination of
398 mechanisms such as hormesis and epigenetics (e.g., Costantini, 2014; Torda et al., 2017).

399

400 *Potential for tuning of reproductive timing*

401 Our multi-life stage perspective identifies carryover effects of adult stressor exposure,
402 with reproductive and offspring consequences. Shifts in reproductive timing can have
403 significant consequences for offspring settlement conditions. It is possible that “bet-
404 hedging” or environmental tuning by the parents may result in release of larvae timed to
405 favorable conditions. For example, a shift in reproductive timing of coral planulation with
406 change in temperature across season was recently documented (Fan et al., 2017). In this
407 case, seasonal acclimatization in the parents resulted in change in summer planulae
408 release timing, which minimizes planulae release during strong, likely stressful,
409 upwelling-induced temperature fluctuations of ~10°C (Lee, Chao, Fan, Wang, & Liang,
410 1997). Adult tuning of larval release of offspring is also possible in our experiment.
411 Kāneohe Bay is a semi-enclosed embayment that has fluctuations in physical

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412 conditions as a function of tidal cycle. Specifically, diurnal pCO₂ fluctuations are greatest
413 when tidal fluctuation is the lowest (Guadayol et al., 2014; Putnam, 2012; Silbiger et al.,
414 2014) in the shallow fringing reefs of Kāneohe Bay. A delay in the peak of planulation
415 from the adults preconditioned to high pCO₂, would then correspond to the timing of
416 lower daily tidal ranges
417 (<https://tidesandcurrents.noaa.gov/stationhome.html?id=1612480>) and thus higher pCO₂
418 fluctuations that are more similar to the high pCO₂ adult conditions. Another hypothesis
419 that could contribute to a shift in larval release under high pCO₂ condition is adult or
420 offspring energetic constraints. Delay in release could indicate energetic costs to
421 maintaining adult calcification and homeostasis (Stumpp et al., 2012), potentially
422 resulting in decreased parental investment, or increased development time necessary in
423 offspring (Stumpp, Wren, Melzner, Thorndyke, & Dupont, 2011). Further, low pH can
424 influence development processes such as sperm performance, fertilization success, and
425 developmental normalcy and timing (Albright, 2011; Byrne & Przeslawski, 2013).

426 Given the trend for a shift in the timing of planulation during July when our
427 offspring experiment was completed, it could be hypothesized that parental effects in the
428 reciprocal exposure are due to slight differences in the larval cohorts by day of release
429 (Cumbo et al., 2013; Cumbo, Fan, & Edmunds, 2012; Putnam et al., 2010; Rivest &
430 Hofmann, 2015). For example, peaks in *Symbiodinium* density and photophysiology, and
431 larval size, are positively correlated to peak larval release in *Pocillopora damicornis* in
432 Taiwan (Putnam et al., 2010). These differences in physiology by day of release also
433 translate to variation in susceptibility to changing temperature and pH in *P. damicornis*
434 (Cumbo et al., 2013; Rivest & Hofmann, 2015). The impact of day of release in our case

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435 is likely to be minimal, given the experiment was not conducted on a single day's larval
436 pool, but over 7 consecutive days (Fig. 2), better representing the full range of larval
437 phenotypes from *P. damicornis/acuta*.

438

439 *Importance of carryover effects for corals*

440 Our work provides further evidence that parental environment matters to offspring
441 performance in this brooding coral species, *Pocillopora acuta*. While ~1 month of
442 exposure to increased temperature and low pH resulted in TGP in this same species
443 (Putnam & Gates, 2015), in our current study with exposure to only OA, reaction norms
444 were primarily parallel, with enhanced performance in those preconditioned. This may
445 suggest that exposure to increased temperature (or the combination of temperature and
446 OA) has more profound, or mechanistically different impacts than OA on processes
447 involved in parental contributions or developmental acclimation (e.g., Byrne, 2012). The
448 enhanced growth of *P. acuta* juveniles under low pH is unexpected given the commonly
449 detrimental effect of ocean acidification on coral calcification (Kroeker, Kordas, Crim, &
450 Singh, 2010). *Pocillopora damicornis* has, however displayed variability in sensitivity
451 of calcification in response to OA, from negative (Putnam et al., 2016) to no effects on
452 growth (Comeau et al., 2014; Comeau, Edmunds, Spindel, & Carpenter, 2013). For
453 instance, ocean acidification did not impact recruitment of *P. damicornis* larvae to the
454 sides of treatment tanks in a mesocosm study also in Kāneohe Bay (Jokiel et al., 2008).
455 Furthermore, physiology at the larvae stage was not strongly affected by OA (Putnam et
456 al 2013), but was affected more so by increased temperature. Enhanced calcification in a
457 trans-generational context has been measured in another marine invertebrate, where

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458 higher shell growth rates in offspring of the Manila clam following exposure of the
459 parents to low pH have been observed (Zhao et al., 2018; Zhao, Schöne, Mertz-Kraus, &
460 Yang, 2017). This positive carryover effect for growth in another marine calcifier
461 supports our findings here with *Pocillopora acuta*, with implications for the presence and
462 importance of TGP beyond a single coral species.

463 ***Potential mechanisms underlying parental effects***

464 Several hypotheses may account for the parental contribution to enhanced
465 settlement, survivorship, and growth we documented. It is possible that adults manipulate
466 the investment in their offspring in the form of *Symbiodinium* communities (Padilla-
467 Gamiño, Pochon, Bird, Concepcion, & Gates, 2012), microbiome (Sharp, Distel, & Paul,
468 2012), size, protein, lipids, or carbohydrates (Hartmann, Marhaver, Chamberland, Sandin,
469 & Vermeij, 2013). Further the role of mitochondrial performance has been posited as a
470 mechanism of rapid adaptation in coral larvae (Dixon et al., 2015) and mitochondrial
471 performance has been linked to parental environment in the trans-generational
472 acclimatization of marine worms (Gibbin et al., 2017). These mechanisms could provide
473 metabolic boosts or conversely detriments during this energetically demanding life stage
474 (Edmunds, Cumbo, & Fan, 2013); e.g., the presence of clade D symbionts reduces
475 growth in coral juveniles (Little, Van Oppen, & Willis, 2004). DNA methylation and
476 other epigenetic mechanisms linked to gene expression regulation (Putnam et al., 2016;
477 Putnam & Gates, 2015; Torda et al., 2017) could also provide a mechanism of heritable
478 cross-generational priming. Identification of differential DNA methylation patterns
479 between the offspring of exposed and unexposed oysters is an initial line of evidence for
480 an epigenetic role in TGP for marine calcifiers (Rondon et al., 2017). The minute

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481 number of methylation changes and the lack of direct impact on RNA transcript
482 abundance or differential splicing (Rondon et al., 2017), however, illustrates how
483 complex these mechanisms can be. While differential provisioning of planulae
484 symbiotically, energetically, and epigenetically is possible, the goal of examining
485 ecological effects on the process of recruitment precluded destructive sampling for such
486 hypotheses in our study, but they remain important considerations in future work.

487 Brooded embryos may experience developmental acclimation while growing
488 within the parental polyp (Putnam & Gates, 2015). It is possible that low pH in the
489 gastrovascular cavity (GVC) at the site of development could condition planulae for low
490 pH when released. This hypothesis would account for the differences seen in our study
491 between ambient and low pH preconditioned parents if the GVCs were modified
492 differently between treatments to retain a treatment offset. To date, limited data are
493 available for GVC pH under a variety of conditions (Agostini et al., 2011; Cai et al.,
494 2016). The data available suggest both a high pH and low pH within the GVC and
495 associated mesenteries (Cai et al., 2016), with no uniform picture of what planulae within
496 the polyp are exposed to relative to external conditions. Further work with multiple coral
497 species is necessary to disentangle the role of developmental acclimation from TGP,
498 including experiments focused on the magnitude and timing of signals that will induce
499 carryover effects and exposures through the F1 and F2 generation (Torda et al., 2017).

500

501 *Environmental hardening through hormetic priming*

502 Acclimatization occurs through short-term compensatory processes including modulation
503 of biochemical activity and gene expression in response to external stimuli, occurring on

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504 daily, seasonal, and annual scales, within a generation, and across a generation. Often
505 implicit in the usage of the term acclimatization is the inference that acclimatory
506 processes are beneficial and fully compensatory, *sensu* the Beneficial Acclimation
507 Hypothesis (BAH; Huey, Berrigan, Gilchrist, & Herron, 1999), but acclimatization is not
508 always adaptive (Edmunds, 2014; Edmunds & Gates, 2008; Huey et al., 1999). One
509 conceptual explanation for inconsistency of BAH is the framework of hormetic priming
510 (Costantini, 2014; Costantini, Metcalfe, & Monaghan, 2010), which deserves
511 consideration with regards to explaining patterns of TGP. Hormesis is defined as the
512 stimulation of function through mild exposure(s) (Southam & Ehrlich, 1943). Hormetic
513 priming thus occurs when exposure to a sub-lethal stressor results in stimulatory response
514 to increasing levels of a condition (e.g., Fig. 4), for example, as we have documented
515 here in the enhanced performance of larvae of *Pocillopora acuta* following parental
516 preconditioning. Hormesis is a biphasic response and therefore does not necessitate
517 positive acclimation to all future exposures (Fig. 4).

518 Hormetic priming as a mechanism of acclimatization could explain both the
519 beneficial and detrimental effects of increased temperature that have been documented in
520 certain types of repeated exposures (Ainsworth et al., 2016; Brown et al., 2000; Grottoli
521 et al., 2014), as well as variability in performance. For example, Ainsworth et al., (2016)
522 identified a “protective trajectory” of sea surface temperatures (SST) that corals
523 experienced, which lead to acquired thermal tolerance in *Acropora aspera*. Conversely a
524 “repetitive bleaching trajectory”, with high frequency bleaching events that lack recovery
525 time resulted in substantial symbiotic cell loss, bleaching, and mortality (Ainsworth et al.,
526 2016). Here it is likely these responses are on differing sides of the zero equivalence

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527 point in terms of the biphasic nature of hormetic processes (Y axis in Fig. 4A; (Costantini
528 et al., 2010; Lushchak, 2014). An example of hormetic priming in corals would be that of
529 mild ROS exposure resulting in protein expression priming, thereby reducing the ROS
530 damage in subsequent events (Brown, Downs, Dunne, & Gibb, 2002). Beyond
531 antioxidant genes, frontloading, or the constitutive up-regulation of expression of
532 canonical heat stress genes in *Acropora hyacinthus* samples from the high thermal
533 variability pool in American Samoa, could be another outcome of hormetic priming, with
534 implications for the thermal tolerance of those primed individuals (Barshis et al., 2013).

535

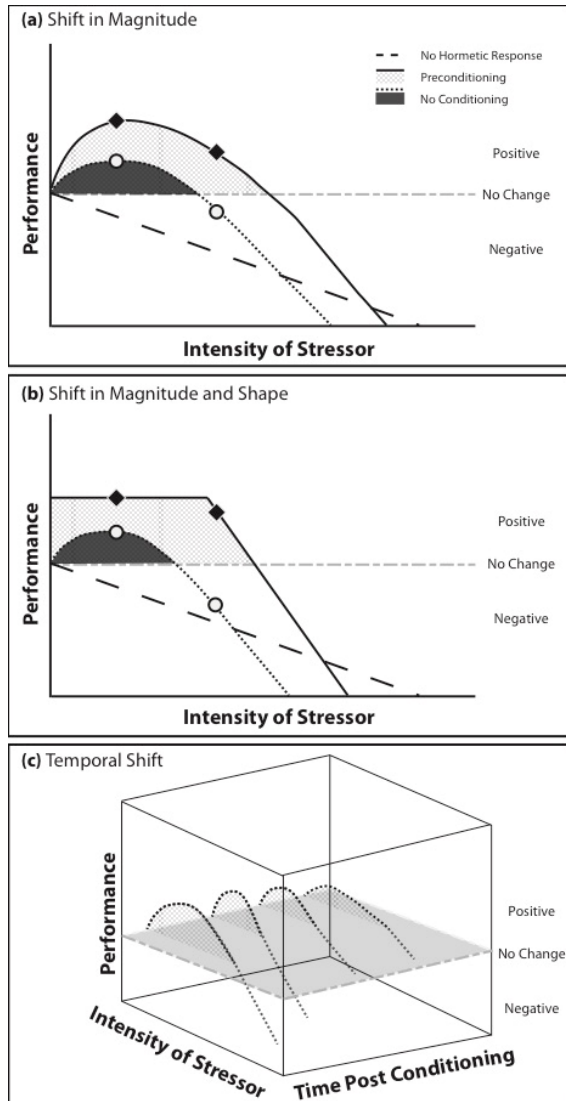


Figure 4. Hormeric priming may contribute to magnitude, pattern, and temporal variation in the benefits of TGP. The dashed line indicates the result of no hormeric priming, the gray dashed line is no change, the dotted line (black area) indicates a hormeric response with no conditioning, while the solid line (hashed area) indicates the hormeric response with preconditioning (Constantini et al., 2010; Lushchak 2014). Shaded areas indicate the hormeric zones, where the stimulation of performance from the increasing stressor is above the line of no change. Variation in the intensity, duration, and life stage of prior exposure may shift the A) magnitude, or B) shape of the hormeric zone. For example, in sessile benthic organisms, carryover effects from parental exposure may result in an enhanced hormeric zone relative to no conditioning. Further there may be C) temporal constraints on hormeric conditioning. For example, the hormeric zone may differ from parental exposure versus developmental exposure, or as in the case of our study, display a decline in positive carryover effects with increasing time post conditioning (as visualized by the temporal shift in hormeric zone).

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536 Corals in our study displayed life stage-dependent TGP. Despite the enhancement
537 in performance seen in early stages, the parental effects of preconditioning to high pCO₂
538 are absent in the offspring by 6 months post release. While maintenance of maternal
539 effects may be expected in short lived organisms, as generation time increases there is a
540 greater potential mismatch between parental and offspring conditions (e.g., Fig. S1). This
541 change in parental effects over time is not unexpected due to potential maladaptive
542 tradeoffs (Burgess & Marshall, 2014), especially the case in long-lived corals (Torda et
543 al., 2017). Seasonal, annual, and decadal environmental changes likely elicit tradeoffs
544 between the early life stage performance benefits of TGP and the costs of TGP the
545 organism may incur later in life. For example, maternal exposure of soil arthropods to
546 high temperatures resulted in increased thermal resistance at the juvenile stage, but later
547 drove reduced F1 fecundity (Zizzari & Ellers, 2014). Further the expectation of positive
548 TGP is linked to the predictability of the stressor (e.g., anticipatory parental effects;
549 APE's; Burgess & Marshall, 2014; Donelson et al., 2017). Specifically, TGP through
550 hormetic priming would likely be optimized by high environmental autocorrelation (i.e.,
551 a strong match between parent and offspring conditions would result in extended
552 enhancement). The greater the temporal shift from the parental environment (e.g., 6
553 months here Fig. S1) the less likely there is to be a benefit from parental enhancement
554 and the more likely within generation priming would become important (e.g., Fig. 4C).
555 Seasonal changes in physical parameters would then be expected to result in a loss of
556 benefit from TGP as pH continues to change, in a biphasic fashion (Fig. 4C).
557 Additionally, with respect to overall growth rates, the growth from months 2-6 would be
558 expected to decline due to seasonal effects associated with decreases in temperature and

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559 light in the winter months (Fig. S1; Fitt, McFarland, Warner, & Chilcoat, 2000; Thornhill
560 et al., 2011). The temporal transience of parental effects documented in our study argues
561 that for parental effects to translate into long term “memory” more constant
562 environmental and biological feedbacks are necessary (Ptashne, 2013).

563

564 *Implications for reef-building corals*

565 Experiments designed to examine TGP and carryover effects provide a glimmer of hope
566 for coral reef organisms that acclimatization may act as a buffer against a rapidly
567 changing climate (Putnam & Gates, 2015; Torda et al., 2017). Further experiments are
568 necessary to distinguish between true TGP, parental effects, and developmental
569 acclimation, and their underlying mechanisms. This could be achieved in spawning coral
570 systems, or by manipulating the timing of exposure in the brooding coral system to target
571 isolated stages (i.e., adult, gametogenesis, brooding, and larval). Additionally, tests of the
572 stability and later-life tradeoffs of TGP, as well as mechanisms of environmental
573 “memory” through aspects such as mitochondrial function (Gibbin et al., 2017), DNA
574 methylation (Putnam et al., 2016), or microbiome inheritance (Putnam, Barott, Ainsworth,
575 & Gates, 2017; Webster & Reusch, 2017) will unveil the complex contributions of the
576 holobiont partners to meta-organism function and acclimatization potential.

577 Our work challenges the paradigm of inevitable coral decline due to rapid climate
578 change by identifying ecologically-relevant beneficial parental effects in offspring, in
579 response to adult preconditioning to ocean acidification. We suggest hormesis, or
580 environmental priming may conceptually explain enhanced tolerance and performance
581 seen in acclimatization studies, as well as explaining the lack of a ubiquitous beneficial

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582 acclimation due to the biphasic nature of hormesis. With regards to a conservation and
583 management actions (i.e. assisted evolution; van Oppen et al., 2017; van Oppen, Oliver,
584 Putnam, & Gates, 2015), environmental priming is not a one-size-fits all phenomenon
585 (i.e., does not always confer beneficial acclimation). Instead conditioning methods would
586 necessitate a Goldilocks approach, as variation in cellular conditions and physiology
587 between species requires a variety of exposures for optimal performance outcomes
588 (Putnam et al., 2017). It is not clear, however, if the duration of the benefits would extend
589 far beyond the exposures, as phenotype-environment mismatches increase with season
590 and anthropogenic effects. The performance and fitness tradeoffs of acclimatization,
591 hormetic triggers, and heritability of potential epigenetic feedbacks present promising
592 areas of further study with respect to carryover effects and the ecological and
593 evolutionary trajectories of reef-building corals.

594

595 **Acknowledgements**

596 This work was supported by funding from NSF OCE-PRF 1323822 to HMP, and NSF
597 EPS-0903833, and NSF URM 0829272. We would like to thank Rashim Khadka and the
598 HIMB facilities staff for their assistance in this work and N. Silbiger, M. Iacchei for
599 constructive comments on the manuscript. This is HIMB contribution number xxx and
600 SOEST contribution number XXX.

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