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2 Re-examination of the effects of food abundance on jaw plasticity 3 in purple sea urchins

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7 Abstract

AQ1 Morphological plasticity is a critical mechanism that animals use to cope with variations in resource availability. During
9 periods of food scarcity, sea urchins demonstrate an increase in jaw length relative to test diameter. This trait is thought to
10 be reversible and adaptive by yielding an increase in feeding efficiency. We directly test the hypotheses that (1) there are
11 reversible shifts in jaw length to test diameter ratios with food abundance in individual urchins, and (2) these shifts alter
12 feeding efficiency. Purple sea urchins, *Strongylocentrotus purpuratus*, were collected and placed in either high or low food
13 treatments for 3 months, after which treatments were switched for two additional months between February and September,
14 2015 in La Jolla, CA (32.8674°N, 117.2530°W). Measurements of jaw length to test diameter ratios were significantly higher
15 in low compared to high food urchins, but this was due to test growth in the high food treatments. Ratios of low food urchins
16 did not change following a switch to high food conditions, indicating that this trait is not reversible within the time frame
17 of this study. Relatively longer jaws were also not correlated with increased feeding efficiency. We argue that jaw length
18 plasticity is not adaptive and is simply a consequence of exposure to high food availability, as both jaw and test growth halt
19 when food is scarce.

20 Introduction

21 Morphological plasticity is a fundamental mechanism that
22 organisms use to cope with changes in resource availabil-
23 ity. Variations in food availability can yield dramatic phe-
24 notypically plastic responses in the morphology of feeding
25 mechanisms across animals (e.g., fishes: Meyer 1987; Mit-
26 telbach et al. 1999; Adams and Huntingford 2004; molluscs:

Drent et al. 2004; barnacles: Marchinko 2003). It has long
27 been thought that changes in food abundance also elicit a
28 morphologically plastic response in the feeding apparatus
29 (Aristotle's Lantern) of sea urchins (Ebert 1980b; Edwards
30 and Ebert 1991; Levitan 1991; Fernandez and Boudouresque
31 1997). Specifically, the lengths of the jaws (demi-pyramids)
32 that comprise the Aristotle's Lantern change relative to
33 test diameter in response to variation in food abundance,
34 whereby jaw length becomes longer relative to test diameter
35 when food is limited (Ebert 1980b; Edwards and Ebert 1991;
36 Levitan 1991; Ling and Johnson 2009).

Urchins are notorious for overgrazing habitats dominated
37 by large macroalgae, resulting in 'urchin barrens'—a world-
38 wide phenomena that is becoming increasingly prevalent
39 with climate change (reviewed in Ling et al. 2015). Urchins
40 that live in macroalgal habitats and barrens exhibit plastic-
41 ity in a variety of morphological structures. For example,
42 urchins from barrens tend to be smaller, less dense, and have
43 thinner tests (Ling and Johnson 2009). These differences
44 are thought to reduce individual performance but ultimately
45 increase population size in barrens by augmenting turnover
46 of the population (Ling and Johnson 2009; Ling et al.
47 2019). Conversely, the relatively longer jaws observed in
48 urchins from barrens are thought to aid their success by
49
50

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51 increasing feeding efficiency on encrusting and calcareous
 52 algae, because longer jaws may facilitate scraping or grab-
 53 bing algae from rocks (Ebert 1980b, 2014; Edwards and
 54 Ebert 1991; Fernandez and Boudouresque 1997).

55 Researchers have further observed that relative jaw length
 56 changes cyclically in the field, following seasonal fluctua-
 57 tions in food abundance, which suggests that this plastic
 58 response is reversible (Ebert 2014). Reversible morphologi-
 59 cal plasticity implies that there costs and benefits associated
 60 with the trait, further advocating a common assumption in
 61 the literature that having a greater jaw length to test diameter
 62 ratio is advantageous (Ebert 1996). In a field experiment
 63 with the sea urchin, *Echinometra mathaei*, for example, indi-
 64 viduals with relatively longer jaws grazed larger areas than
 65 those with relatively shorter jaws (Black et al. 1984).

66 These field and laboratory observations of jaw plasticity
 67 are compelling and suggest that sea urchins have the capaci-
 68 ty to cope with wide variations in resource abundance, if
 69 this trait is indeed adaptive. What has yet to be determined,
 70 however, is how relatively longer jaws actually increase
 71 feeding efficiency and if observed population level variance
 72 in relative jaw length is due to strong selection pressure
 73 from changes in food abundance (Fansler 1983). If this trait
 74 is both phenotypically plastic and adaptive, we postulate
 75 that physical changes in jaw size within individual urchins
 76 should occur, as opposed to body tissue being gained or lost
 77 according to resource availability, which occurs naturally
 78 (Ebert 1968) and is not an adaptive response to changes in
 79 food availability.

80 We sought to determine if the relationship between jaw
 81 length and test size changes in response to food availabil-
 82 ity in individual juvenile *S. purpuratus* and whether such
 83 changes arise from the jaw length, test size, or both. We
 84 examined juveniles because they are known to have faster
 85 growth rates than adults (Ebert 1968) and exhibit larger
 86 relative jaw lengths in urchin barrens versus kelp forests
 87 (Pederson and Johnson 2008). Thus, juveniles may show
 88 greater responses to changes in food availability over shorter
 89 timescales. We also tested the hypotheses that individual
 90 changes in relative jaw length are reversible under shift-
 91 ing food abundances and that relatively longer jaws yield
 92 greater feeding efficiency on algae (and are therefore adap-
 93 tive) based on consumption rates and bite size.

94 **Materials and methods**

95 **Urchin collection and maintenance**

96 Juvenile purple sea urchins, *Strongylocentrotus purpuratus*,
 97 were collected in February 2015 at Point Loma, San Diego
 98 County, California (32.7000°N, 117.2467°W) and brought to
 99 the Scripps Institution of Oceanography (SIO), University of

California, San Diego, where they were held together in a 100
 gallon aquarium for 2 months prior to the start of the experi- 101
 ment. The flow through aquarium received filtered seawater 102
 pumped in from the SIO pier (3–4 m depth, 300 m off- 103
 shore) at ambient conditions [temperature = 19.05 ± 2.55 °C, 104
 pH = 8.08 ± 0.05, salinity = 230–235 PSU; from Kram S. 105
 L. et al. Scripps Ocean Acidification Real-time (SOAR) 106
 Dataset, SIO]. The urchins in this holding tank were given 107
 5–6 large blades of giant kelp, *Macrocystis pyrifera*, their 108
 preferred food source (Leighton 1966; Foster et al. 2015), 109
 3–4 days per week, which was considered to be an interme- 110
 diate amount of food relative to the experimental treatments. 111

112 One week prior to the start of the experiment, 90 urchins
 113 were measured (see growth measurements) and placed in
 114 individual mesh planting pots (Hydrofarm Net Cup, 3-in.,
 115 Hydrofarm, Inc., CA, USA), which were suspended from
 116 custom built PVC frames (15 pots per PVC frame, 6 frames
 117 total) and placed in one of six plastic bins. Ambient seawater 118
 was continuously supplied directly to each bin through 119
 separate rubber hosing. Three bins housed the high food 120
 treatment urchins and three bins housed the low food treat- 121
 ment urchins to keep the food treatments separated. Bins 122
 were staggered on an empty water table, alternating high 123
 and low treatment bins.

124 At the start of the experiment, all urchins were weighed,
 125 and their test diameter and height were measured (see
 126 growth measurements section). To track jaw growth, urchins
 127 were soaked in a solution of calcein (0.125 mg calcein/1L
 128 seawater) adjusted to a pH of 8.0 in a 10 L beaker that was
 129 aerated for 24 h, following (Ebert 1977). Calcein stains the
 130 calcium of the jaws during the soak, but not new accretion,
 131 thereby enabling measurement of new jaw growth (see
 132 growth measurements section).

133 All urchins were randomly assigned to one of two treat-
 134 ments: high food, in which individuals were given constant
 135 food and supplied with fresh kelp every 2 days, and low
 136 food, in which individuals were only given fresh kelp every
 137 12–14 days for 24 h, with uneaten kelp removed (Fansler
 138 1983). At feedings, three 6 cm² sized pieces of *M. pyrifera*
 139 were cut and placed in each urchin pot. Individuals were
 140 checked daily and their bins were emptied and cleaned every
 141 2 days for the duration of the experiment.

142 Urchins were maintained in these food treatments for
 143 approximately 3 months (85 days), after which 15 individu-
 144 als from each treatment (30 total) were subsampled to record
 145 their feeding behavior and then sacrificed to measure their
 146 jaw growth and test diameters. One individual from the low
 147 food treatment died and was not included in the analyses.
 148 Additionally, three urchins (one from the low treatment, two
 149 from the high treatment) had no visible tag lines and were
 150 therefore not analyzed for jaw growth.

151 Of the remaining urchins (60 individuals), 15 from each
 152 treatment were soaked in a solution of calcein for a second

153 time to monitor growth at multiple time points. The treat-
 154 ments were then switched; urchins that were initially in the
 155 low food treatment were switched to a high food treatment
 156 (hereafter referred to as low/high) and urchins that were initially
 157 in the high food treatment were switched to a low food
 158 treatment (hereafter referred to as high/low). The experiment
 159 continued for 2 months (67 days), until it was terminated
 160 due to mortality associated with an unseasonably warm
 161 water event (Cavole et al. 2016). Seven urchins died (three
 162 from the low/high treatment, four from the high/low treat-
 163 ment) and were not included in the analyses. The second
 164 tagging attempt failed; a second tagging line was not visible
 165 on urchin jaws and the first tagging line was masked by the
 166 second tagging attempt. These urchins were thus excluded
 167 from analyses, leaving 23 urchins to be euthanized and
 168 measured for jaw length, growth, and test diameter after the
 169 diet switch.

170 Growth measurements

171 Test diameter was measured at the centroid of the test to the
 172 nearest 0.01 mm using digital calipers at the beginning of the
 173 experiment, at 3 months, and at 5 months. Care was taken to
 174 avoid spines and compressing the test. Each measurement
 175 was repeated 3 times and averaged (maximum measurement
 176 error = 0.51 ± 0.29 mm). Urchins ranged in size from 15 to
 177 22 mm test diameter at the start of the experiment, and there-
 178 fore did not exceed 25 mm, the minimum size at which purple
 179 urchins reach sexual maturity (Conor 1972; Bay-Schmith
 180 and Pearse 1987). Urchins were also weighed (wet weight)
 181 to the nearest 0.01 g.

182 The jaws were dissected and soaked in 5% hypochlorite
 183 bleach solution for 20 min and then rinsed with deionized
 184 water (Black et al. 1984). One jaw (demi-pyramid) from
 185 each individual was dissected and imaged under a dissecting
 186 microscope with a fluorescent light source (Leica M165 FC,
 187 Buffalo Grove, IL, USA) equipped with a camera (Canon
 188 EOS 60D DSLR) at 3 months and 5 months. When initially
 189 tagged, the calcein dye left a thin, fluorescent band along the
 190 base (proximal end) of each jaw, and new jaw material was
 191 laid down adjacent to this fluorescent band. As such, jaw
 192 growth was measured as the distance from the base of the
 193 jaw to the fluorescent band using ImageJ (v. 1.49) (Fig. 1)
 194 (Schneider et al. 2012). The length of the jaw was meas-
 195 ured as the distance from the base of the jaw to the base
 196 of the tooth (Fig. 1). Each side of one intact jaw from each
 197 individual was measured five times and a mean measure-
 198 ment for each jaw was calculated. It was not possible to
 199 measure initial jaw length of live urchins, therefore initial
 200 jaw length was estimated by subtracting the thickness of the
 201 growth band from the total jaw length following (Pederson
 202 and Johnson 2008).

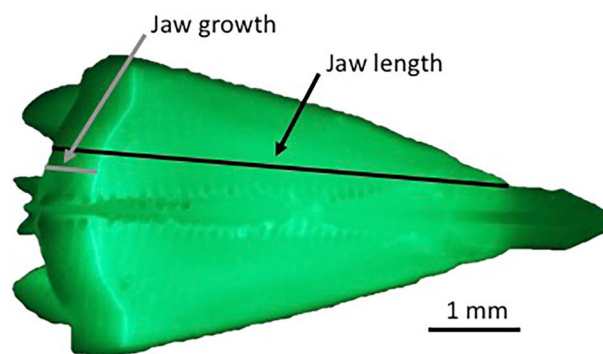


Fig. 1 One jaw (demi-pyramid) tagged with calcein dye. Lines illustrate the measurements of jaw length (black line, base of the jaw to the base of the tooth) and jaw growth (grey line, base of the jaw to the fluorescent band)

Gonads were carefully dissected and weighed to the near- 203
 est 0.01 g for individuals in the high and low food treatments 204
 sacrificed at 3 months. To correct for body size, the gonad 205
 index, a proxy for resource allocation (Ebert et al. 2012), was 206
 calculated following (Ebert 1968) as: 207

$$\text{Gonad index} = \frac{\text{Gonad dry weight}}{(\text{Test diameter})^2(\text{Test height})} \quad (1) \quad 208$$

209 Feeding efficiency

210 Prior to being measured and sacrificed, the feeding behavior 210
 of urchins in the low and high food treatments at 3 months 211
 was examined, following a 4 day starvation period. Fifteen 212
 individuals from the high food treatment and fourteen indi- 213
 viduals from the low food treatment were each observed 214
 for 3 h while feeding on *M. pyrifera*. One piece of kelp 215
 (approximately 6 cm²) was weighed to the nearest 0.01 g 216
 before being given to an urchin and weighed again follow- 217
 ing the feeding trial to determine the mass consumed. The 218
 kelp pieces were cut into squares with scissors to produce 219
 straight edges, along which individual bites could be easily 220
 identified. 221

222 The rate of kelp consumed was calculated by subtracting 222
 the final kelp weight from the initial weight, divided by 223
 final urchin mass and converted to a rate by dividing by the 224
 3 h observation period. The kelp pieces were also imaged 225
 using a dissection microscope with camera. The diameter of 226
 the three largest, discernable bites from each individual was 227
 measured using ImageJ. Maximum bite size was calculated 228
 as the mean bite diameter. 229

230 Statistics

231 All data were tested for normality using the Shapiro–Wilk 231
 test and for homogeneity of variances using Bartlett’s test. 232

233 To confirm that the experimental bins in which the urchin
 234 pots were placed had no effects on the results, two of the
 235 key measurements (test diameter and jaw length) were
 236 compared post hoc between bins within treatment and
 237 sample periods using ANOVA's. No significant differences
 238 were found (test diameter: 3 months: low: $P=0.54$, high:
 239 $P=0.61$, 5 months: low: $P=0.63$, high: $P=0.62$, jaw
 240 length: 3 months: low: $P=0.59$, high: $P=0.66$, 5 months:
 241 low: $P=0.31$, high: $P=0.53$).

242 Two-way ANOVA's or Kruskal–Wallis non-parametric
 243 tests were used to evaluate differences in measured metrics
 244 between treatments. Linear regressions were used to evalu-
 245 ate changes in jaw length, test diameter, and the jaw length
 246 to test diameter ratio over the course of the experiment.
 247 The rate of kelp consumption and maximum bite size
 248 between the high and low treatments were compared using
 249 *t*-tests. A Bonferroni-corrected $\alpha=0.002$ for 33 multiple
 250 comparisons was used. All analyses were conducted using
 251 R v. 3.3.0 (R Development Core Team 2014). Summary
 252 statistics are represented as mean \pm standard deviation.
 253 Datasets analyzed during the current study are available
 254 on Dryad (<https://doi.org/10.5061/dryad.37rp8r9>).

Results

Jaw length and growth

257 Mean estimates of initial jaw lengths were not significantly
 258 different between treatments (high = 4.46 ± 0.28 mm,
 259 high/low = 4.55 ± 0.28 mm, low = 4.24 ± 0.30 mm, and
 260 low/high = 4.46 ± 0.34 mm) (one-way ANOVA: $P=0.08$,
 261 $F_{3,45} = 2.41$, $N=48$).

262 Final lengths of the jaws from the high food treatments
 263 (high = 4.98 ± 0.31 mm, high/low: 5.15 ± 0.38 mm) were
 264 significantly longer than those from the low food treatments
 265 (low = 4.25 ± 0.34 mm, low/high = 4.72 ± 0.34 mm) (two-
 266 way ANOVA: $P \ll 0.001$, $F_{1,48} = 35.70$, $N=52$) (Table 1).

267 Jaw growth was significantly higher in individuals from
 268 the high (0.54 ± 0.12 mm) and high/low (0.60 ± 0.18 mm)
 269 treatments compared to individuals from the low
 270 (0.08 ± 0.06 mm) and low/high treatments (0.27 ± 0.07 mm)
 271 (two-way ANOVA: $P \ll 0.001$, $F_{1,45} = 12.65$, $N=48$). There
 272 was also significantly more jaw growth in the low/high
 273 treatment compared to the low treatment (*t* test: $P \ll 0.001$,
 274 $t_{22,96} = -6.17$, $N=25$). However, there was no difference in
 275 jaw growth between the high/low treatment and the high
 276 treatment ($P=0.36$, $t_{16,67} = -0.95$, $N=24$) (Table 1).

Table 1 Test and jaw measurements of urchins (mean \pm SD) on their final sampling days (e.g. 3 months for the high and low treatments, 5 months for the high/low and low/high treatments)

Metric	Low	Low/High	High	High/low
Jaw length: test diameter	0.24 ± 0.01 ($N=14$)	0.24 ± 0.01 ($N=12$)	0.21 ± 0.01 ($N=15$)	0.21 ± 0.01 ($N=11$)
Jaw length (mm)	4.31 ± 0.30 ($N=14$)	4.72 ± 0.34 ($N=12$)	4.98 ± 0.31 ($N=15$)	5.15 ± 0.38 ($N=11$)
Jaw growth (mm)	0.08 ± 0.08 ($N=12$)	0.27 ± 0.07 ($N=12$)	0.54 ± 0.12 ($N=13$)	0.60 ± 0.18 ($N=11$)
Jaw growth (%)	1.85 ± 1.97 ($N=12$)	6.20 ± 1.79 ($N=12$)	12.13 ± 2.48 ($N=13$)	13.16 ± 3.66 ($N=11$)
Test diameter (mm)	17.76 ± 1.29 ($N=14$)	19.55 ± 1.60 ($N=12$)	23.49 ± 2.04 ($N=15$)	24.79 ± 2.75 ($N=11$)
Test diameter growth (mm)	-0.02 ± 0.38 ($N=14$)	2.02 ± 0.67 ($N=12$)	5.61 ± 1.36 ($N=15$)	6.04 ± 1.97 ($N=11$)
Test diameter growth (%)	-0.12 ± 2.10 ($N=14$)	11.72 ± 4.22 ($N=12$)	31.45 ± 7.38 ($N=15$)	32.52 ± 10.54 ($N=11$)
Mass growth (mm)	-0.15 ± 0.10 ($N=14$)	-0.19 ± 0.09 ($N=12$)	3.00 ± 0.76 ($N=15$)	3.51 ± 1.20 ($N=11$)
Mass growth (%)	-5.84 ± 3.92 ($N=14$)	-7.73 ± 3.95 ($N=12$)	111.67 ± 23.16 ($N=15$)	115.72 ± 32.09 ($N=11$)
Gonad index	0.06 ± 0.08 ($N=10$)	–	1.75 ± 0.48 ($N=9$)	–
Kelp consumed (g)	0.002 ± 0.001 ($N=14$)	–	0.003 ± 0.001 ($N=15$)	–
Bite size (mm)	0.009 ± 0.005 ($N=14$)	–	0.007 ± 0.002 ($N=15$)	–

Dashes indicate that sampling did not occur for those particular treatments. All measurements, except for the kelp consumed and bite size, showed a significant difference between the high (high and high/low) and low (low and low/high) treatments

277 The slopes between the initial and final jaw lengths
 278 were not significantly different from zero for the low
 279 treatment individuals (linear regression: $P = 0.59$,
 280 slope = 0.03 ± 0.06 , $df = 78$, $N = 42$) nor the low/high treat-
 281 ment individuals [$P = 0.04$ (Bonferroni-corrected $\alpha = 0.002$),
 282 slope = -0.06 ± 0.03 , $df = 78$, $N = 42$], indicating no change
 283 in jaw length for the duration of the experiment. However,
 284 the slopes were significantly positive for both the high
 285 ($P \ll 0.001$, slope = 0.12 ± 0.03 , $df = 78$, $N = 42$) and the
 286 high/low treatment individuals (linear regression: $P \ll 0.001$,
 287 slope = 0.18 ± 0.04 , $df = 78$, $N = 42$), indicating an increase
 288 in jaw length.

289 The percent jaw growth data reflected these results for
 290 the low treatment ($P = 0.11$, slope = 0.80 ± 0.50 , $df = 78$,
 291 $N = 44$), high treatment ($P \ll 0.001$, slope = 4.14 ± 0.33 ,
 292 $df = 78$, $N = 44$) and high/low treatment ($P \ll 0.001$,
 293 slope = 2.11 ± 2.22 , $df = 78$, $N = 44$). However, unlike for
 294 jaw length, the percent jaw growth slope for the low/high
 295 treatment individuals was significantly positive ($P \ll 0.001$,
 296 slope = 1.24 ± 0.21 , $df = 78$, $N = 44$) (Table 1, Fig. 2).

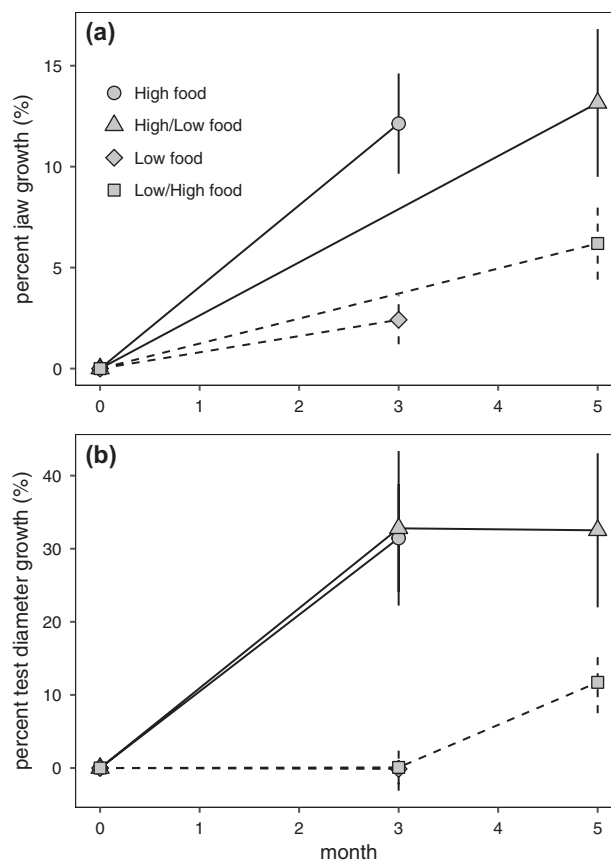
297 **Test size and growth**

298 Initial test diameters were not significantly differ-
 299 ent between treatments (high = 17.89 ± 1.41 mm, high/
 300 low = 18.68 ± 1.53 mm, low = 17.79 ± 1.28 mm, and low/
 301 high = 17.52 ± 1.67 mm) (one-way ANOVA: $P = 0.28$,
 302 $F_{3,38} = 1.3$, $N = 52$).

303 Final test diameters were significantly different between
 304 the high and low food treatments (high = 23.49 ± 2.04 mm,
 305 high/low = 24.71 ± 2.50 mm, low = 17.76 ± 1.29 mm, low/
 306 high = 19.55 ± 1.60 mm) (two-way ANOVA: $P \ll 0.001$,
 307 $F_{1,48} = 107.70$, $N = 52$) (Table 1). There was a trend for
 308 larger test diameters in the low/high treatment compared to
 309 the low treatment [t test: $P = 0.005$ (Bonferroni-corrected
 310 $\alpha = 0.002$), $t_{21,11} = 3.1023$, $N = 26$]. There were no differ-
 311 ences in test diameters between the high/low treatment and
 312 the high treatment ($P = 0.20$, $t_{18,95} = 1.33$, $N = 26$) (Table 1).

313 The slopes between the initial and final test diameters
 314 were significantly positive for both the high ($P \ll 0.001$,
 315 slope = 1.27 ± 0.16 , $df = 119$, $N = 52$) and the high/low treat-
 316 ments (linear regression: $P \ll 0.001$, slope = 1.87 ± 0.24 ,
 317 $df = 119$, $N = 52$), indicating an increase in test diameter over
 318 the course of the experiment. There was a slight increase
 319 in test diameter in the low/high treatment individuals once
 320 they were switched to the high food diet [$P = 0.02$ (Bon-
 321 ferroni-corrected $\alpha = 0.002$), slope = 0.37 ± 0.16 , $df = 119$,
 322 $N = 52$]. However, for the low treatment individuals, the
 323 slope was not significantly different from zero for indicat-
 324 ing no change in test diameter (linear regression: $P = 0.97$,
 325 slope = -0.01 ± 0.24 , $df = 119$, $N = 52$) (Table 1).

326 The percent growth of the test diameter reflected these
 327 results as well (high: $P \ll 0.001$, slope = 10.48 ± 0.79 ,



328 **Fig. 2** Percent growth of the **a** jaws and **b** test diameter over time
 329 across treatments. Growth was significantly greater but not different
 330 from one another in the high food treatments (solid lines) for both the
 331 jaws and test diameter compared to the low food treatments (dashed
 332 lines). Lines indicate that growth of both the jaws and the test diame-
 333 ter in the high food treatments increased compared to initial measure-
 334 ments. Percent growth in the low treatment did not increase in either
 335 jaws or the test, but growth in the low/high treatment increased in the
 336 jaws but not the test

336 $df = 119$, $N = 52$; high/low: $P \ll 0.001$, slope = 6.85 ± 0.55 ,
 337 $df = 119$, $N = 52$; low: $P = 0.96$, slope = -0.004 ± 0.82 ,
 338 $df = 119$, $N = 52$), except for the low/high treatment
 339 ($P \ll 0.001$, slope = 2.16 ± 0.53 , $df = 119$, $N = 52$), which
 340 showed a significant increase (as opposed to a slight
 341 increase) in test diameter once the individuals were switched
 342 to a high food diet (Table 1, Fig. 2).

335 **Jaw length to test diameter ratio**

336 Urchins in the low (0.24 ± 0.01 mm) and low/high food
 337 (0.24 ± 0.01 mm) treatments had significantly greater
 338 jaw length to test diameter ratios than urchins in the high
 339 (0.21 ± 0.01 mm) and high/low food (0.21 ± 0.01 mm) treat-
 340 ments (two-way ANOVA: $P \ll 0.001$, $F_{1,48} = 111.76$, $N = 52$)
 341 (Table 1).

The slope between the initial and final jaw length to test diameter ratios for the low treatment individuals was not significantly different from zero, indicating that the initial and final ratios did not change (linear regression: $P = 0.36$, slope \pm standard error = 0.002 ± 0.002 , $df = 78$, $N = 42$). The slope decreased slightly for the low/high treatment individuals [$P = 0.01$ [Bonferroni-corrected $\alpha = 0.002$], slope = -0.003 ± 0.001 , $df = 78$, $N = 42$], but decreased significantly for both the high ($P \ll 0.001$, slope = -0.012 ± 0.002 , $df = 78$, $N = 42$) and the high/low treatment individuals ($P \ll 0.001$, slope = -0.007 ± 0.001 , $df = 78$, $N = 42$) (Fig. 3).

Urchin mass and development

Growth in mass, both absolute and percentage, differed between food treatments. Absolute mass growth was positive and significantly greater in high food treatments compared to negative growth in low food treatments (high = 3.00 ± 0.76 g, high/low = 3.51 ± 1.20 g, low = -0.15 ± 0.10 g, low/high = -0.19 ± 0.09 g; Kruskal–Wallis: $P \ll 0.001$, $H_1 = 39.02$, $N = 53$; negative growth, Wilcoxon sign rank test, low: $P \ll 0.001$, low/high: $P \ll 0.001$). Percent mass growth was also positive and significantly greater in the high food treatments compared to the low food treatments, which showed negative percent growth (high = $111.67 \pm 23.16\%$, high/low = $115.72 \pm 32.09\%$, low = $-5.84 \pm 3.92\%$, low/high = $-7.73 \pm 3.95\%$; Kruskal–Wallis: $P \ll 0.001$, $H_1 = 38.26$, $N = 53$; negative growth, Wilcoxon sign rank test, low: $P < 0.001$, low/high: $P < 0.001$) (Table 1).

There were significant differences in the gonad index between urchins in the high and low food treatments (high

food = 1.75 ± 0.48 , low food = 0.06 ± 0.08 ; Kruskal–Wallis: $P \ll 0.001$, $H_1 = 13.5$, $N = 19$) (Table 1). Twelve individuals in the high and high/low food treatments grew to have test diameters of 25 mm or greater during the experiment, with five of these individuals being greater than 27 mm, indicating that they were sexually mature.

Feeding efficiency

The rate of kelp consumed was slightly higher but not significant in individuals in the high food compared to the low food treatment (low = 0.005 ± 0.001 g/h, high = 0.008 ± 0.001 g/h) [t test: $P = 0.03$ (Bonferroni-corrected $\alpha = 0.002$), $t_{26,8} = 2.36$, $N = 29$] (Fig. 4).

Measurements of maximum bite size relative to final jaw length were not significantly different between the low and high food treatments (low = 0.036 ± 0.020 , high = 0.03 ± 0.009) (t test: $P = 0.33$, $t_{18,14} = -1.0$, $N = 29$) (Fig. 4). The regression of bite size as a function of jaw length was not significantly different from zero for either the high (ordinary least-squares: $r^2 = 0.02$, $P = 0.33$, slope = 0.02 , $N = 15$), or low ($r^2 = 0.08$, $P = 0.15$,

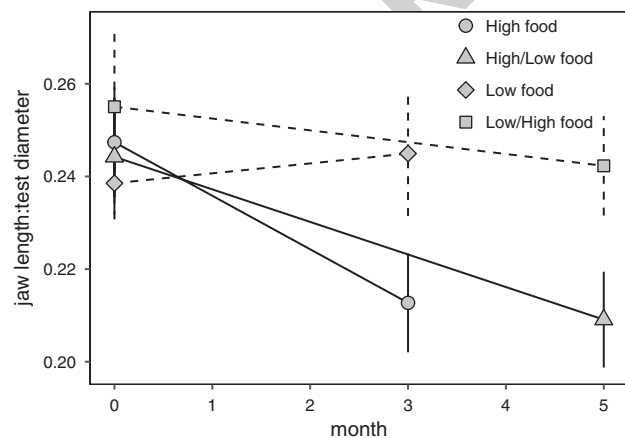


Fig. 3 Jaw length to test diameter ratios over time across treatments. The ratio was significantly greater in the low food treatments (dashed lines) compared to the high food treatments (solid lines) regardless of whether the treatments were reversed. Lines indicate that the ratios of the high food individuals decreased from the initial ratios, but the ratios of the low food individuals did not

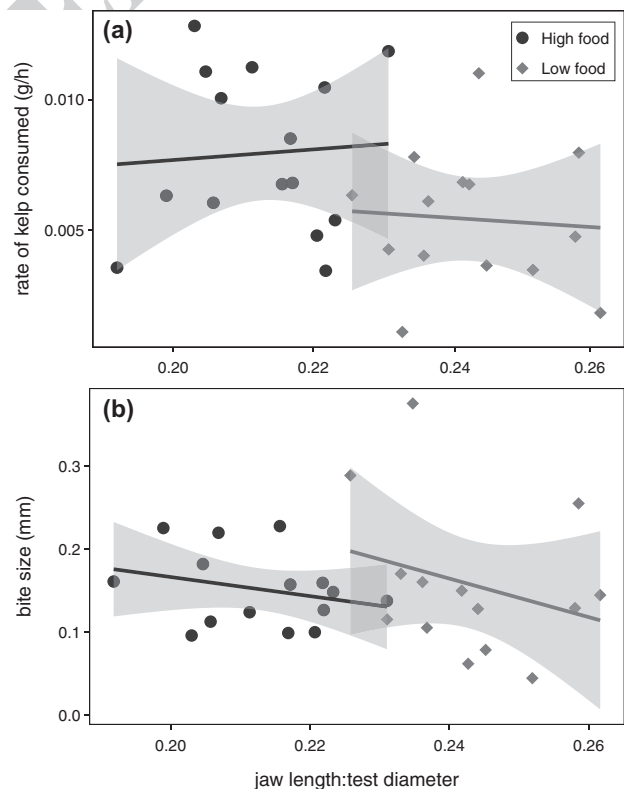


Fig. 4 Urchin feeding efficiency depicted as **a** feeding rate corrected for body mass and **b** bite size relative to jaw length to test diameter ratio. Feeding rate and bite size are not significantly correlated with the jaw length to test diameter ratio for both the high (black circles) and low (grey diamonds) treatments. Shaded areas are 95% confidence intervals

392 slope = 0.09, $N = 14$) food treatment. The regression of
 393 bite size as a function of jaw length to test diameter ratio
 394 was also not different from zero for either treatment (high:
 395 $r^2 = 0.07$, $P = 0.12$, slope = -1.15 , $N = 15$; low: $r^2 = 0.08$,
 396 $P = 0.18$, slope = -2.32 , $N = 14$).

397 Discussion

398 Phenotypic plasticity implies that an organism has an ability
 399 to adapt its phenotype to changing environmental or resource
 400 conditions (Kelly et al. 2012). The feeding apparatus of sea
 401 urchins has long been considered an example of phenotypic
 402 plasticity in response to food availability, with jaw length
 403 to test diameter ratios increasing during periods of food
 404 scarcity. In this study, we found that under low food condi-
 405 tions, growth of the jaws, test, and mass all appear to halt, or
 406 even decrease in the case of mass. When food is abundant,
 407 however, urchins grow significantly, especially in terms of
 408 their test diameter and body mass. We therefore question
 409 whether increasing relative jaw length is an example of phe-
 410 notypic plasticity, given that halting growth is a common
 411 physiological response to starvation. Furthermore, we found
 412 that relative jaw length did not change for food deprived
 413 urchins when provided with abundant food, thereby refuting
 414 the notion of reversibility in this trait. Finally, there was no
 415 evidence that having relatively longer jaws improves feed-
 416 ing efficiency on macroalgae, suggesting that this phenotype
 417 may not be an adaptive response to starvation.

418 Jaw length to test diameter ratio changes with high 419 food abundance

420 Explanations for the mechanisms underlying changes in jaw
 421 allometry with variations in food availability center around
 422 whether resources are being directed towards or away from
 423 jaw construction. During food scarcity, resources may be
 424 reallocated to the jaws to increase the jaw length relative
 425 to test diameter (Fansler 1983; Edwards and Ebert 1991;
 426 Ebert 1996), while during food abundance, resources may
 427 be allocated to other parts of the body, rather than to the
 428 jaws, which may be less energetically costly (Ebert 2014).
 429 In contrast, we show that significant changes in jaw length
 430 appeared to occur only when food abundance was high.
 431 When food abundance was low, the urchins maintained
 432 their jaw lengths and consequently their jaw length to test
 433 diameter ratios.

434 Specifically, neither the jaws nor the tests grew in the
 435 low food treatments, yielding no corresponding change in
 436 the jaw to test diameter ratio. We also found no evidence
 437 of reallocation of calcified material to the jaws when food
 438 abundance was low; the fluorescent tag line remained at the
 439 base of the jaw in almost all individual urchins in the low

440 food treatment, indicating that there was no accretion of new
 441 material. If there had been significant reallocation of calci-
 442 fied material to the jaws, measureable growth would have
 443 been detectable, as was the case for individuals in the high
 444 food treatments. Stunted jaw growth is especially evident
 445 when the high and high/low treatment animals are compared;
 446 there was no significant difference in jaw growth between
 447 the high treatment (new growth from the site of calcein
 448 stain = 0.54 ± 0.12) and the high/low treatment (0.60 ± 0.18),
 449 indicating that growth ceased when urchins were switched to
 450 the low food diet. While this result counters previous claims
 451 that material is reallocated to the jaws when food is scarce
 452 (Fansler 1983; Edwards and Ebert 1991; Ebert 1996), it cor-
 453 responds to observations in natural urchin populations where
 454 jaws from urchins in barrens grow at highly reduced rates
 455 compared to those in urchins from macroalgal beds (Peder-
 456 son and Johnson 2008; Ling and Johnson 2009; Ling et al.
 457 2019). It remains unclear whether these field observations
 458 result from reallocating material to the jaws to maintain even
 459 minimal growth or from simply a slowing of urchin growth
 460 rate overall.

461 No detectable changes in the test diameter in the low
 462 food treatments indicate that calcified material was also not
 463 allocated to test construction. Some sea urchins, including
 464 *Strongylocentrotus purpuratus*, *Diadema antillarum*, and
 465 *Heliocidaris erythrogramma*, have been shown to shrink,
 466 or decrease, their test diameter when food abundance is low
 467 (Ebert 1968; Levitan 1989, 1991; Constable 1993). Indi-
 468 viduals in this study maintained their test size, possibly
 469 because they were not exposed to starvation levels sufficient
 470 to stimulate reabsorption of somatic and gonadal tissue, the
 471 purported mechanism yielding test shrinkage (Fansler 1983;
 472 Levitan 1989, 1991; Constable 1993). However, the gonad
 473 index was lower in the low food treatment, and none of these
 474 individuals reached sexual maturity according to their test
 475 diameters, suggesting that this treatment did in fact induce
 476 considerable stress. Despite the starvation level in our study
 477 being less extreme than that of previous studies, our data
 478 show that urchins experienced food limitation sufficient to
 479 cause a significant decrease in mass. As a result, there were
 480 likely too few available resources to allocate to the accretion
 481 of new test material in both the low food treatments, sug-
 482 gesting that test reconstruction does not occur when food
 483 availability is low.

484 Conversely, when food availability was high, both the
 485 jaws and the tests grew significantly, demonstrating accre-
 486 tion of material to these calcified parts that was sufficient to
 487 yield changes in the jaw length to test diameter ratio. The
 488 test accreted more material than the jaws (Table 1), thereby
 489 decreasing the ratio of jaw length to test diameter in the high
 490 food treatments compared to the low food treatments. Thus,
 491 even though both the tests and the jaws grew significantly
 492 when supplied with increased food, it was the greater growth

of the test that changed the jaw length to test diameter ratio, and not changes in the jaw, contrary to what has been reported previously (Ebert 1980b; Fansler 1983; Levitan 1991; Ebert 1996). Given that the test appears to grow at high rates in macroalgal beds (Pederson and Johnson 2008; Ling and Johnson 2009; Ling et al. 2019), we hypothesize that test diameter is also important for defining relative jaw length in the field as well.

In light of these results, we question whether changes in relative jaw length with food abundance are an example of phenotypic plasticity, given that halting or at least greatly reducing growth is a common physiological response to starvation that is not necessarily considered an adaptive mechanism to cope with changes in resource availability. Instead, we hypothesize that the documented changes likely have little adaptive value and are simply a physiological consequence of growing when food is available and stunting growth when food is not available.

Reversibility of jaw length to test diameter ratio

When food abundance was switched, urchins that were shifted from low food to high food (low/high) showed no change in their jaw length to test diameter ratio, which remained greater than that of the urchins that were switched from high food to low food (high/low). This finding implies that relative jaw length was not reversible in our experiment. It is possible that a lag time in the reversibility of plastic responses (Ebert 2014) prevented its detection in this study. Adult *S. purpuratus* individuals demonstrated reversibility at 32 weeks following a food shift, though significant changes to jaw size were detected within 12 weeks (Fansler 1983). Thus, it would be reasonable to observe some evidence of reversibility within the timeframe of this study, particularly for juvenile urchins that typically experience faster growth rates (Ebert 1968).

This was the first experiment of this nature conducted on juvenile urchins. That we did not document a reversibly plastic response in juveniles raises the possibility that the food environment experienced as a juvenile carries forward into adulthood and that if long periods of starvation are experienced as juveniles, individuals will continue to have higher relative jaw lengths as adults compared to their well-fed counterparts. Thus, we speculate that there may be an age threshold for establishing allometric relationships in the body, whereby if an individual is exposed to food stress early in life, its ability to express a plastic response is altered (Searcy et al. 2004; Byrne et al. 2008; Kucharski et al. 2008).

The possible effects of early life food stress on jaw plasticity suggest that, in addition to habitat, urchin density, and species differences (Constable 1993; Fernandez and Boudouresque 1997; Epherra et al. 2015; Haag et al. 2016),

resource limitation, which is closely linked to habitat and density differences, may be an important factor underlying the presence or absence of cyclical reversibility to seasonal changes in food abundance (Ebert 2014). It may also help to explain why differences in relative jaw lengths between urchins in barrens and macroalgal beds persist and appear to be reinforced over time (Ling et al. 2019). If urchins were affected by food limitation as juveniles, then even if food conditions shift in the future, they will maintain the relative jaw lengths acquired as juveniles.

Relative jaw length does not affect feeding efficiency

Documenting changes in jaw length to test diameter ratios in response to food availability is relatively common (Ebert 1980b; Fansler 1983; Edwards and Ebert 1991; Levitan 1991; Brockington et al. 2001; Pederson and Johnson 2008; Ebert 2014; Epherra et al. 2015; Haag et al. 2016), and relative jaw length is considered a useful tool for evaluating resource limitation in urchin populations (Ebert 1980a; Black et al. 1984; Levitan 1991; Pederson and Johnson 2008; Ling et al. 2019). Indeed, our results confirm this finding and show that juvenile *S. purpuratus* individuals experience similar changes in relative jaw length. Thus, it is tempting to give an adaptive explanation for observing these patterns in nature. This study is the first to directly test whether an increase in relative jaw length increases feeding efficiency on macroalgae. The rates of kelp consumed and maximum bite size were both independent of relative jaw length. Despite having relatively larger jaws, urchins in the low food treatment did not consume kelp at higher rates nor did they take larger bites of kelp. The fact that the low food urchins, which were smaller overall, consumed kelp at similar suggests that these individuals were simply more hungry compared to those in the high food treatment.

Our finding that relatively longer jaws have no effect on feeding efficiency should be considered in the context of the type of food available. While we measured feeding efficiency using *M. pyrifera*, the mechanics of consuming macroalgae differ from those used to scrape and consume encrusting or calcareous algae. Indeed, the presence of longer jaws in urchin species may be associated with the availability of different types of food (reviewed in Ling et al. 2019). For example, larger jaws have been associated with active benthic grazing for efficiently scraping algae off of substrates in urchin barrens (Byrne et al. 2008; Ling and Johnson 2009; Epherra et al. 2015; Haag et al. 2016). The sea urchin, *Arbacia dufresnii*, has shorter absolute jaw lengths in habitats where algae is available compared to individuals in habitats where filamentous and calcareous algae and molluscs are more available (Epherra et al. 2015). Similarly, longer relative jaws have been measured

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595 in *Heliocidaris erythrogramma* urchins found in barrens
596 compared to those living in habitats with a dense mac-
597 roalgae canopy (Pederson and Johnson 2008; Ling and
598 Johnson 2009). While the switch to a durophagous diet
599 generally leads to reduced growth and recruitment for
600 urchins, there is an overall population size increase that
601 creates positive feedback on population growth even as
602 kelp declines (Ling et al. 2019). Thus, having relatively
603 longer jaws may allow for consuming calcified organ-
604 isms more efficiently, thereby further facilitating the diet
605 switch. This would suggest that food type is the driver of
606 the response, not food availability.

607 The functional significance of having longer jaws for
608 scraping, however, has yet to be tested. It remains unclear,
609 for example, how longer jaws, as opposed to other biome-
610 chanical or material traits, such as harder jaws, would aid
611 in a durophagous feeding mechanism. Given that on an
612 individual level, a durophagous diet does not provide great
613 nutritional value (reviewed in Ling et al. 2015), it is hard to
614 imagine that a persistent durophagous diet is an important
615 driver of morphological changes in relative jaw length. If
616 longer jaws indeed facilitate durophagy, then this is likely
617 a consequence of the plasticity of the test rather than the
618 jaw material. This would suggest that the changes in rela-
619 tive jaw length are not adaptive and simply a consequence
620 of a changing test. More broadly, these findings imply that
621 a change in feeding ecology is not the main strategy that
622 urchins use to maintain population sizes in urchin barrens;
623 rather is it their ability to sustain reproductive potential in
624 the face of low food availability. This idea reinforces the
625 notion that it is not a durophagous diet that helps to maintain
626 urchin barren states, but instead the allocation of resources
627 to reproduction (Ling et al. 2019) that yields continued suc-
628 cess even in low food environments such as urchin barrens.

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639 SJW. MSdV and SJW designed the study with input from JRAT. SJW
640 conducted the experiments and collected the data with help from
641 MSdV. MSdV analyzed the data. MSdV wrote the manuscript but SJW
642 wrote the methods section. JRAT had significant input in manuscript
643 preparation. All authors contributed substantially to manuscript editing.

644 Compliance with ethical standards

645 **Conflict of interest** The authors declare that they have no conflict of
646 interest.

Ethical approval This research complied with animal welfare guide-
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