Effects of five southern California macroalgal diets on consumption, growth, and gonad weight, in the purple sea urchin *Strongylocentrotus purpuratus*

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Consumer growth and reproductive capacity are direct functions of diet. Strongylocentrotid sea urchins, the dominant herbivores in California kelp forests, strongly prefer giant kelp (*Macrocystis pyrifera*), but are highly catholic in their ability to consume other species. The biomass of *Macrocystis* fluctuates greatly in space and time and the extent to which urchins can use alternate species of algae or a mixed diet of multiple algal species to maintain fitness when giant kelp is unavailable is unknown. We experimentally examined the effects of single and mixed species diets on consumption, growth and gonad weight in the purple sea urchin *Strongylocentrotus purpuratus*. Urchins were fed single species diets consisting of one of four common species of macroalgae (the kelps *Macrocystis pyrifera* and *Pterygophora californica,* and the red algae *Chondracanthus corymbiferus* and *Rhodymenia californica* (hereafter referred to by genus) or a mixed diet containing all four species *ad libitum* over a 13-week period in a controlled laboratory setting. Urchins fed *Chondracanthus*, *Macrocystis* and a mixed diet showed the highest growth (in terms of test diameter, wet weight and jaw length) and gonad weight while urchins fed *Pterygophora* and *Rhodymenia* showed the lowest. Urchins consumed their preferred food, *Macrocystis* at the highest rate when offered a mixture, but consumed *Chondracanthus* or *Macrocystis* at similar rates when the two algae were offered alone. The differences in urchin feeding behavior and growth observed between these diet types suggest the relative availability of the algae tested here could affect urchin populations and their interactions with the algal assemblage. The fact that the performance of urchins fed *Chondracanthus* was similar or higher than those fed the preferred *Macrocystis* suggests that the availability of the former could could sustain growth and reproduction of purple sea urchins during times of low *Macrocystis* abundance as is common following large wave events.

1 **Effects of five southern California macroalgal diets on consumption, growth**

2 **and gonad weight in the purple sea urchin *Strongylocentrotus purpuratus***

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Introduction

10   Sea urchins are dominant grazers in many benthic marine systems around the world and

11 can exert a strong top-down influence on community structure (Lawrence 1975). In kelp forests

12 along the west coast of North America strongylocentrotid sea urchins can have a large effect on

13 the standing biomass of the giant kelp *Macrocystis pyrifera* and understory algal species (North

14 & Pearse 1970; Leighton 1971; Dayton 1985). The standing biomass of giant kelp, a preferred

15 food of sea urchins (Leighton 1971), fluctuates greatly in response to a range of physical and

16 biological processes (Dayton et al. 1999; Reed, Rassweiler & Arkema 2008; Reed et al. 2011,

17 Cavanaugh et al. 2011), and when its abundance is low sea urchins are known to shift their diet to

18 consume the remaining algal assemblage (Ebeling, Laur & Rowley 1985; Harrold & Reed 1985).

19 Increased knowledge of diet's effects on sea urchin consumption, growth and reproduction should

20 lead to a better understanding of when and where they can have strong ecosystem effects.

21   The feeding rates, food selectivity, growth and reproduction of a variety of species of sea

22 urchins vary with changes in quantity and types of available foods. This variation is due to

23 consumer food preferences and the digestibility, absorption efficiency and composition of

24 available food (Lawrence 1975). Feeding and nutrient allocation to somatic and gonadal growth

25   and gametogenesis also vary with diet, time of year, and environmental conditions (Lawrence &

26   Lane 1982). Some species of sea urchins exhibit strong food preferences in the presence of a

27   mixture of algae (Leighton 1968). Many perform better when consuming mixed diets

28   (Beddingfield & McClintock 1997; Fernandez & Boudouresque 1998; Fernandez & Pergent

29   1998; Vadas et al. 2000), suggesting that algal assemblage diversity could affect sea urchin

30   performance. A comprehensive understanding of the interactions between sea urchins and

31   macroalgal assemblages in any system requires knowledge of the factors that affect sea urchin

32   feeding behavior, and performance.

33   Here we experimentally evaluated the effects of algal diet on consumption, growth, and

34   gonad weight of the purple sea urchin *Strongylocentrotus pupuratus* using four co-occurring

35   species of macroalgae known to be part of its diet: the kelps *Macrocystis pyrifera* and

36   *Pterygophora californica*, and the red algae *Chondracanthus corymbiferus* and *Rhodymenia*

37   *californica* (all algal species hereafter referred to by genus). These four species were chosen

38   because they represented a large proportion (> 75%) of the algal biomass in our study region in

39   southern California (Miller, Harrer & Reed 2012) and are consumed by purple sea urchins in the

40   field (Byrnes, Cardinale & Reed 2013). Thus, changes in the performance of purple sea urchins

41   resulting from changes in the availability of these four species of macroalgae could have large

42   implications for the structure of subtidal reef communities.

43   Methods

44   We measured algal consumption, test growth, jaw growth, change in whole body wet

45   weight and gonad weight of urchins fed one of five experimental diets over an 89-day period in a

46   controlled laboratory setting. Urchins used in the experiment were collected on October 2010

47   from a shallow (~4 m depth) boulder reef (34º 24.9 N 119º 49.8 W) located offshore of the

48   University of California, Santa Barbara. To minimize inherent variation in growth potential,

49   consumption potential, and initial gonad weight, urchins were chosen to be relatively uniform in

50   size (horizontal test diameter 33.5 ± 0.4 mm, mean ± SE) and presumably age (Ebert 1968; Ebert

51   1977; Kenner 1992; Russell 1987), and collected from a denuded urchin barren where their gonad

52   weight was predicted to be uniformly low.

53   Upon collection, urchins were transported to the laboratory in insulated containers, placed

54   in aquaria with running seawater and starved for one week prior to the start of the experiment.

55   Blotted dry urchins (placed with the aboral end facing down on paper towels for 5 minutes) were

56   weighed to the nearest 0.01 gram and their horizontal test diameter was measured to the nearest

57   0.1 mm using Vernier calipers. To measure jaw growth, each urchin was injected with the

58   fluorescent marker tetracycline following Ebert (1982). 1.0 g of tetracycline was mixed with 100

59   mL seawater and 0.2 mL of the resulting solution was injected into each urchin through the

60   peristomal membrane with a hypodermic needle. Tetracycline binds to actively calcifying tissues,

61   effectively labeling jaw material present at the start of the experiment. Jaw material calcified after

62   tetracycline administration was therefore unlabeled.

63   Each urchin was assigned to one of 35 labeled plastic containers (32 x 19 x 11 cm)

64   supplied with flow-through seawater. This setup allowed us to keep track of individuals without

65   the use of external tags. Each container was supplied from the same head water tank, however the

66   containers were not connected and therefore water supplies were independent. Seawater

67   temperatures ranged from 11.6 to 16.3 ºC during the experiment and matched ambient conditions.

68   Urchins were fed one of five macroalgal diets: a monospecific diet of either *Macrocystis pyrifera*,

69   *Pterygophora californica*, *Rhodymenia californica*, or *Chondracanthus corymbiferus*, or an equal

70   mixture of all four species (hereafter referred to as a mixed diet) with n = 7 urchins per diet type.

71   Sea urchin containers assigned to each treatment were spread out randomly in space. Algae were

72   added to the tanks during nine periods ranging in length from 4 to 8 days in which all

73   experimental urchins were given a known amount of algae (on average either 34 g of one species,

74   or in the mixed diet treatment 10 g of each of the four species). Sea urchins were given more

75   algae than they consumed in all cases, except during one feeding period in which urchins in

76   mixed diet treatments consumed all *Macrocystis* approximately 48 hours before algae was

77   removed and the feeding period terminated. During the 89-day experiment, urchins were exposed

78   to algae for approximately 54 days. *Rhodymenia* was absent from the monospecific *Rhodymenia*

79   treatment and from the mixed diet treatment for one of the feeding periods (14% of the total

80   exposure time) due to its lack of availability in the field. Feeding periods were kept relatively

81   short to prevent degradation of the algae, and algae were not immediately replaced due to

82   logistical constraints on field collections. To study algal consumption, algal wet weight (after

83   removing excess water with a spinning colander) was measured at the beginning and end of each

84   feeding period. Consumption was calculated as wet weight (g) of algae consumed per urchin per

85   hour using the total amount of hours urchins were exposed to algae (exposure time). We used

86   consumption rate rather than amount consumed to standardize for different exposure times in the

87   *Rhodymenia* treatment. To evaluate the nutritional content of the algae, tissue samples of each

88   species of algae were collected at three time points during the experiment and analyzed for

89   carbon and nitrogen content (% dry weight). Samples were weighed wet (after removing excess

90   water with a spinning colander), placed in a drying oven at 60 ℃ until dry, ground to a fine

91   powder, and stored in a desiccator until analyzed by the UCSB Marine Science Institute

92   Analytical Laboratory using the Dumas combustion method (duplicate samples from each species

93   at each time point were tested). Mean carbon:nitrogen (C:N) ratios were calculated for each algal

94   species and linear models were fit for each measure of urchin performance (see below) using C:N

95   as the independent variable in each case.

96   At the end of the experiment the horizontal test diameter and wet weight (measured to the

97   nearest 0.01 g in blotted dry urchins) of each urchin was measured. The change in test diameter

98   and change in wet weight of each individual over the experiment was calculated by subtracting

99   the initial value measured at the beginning of the experiment from that measured at the end of the

100   experiment. Gonads were removed from each urchin upon dissection, placed in an oven at 60 ºC

101   until dry and weighed to the nearest 0.01g. Final gonad dry weight was used as a measure of

102   gonad growth because initial gonad weight was presumed to be nil as all individuals used in the

103   experiment were similar in size and collected from a barren. We verified this assumption by

104   taking eight urchins (test diameter 34.3 ± 1.0 mm (mean ± SE)) from the original collection site

105   in the middle of the experiment (inadvertently, no data from the source population were taken at

106   the beginning of the experiment) and measuring the mass of their gonads (see Results) following

107   the same procedure described above.

108   Jaw growth was measured using half-pyramids of the aristotle's lantern following Ebert

109   (1982). Half pyramids were removed from each urchin and soaked in a 5% sodium hypochlorite

110   solution for 24 hours. For one half-pyramid per urchin, the total length from the oral tip to the flat

111   shoulder at the aboral end (see Ebert (1980a) for pictures of points of measurement) was

112   measured to the nearest 0.01 mm using a dissecting microscope equipped with an ultraviolet lamp

113   and an ocular micrometer. Fluorescence from labeled tetracycline was observed from the oral tip

114   to part way up the length of the jaw, indicating that this material had been present at the start of

115   the experiment. Jaw growth was measured as the length of the non-fluorescent "band" extending

116   from the top of the fluorescent area to the flat shoulder at the aboral end.

117   Differences among treatments were analyzed separately for each response variable

118   (consumption rate (g of algae consumed · h^{-1} averaged over the experiment), change in test

119   diameter, change in jaw length, change in whole body wet weight, and final gonad dry weight)

120   using one-way ANOVA. Diet selectivity was studied by examining the rate at which individual

121   species of algae were consumed in mixture treatments by fitting a linear model with algal species

122   as a fixed effect and container (individual urchin enclosure) included as a random effect (Gelman

123   & Hill 2006) as consumption rates of individual species of algae in a single container were not

124 independent. After fitting linear models, assumptions of normality were tested by performing the

125 Shapiro-Wilk test on the linear regression residuals, and homogeneity of variance was tested

126 using Bartlett's test on the residuals across treatments (or across algal species, in the case of the

127 mixed model). Homogeneity of varianace was not supported for the linear models of change in

128 wet weight, consumption across treatments, and consumption within the mixed diet. ($p < 0.05$).

129 Given that our data were from consumption and growth processes (implying multiplicative error)

130 these three models were re-fit with log base 10 transformed data, and the resulting regression

131 residuals exhibited normality and homogeneity of variance ($p > 0.05$). A post-hoc Tukey test was

132 used to compare means (with statistical significance determined at the $p < 0.05$ level)—False

133 Discovery Rate corrected p-values (Benjamini & Hochberg 2000) were used in the case of the

134 mixed model. For the log-transformed data, least-squares means and standard errors were back-

135 transformed for plotting purposes. All statistical models were fit using R version 2.15-3 (R

136 Development Core Team 2012) with the nlme package for mixed models (Pinhero et al. 2012)

137 and the multcomp library for post-hoc analyses (Hothorn et al 2008).

138

139 # Results

140   Diet type had a significant effect on all performance measures (Table 1). Sea urchins fed

141 *Chondracanthus, Macrocystis* and mixed diets exhibited the highest test growth, jaw growth, wet

142 weight gain, and gonad weight, with no significant differences between these three diets (Figure

143 1). Urchins fed *Pterygophora* exhibited significantly lower test growth compared to those fed

144 *Chondracanthus* and *Macrocystis* diets, but had jaw growth and gonad weight that were not

145 statistically different from either of them (Figure 1). Urchins fed *Rhodymenia* exhibited the

146 lowest values of all growth metrics and gonad weight (except that urchins fed *Pterygophora* had

147 slightly lower mean test growth), with values significantly lower than those of urchins fed

148   *Chondracanthus, Macrocystis* and mixed diets, in most cases (Figure 1). Urchins collected from

149   the field as a control group in the middle of the experiment had a gonad weight of 0.20 ± 0.06 g

150   (mean $\pm$ SE) which was statistically not detectably different (p = 0.24, Welch two-sample t-test—

151   the assumption of normality was met for both samples (Shapiro-Wilk p > 0.05)—from the gonad

152   weight of experimental urchins fed *Rhodymenia*, the least nutritious diet (Figure 1c).

153   Within the mixed diet, sea urchins consumed *Macrocystis* at the highest rate, over twice as

154   fast as any other species (Figure 2a, Table 2). When algae were offered alone, however, the

155   consumption rate of *Chondracanthus* and the mixed diet were similar to that of *Macrocystis*

156   (Figure 2b). In contrast, urchins consumed *Pterygophora* and *Rhodymenia* offered singly at the

157   lowest rates.

158   The four species of algae used in the experiment differed in nutritional value as

159   determined by their C:N ratios (Figure 3). Importantly, we found no relationship between an

160   alga's C:N ratio and food quality as measured by urchin performance (p > 0.27 for all

161   correlations between the various measures of urchin performance and algal C:N ratio), with the

162   exception of a correlation between gonad weight and algal C:N ratio (slope = 0.04 ± 0.02

163   (estimate $\pm$ SE), p = 0.01). Counter to expectations, the species with the lowest C:N ratio (and

164   thus the highest expected nutritional value) was *Rhodymenia*, which proved to be the least

165   nutritional to urchins in terms of somatic and gonadal growth.

166

Discussion

167

168   We found test growth, wet weight gain, jaw growth, and gonad weight varied significantly

169   among purple sea urchins as a function of diet. Overall, urchins fed monospecific diets of

170   *Chondracanthus, Macrocystis,* and those fed a mixed diet grew significantly faster than those that

171   were fed monospecific diets of *Pterygophora* or *Rhodymenia*, while urchins fed *Rhodymenia* had

172   the lowest gonad weights. Urchins showed a strong preference for the naturally abundant

173   *Macrocystis*, even when other algae were offered alongside. Our results suggest, however, that a

174   diet consisting of other less preferred species of algae can sustain *S. purpuratus* at equally high

175   levels of fitness at least over the short-term. This feature may be critically important in

176   maintaining the reproductive capacity of purple sea urchins during the peak winter spawning

177   season when *Macrocystis* is least abundant due to intensive wave disturbance (Reed, Rassweiler

178   & Arkema 2008; Reed et al. 2011).

179   Since no differences in performance were observed among urchins fed *Chondracanthus*,

180   *Macrocystis* (monospecific) and mixed diets, we found little evidence that purple sea urchins fed

181   a mixed diet benefitted over and above those fed a monospecific diet as long as either

182   *Macrocystis* or *Chondracanthus* were present in the mixture. Because our particular mixed diet

183   did not lead to increased performance, there appeared to be no benefit of diet complementarity

184   (as assumed by the balanced diet hypothesis (Pennings, Nadeau & Paul 1993)). Furthermore,

185   since consumption was not higher in urchins fed a mixed diet, as could be permitted if species-

186   specific toxins limited consumption of any one species, it does not seem likely that toxin

187   minimization played a large role.

188   Despite these results, *Macrocystis* was consumed at the highest rate in mixed diets,

189   suggesting that the effects of a mixed diet in the absence of this preferred food might prove

190   different. Understanding urchin performance from algal mixtures in the absence of *Macrocystis*

191   would be useful for understanding urchin dynamics after major kelp removal, as is common

192   following large wave events. In this framework, Byrnes, Cardinale & Reed (2013) found that

193   reduction in the abundance of sessile species by grazing purple sea urchins was positively

194   correlated with species richness in plots where *Macrocystis* had been removed.

195   The low values for growth and gonad weight observed in purple sea urchins that were fed

196   a monospecific diet of *Rhodymenia* occurred in spite of the fact that this species was often

197   covered with epiphytic invertebrates such as hydroids and encrusting bryozoans, which have been

198   shown to increase urchin somatic and gonad growth (Knip & Scheibling 2007 and references

199   therein). The fact that this alga was absent from the *Rhodymenia* monospeicifc diet and mixed

200   diet for 14% of the total exposure time (due to low availability for collection) most likely did not

201   bias results of performance measurements by much; test growth, jaw growth, change in wet

202   weight, and gonad weight for urchins fed *Rhodymenia* were at least 40% lower than those for

203   *Chondracanthus*, *Macrocystis* (monospecific), and mixed diets each case. Furthermore Leighton

204   (1968) found test growth and gonad index were lower in purple sea urchins fed *Rhodymenia* than

205   those fed either *Macrocystis* or *Pterygophora*. While our results with respect to urchins fed

206   *Rhodymenia* should be interpreted cautiously, they suggest it is likely poor forage for purple sea

207   urchins.

208   Like many organisms urchins display a trade-off in allocating resources to somatic vs.

209   gonadal growth (Lawrence & Lane 1982; Steinberg & van Altena 1992). Our findings pertaining

210   to the performance of urchins fed *Pteryoghora* are consistent with those of Leighton (1968)—

211   purple sea urchins fed *Pterygophora* produced relatively large gonads and grew slowly during

212   periods leading up to the peak spawning season. Leighton (1968), however, showed evidence that

213   somatic growth may increase as a proportion of total growth during the time period after

214   spawning, highlighting that the effects of diet may vary with time of year among other factors.

215   Additionally, concerning the jaw growth of urchins fed *Pterygophora,* Ebert (1980) and Levitan

216   (1991) related increased jaw size and decreased test size to lower food availability in two species

217   of *Diadema*, suggesting resource allocation toward jaw growth facilitated food gathering ability.

218   The fact that sea urchins in our experiment fed *Pterygophora* exhibited relatively high jaw

219   growth relative to test growth provides preliminary evidence of a similar phenomenon in *S.*

220   *purpuratus*. While the urchins in our experiment were not food limited, (as in Ebert (1980a) and

221   Levitan (1991)), it seems possible that some effect of a *Pterygophora* diet could have triggered a

222 similar mechanism as that by which food limitation caused resource allocation toward jaws in

223 *Diadema.*

224   C:N ratio, used in our study as a rough measure of algal nitrogen and therefore protein

225 content, was not correlated to any of the performance measures, as *Chondracanthus* and

226 *Macrocystis*, which produced similar urchin performance had dissimilar C:N ratios (12.6 and 8.7,

227 respectively, where the range of C:N values for all species was 7.4 – 15.6), suggesting that

228 additional factors affected urchin performance. Leighton (1968) found that absorption efficiency

229 was higher for purple sea urchins fed *Macrocystis* (70%) than *Pterygophora* (50%) or

230 *Rhodymenia* (34%), and that protein and carbohydrates were absorbed more efficiently with

231 *Macrocystis* than with *Pterygophora*. These results may explain some of the differences that we

232 observed in performance as a function of diet. Concentrations of fatty acids, minerals

233 Khotimchenko, Vaskovsky & Titlyanova 2002) and chemical deterrents (Hall et al. 1973; Crews

234 & Kho-Wiseman 1977; Estes & Steinberg 1988; Iken & Dubois 2006) also vary in other algae

235 that are encountered by purple sea urchins and may play a role in nutritional quality, urchin food

236 preference and consumption rates. Additional work is needed to uncover the relative

237 contributions of different factors that may have led to the differences in consumption and

238 performance that we observed.

239   We acknowledge that the sea urchins used in our experiment were collected from a single

240 site, and the barren conditions present there suggest that the urchins had low food availability for

241 some time prior to the experiment. Consumer history has been shown to influence urchin somatic

242 and gonad growth (Livore & Connell 2012, Williamson & Steinberg 2012), and the proportion of

243 time food is available has been shown to affect their grazing, growth and resource allocation

244 (Spirlet et al. 1998). Thus, our results could have been affected by the prior history of the

245 individual urchins used in our experiment. However Leighton (1966) found that purple urchins'

246 food preferences did not vary among groups of individuals collected from a variety of habitats.

247   This coupled with the fact that Leighton (1968) observed the same rankings among *Macrocystis*,

248   *Pterygophora*, and *Rhodymenia* in terms of promoting gonadal growth, and similar differences in

249   allocations to somatic and gonadal growth in sea urchins fed *Pterygophora*, suggests that our

250   results are generally applicable to purple sea urchins.

251   *S. purpuratus* and the four algae we tested co-occur only along the west coast of North

252   America (Watanabe 2010). Nonetheless, strong preferences among algae, as well as marked

253   effects of algal nutritional value in terms of fostering growth and reproduction in sea urchins have

254   been noted in temperate and tropical systems around the world, including *Lytechinus variegatus*

255   in the Gulf of Mexico (Beddingfield & McClintock 1998), *Strongylocentrotus droebachiensis* in

256   the Northwestern Atlantic (Larson, Vadas & Keser 1980), *Centrostephanus rodgersii* and

257   *Tripneustes gratilla* in Australia (Steinberg & van Altena 1992) , *Paracentrotus lividus* in the

258   Mediterranean and eastern Atlantic (Boudouresque & Verlaque 2007), and various species of

259   *Diadema* throughout the tropical Indo-Pacific (Muthiga & McLanahan 2007). Such effects likely

260   play a role in the overall consequences of grazing in many systems. For example, the food

261   preferences of *Paracentrotus lividus*, which favor leafy algae over corallines or seagrasses have

262   been shown to affect algal assemblage composition (Boudouresque & Verlaque 2007). Likewise,

263   Scheibling and Anthony (2001) suggested that *Strongylocentrotus droebachiensis'* preference for

264   local brown algae over the invasive alga *Codium fragile* may spare patches largely composed of

265   this alga that would otherwise be denuded under barren-forming conditions.

266   Our results focus on the four species of algae that collectively comprised > 75% of the

267   biomass in kelp forests off Santa Barbara (Miller, Harrer & Reed 2012) and elucidate the effects

268   of these algae on performance of purple sea urchins, which may have implications for urchin

269   populations in the wild. First, the ability to switch between diets, namely diets of

270   *Chondracanthus* and *Macrocystis* (the urchin's preferred food)*,* with little or no cost to growth

271   and reproduction suggests that *Chondracanthus* could serve as an important alternative food

272   source when *Macrocystis* is disproportionately removed by large waves (Dayton & Tegner 1984;

273   Dayton et al. 1999; Gaylord, Denny & Koehl 2008). Upon the removal of *Macrocystis*,

274   understory algae such as *Chondracanthus* become more abundant (Arkema, Reed & Schroeter

275   2009; Miller, Reed & Brzezinski 2011) and may serve as a suitable food that can sustain urchin

276   populations and promote high growth and reproduction. *Chondracanthus'* relatively low rate of

277   primary production (Miller, Harrer & Reed 2012), however, indicates it might not be a long-term

278   sustainable food source. Additionally our results suggest that in the context of the four abundant

279   algae we tested, algal assemblage diversity may not be as important as the availability of one or

280   two high quality food sources. We saw little evidence of a diversity effect; in mixed diets urchins

281   mostly consumed *Macrocystis*, and performed no differently than had they consumed

282   *Macrocystis* alone.

283   Urchin preferences among these algae may also have implications for subtidal community

284   structure, and more work is needed to better understand relative consumption rates of these

285   dominant algae in nature (and the factors affecting these relative consumption rates, such as

286   ambient oceanographic conditions and community interactions). Considering the model of

287   urchin-algal dynamics presented by Harrold & Reed (1985), where following the disappearance

288   of *Macrocystis* urchins shift their behavior from occupying protected cracks and crevices while

289   consuming drift *Macrocystis* to actively grazing the understory on the open substratum, the

290   relative availability of the algae tested here could influence the extent of grazing that occurs after

291   such shifts. Our experiment suggests that algal assemblage composition, along with total

292   abundance and urchin density, all may play a role in shifting urchin dynamics in the wake of

293   environmental perturbations to subtidal systems. More work is needed to understand whether

294   these differences in diet translate to differences in urchin populations at the local and regional

295   scale in pre- and post-disturbance temperate rocky reefs.

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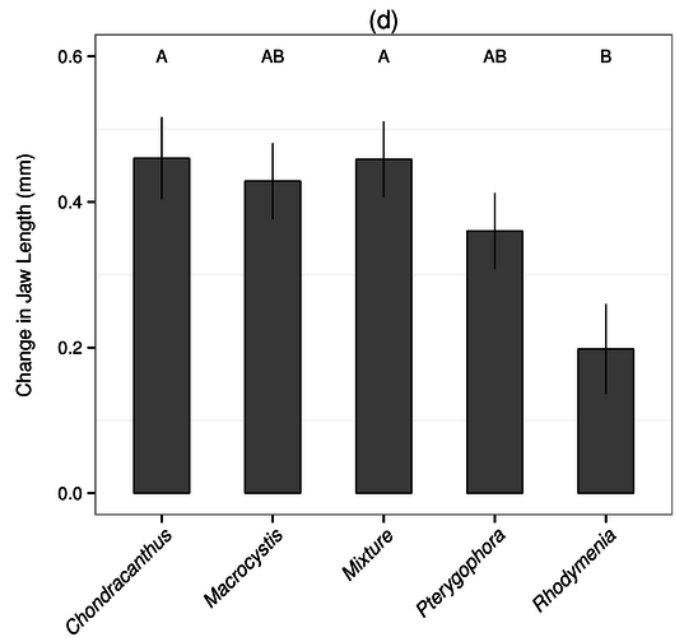
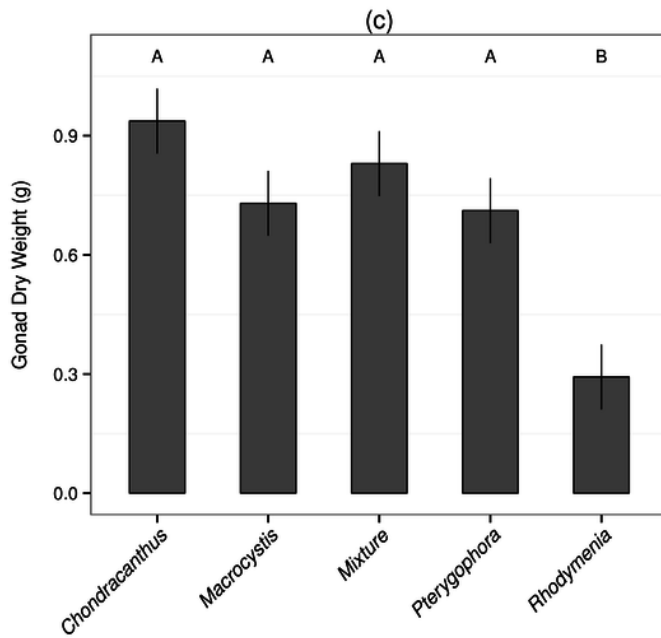
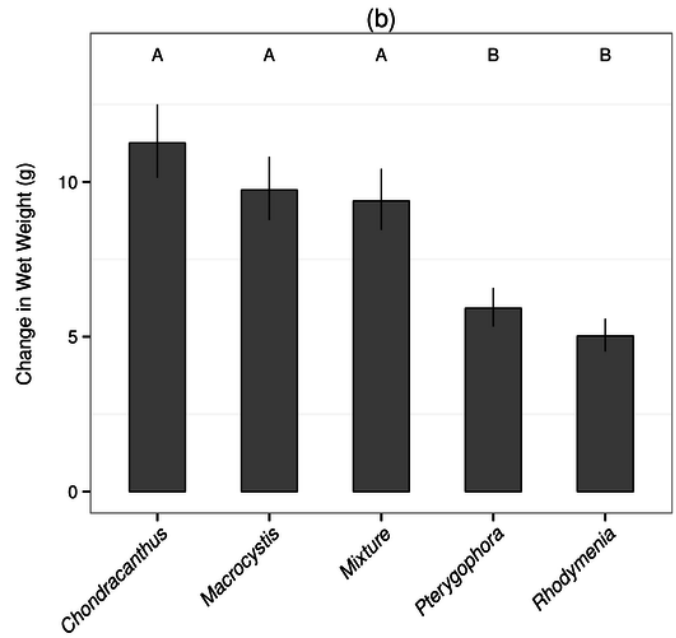
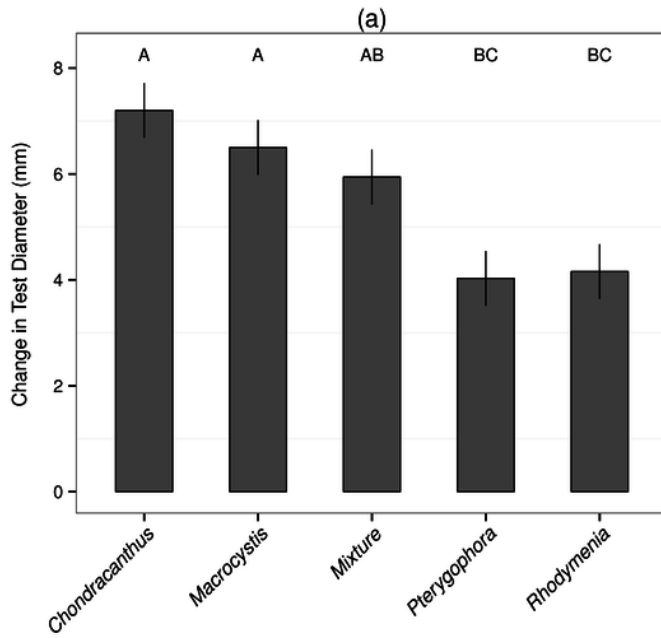
1

Performance Measures

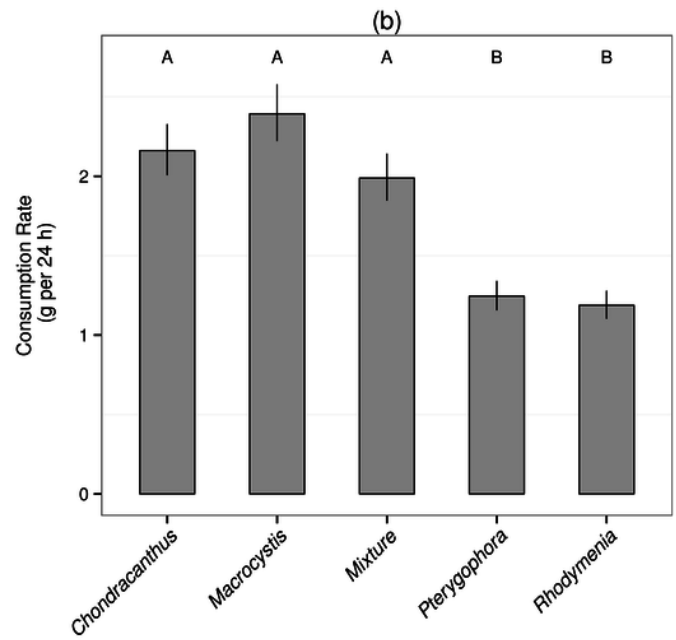
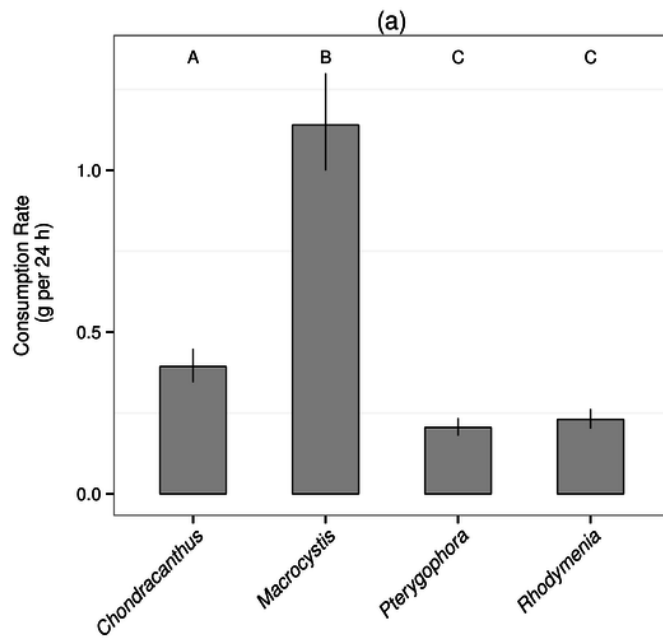
Bars represent mean (± 1 SE) for (a) change in test diameter, (b) change in wet weight, (c) gonad dry weight, and (d) change in jaw length, over the course of the experiment. Letters indicate groups of means as determined by post-hoc general linear hypothesis tests with different letters signifying means that are different at the $p < 0.05$ level.

Performance and Consumption Across Diets

F-tables for linear models fit with different aspects of urchin performance as response variables and diet as a fixed factor.

		df	*SS*	*MS*	*F*	*Pr(>F)*
Change in Test Diameter	Diet	4	56.2	14.1	7.52	< 0.001
	Residual Error	30	56.0	1.87		
Change in Wet Weight	Diet	4	0.642	0.160	11.1	< 0.001
	Residual Error	30	0.434	0.014		
Gonad Dry Weight	Diet	4	1.68	0.420	8.99	< 0.001
	Residual Error	30	1.40	0.047		
Change in Jaw Length	Diet	4	0.263	0.066	3.44	0.021
	Residual Error	27	0.516	0.019		
Consumption Rate	Diet	4	0.559	0.140	19.1	< 0.001
	Residual Error	30	0.220	0.007		

2

Consumption Rate

Bars represent mean consumption rate (± 1 SE) averaged over the experiment. Letters indicate groups of means as determined by post-hoc general linear hypothesis tests with different letters signifying means that are different at the $p < 0.05$ level. (a) Consumption rate of the different algal species in the mixed diet. (b) Consumption rate of all diets.

Consumption Rate within the Mixed Diet

F-table for a linear model fit with consumption rate as the response variable, algal species as a fixed factor and urchin container included as a random effect.

		df (numerator)	df (denominator)	F	Pr(>F)
Fixed Effects	Species	4	18	80.7	< 0.001

		Standard Deviation			
Random Effects	Container	1.05×10^{-5}			
	Residual Error	0.150			

Algal C:N

Each path corresponds to a different a algal species (indicated on right), passing through the mean carbon:nitrogen ratio (C:N) calculated for each collection date. Individual points represent C:N values obtained for each species on each collection date (n = 2).