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

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 purple sea urchins could sustain growth and reproduction during times of low *Macrocystis* abundance as is common following large wave events.

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

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Introduction

Sea urchins are dominant grazers in benthic marine systems around the world and can exert a strong top-down influence on community structure (Lawrence 1975). In kelp forests along the west coast of North America Strongylocentrotid sea urchins can have a large effect on the standing biomass of the giant kelp *Macrocystis pyrifera* and understory algal species (North & Pearse 1970; Leighton 1971; Dayton 1985). The standing biomass of giant kelp, a preferred food of sea urchins (Leighton 1971), fluctuates greatly in response to a range of physical and biological processes (Dayton et al. 1999; Reed, Rassweiler & Arkema 2008; Reed et al. 2011, Cavanaugh et al. 2011), and when its abundance is low sea urchins are known to shift their diet to consume the remaining algal assemblage (Ebeling, Laur & Rowley 1985; Harrold & Reed 1985). Increased knowledge of diet's effects on sea urchin consumption, growth and reproduction should lead to a better understanding of when and where they can have strong ecosystem effects.

The feeding rates, food selectivity, growth and reproduction of a variety of species of sea urchins vary with changes in quantity and types of available foods. This variation is due to consumer food preferences and the digestibility, absorption efficiency and composition of available food (Lawrence 1975). Feeding and nutrient allocation to somatic and gonadal growth and gametogenesis also vary with diet, time of year, and environmental conditions (Lawrence & Lane 1982). Some species of sea urchins exhibit strong food preferences in the presence of a mixture of algae (Leighton 1968). Many perform better when consuming mixed diets (Beddingfield & McClintock 1997; Fernandez & Boudouresque 1998; Fernandez & Pergent 1998; Vadas et al. 2000), suggesting that algal assemblage diversity could affect sea urchin performance. A comprehensive understanding of the interactions between sea urchins and macroalgal assemblages in any system requires knowledge of the factors that affect sea urchin feeding behavior, and performance.

Here we experimentally evaluated the effects of algal diet on consumption, growth, and gonad weight of the purple sea urchin *Strongylocentrotus pupuratus* using four co-occurring species of macroalgae known to be part of its diet: the kelps *Macrocystis pyrifera* and *Pterygophora californica*, and the red algae *Chondracanthus corymbiferus* and *Rhodymenia californica*. These four species were chosen because they represented a large proportion (> 75%) of the algal biomass in our study region in southern California (Miller, Harrer & Reed 2012) and are consumed by *Strongylocentrotus* in the field (Byrnes, Cardinale & Reed 2013). Thus, changes in the performance of purple sea urchins resulting from changes in the availability of these four species of macroalgae could have large implications for the structure of subtidal reef communities.

Methods

We measured algal consumption, test growth, jaw growth, change in whole body wet weight and gonad weight of urchins fed one of five experimental diets over an 89-day period in a controlled laboratory setting. Urchins used in the experiment were collected on October 2010 from a shallow (~4 m depth) boulder reef (34º 24.9 N 119º 49.8 W) located offshore of the

University of California, Santa Barbara. To minimize inherent variation in growth potential, consumption potential, and initial gonad weight, urchins were chosen to be relatively uniform in size (horizontal test diameter 33.5 ± 0.4 mm, mean ± SE) and collected from a denuded urchin barren where their gonad weight was predicted to be uniformly low. Upon collection, urchins were transported to the laboratory in insulated containers, placed in aquaria with running seawater and starved for one week prior to the start of the experiment. Blotted dry urchins (placed with the aboral end facing down on paper towels for 5 minutes) were weighed to the nearest 0.01 gram and their horizontal test diameter was measured to the nearest 0.1 mm using Vernier calipers. To measure jaw growth, each urchin was injected with the fluorescent marker tetracycline following Ebert (1982). 1.0 g of tetracycline was mixed with 100 mL seawater and 0.2 mL of the resulting solution was injected into each urchin through the peristomal membrane with a hypodermic needle. Tetracycline binds to actively calcifying tissues, effectively labeling jaw material present at the start of the experiment. Jaw material calcified after tetracycline administration was therefore unlabeled.

Each urchin was assigned to one of 35 labeled plastic containers (32 x 19 x 11 cm) supplied with flow-through seawater. This setup allowed us to keep track of individuals without the use of external tags. Seawater temperatures ranged from 11.6 to 16.3 ºC during the experiment and matched ambient conditions. Urchins were fed one of five macroalgal diets: a monospecific diet of either *Macrocystis pyrifera*, *Pterygophora californica*, *Rhodymenia californica*, or *Chondracanthus corymbiferus* (all species hereafter referred to by genus), or an equal mixture of all four species (hereafter referred to as the mixed diet) with n = 7 urchins per diet type. Algae were introduced into the tanks during nine periods ranging in length from 4 to 8 days in which all experimental urchins were fed a known amount of algae (either approximately 34 g of one species, or in the mixed diet treatment approximately 10 g of each of the four species). During the 89-day experiment, urchins were exposed to algae for approximately 54 day. *Rhodymenia* was absent from the monospecific *Rhodymenia* treatment and from the mixed diet treatment for one of the feeding periods (14% of the total exposure time) due to its lack of availability in the field. To study algal consumption, algal wet weight (after removing excess water with a spinning colander) was measured at the beginning and end of each feeding period. Consumption was calculated as wet weight (g) of algae consumed per urchin per hour using the total amount of hours urchins were exposed to algae (exposure time). We used consumption rate rather than amount consumed to standardize for different exposure times in the *Rhodymenia* treatment. To evaluate the nutritional content of the algae, tissue samples of each species of algae were collected at three time points during the experiment and analyzed for carbon and nitrogen content (% dry weight). Samples were weighed wet (after removing excess water with a spinning colander), placed in a drying oven at 60 ºC until dry, ground to a fine powder, and stored in a desiccator until analyzed by the UCSB Marine Science Institute Analytical Laboratory using the Dumas combustion method (duplicate samples from each species at each time point were tested).

At the end of the experiment the horizontal test diameter and wet weight (measured to the nearest 0.01 g in blotted dry urchins) of each urchin was measured. The change in test diameter and change in wet weight of each individual over the experiment was calculated by subtracting the initial value measured at the beginning of the experiment from that measured at the end of the experiment. Gonads were removed from each urchin upon dissection, placed in an oven at 60 ºC until dry and weighed to the nearest 0.01g. Final gonad dry weight was used as a measure of gonad growth because initial gonad weight was presumed to be nil as all individuals used in the experiment were similar size and collected from a barren. We verified this assumption by taking eight urchins (test diameter 34.3 ± 1.0 mm (mean ± SE)) from the original collection site in the middle of the experiment and measuring the mass of their gonads following the same procedure described above (see Results).

Jaw growth was measured using half-pyramids of the aristotle's lantern following Ebert (1982). Half pyramids were removed from each urchin and soaked in a 5% sodium hypochlorite solution for 24 hours. For one half-pyramid per urchin, the total length from the oral tip to the flat shoulder at the aboral end (see Ebert (1980) for pictures of points of measurement) was measured to the nearest 0.01 mm using a dissecting microscope equipped with an ultraviolet lamp and an ocular micrometer. Fluorescence from labeled tetracycline was observed from the oral tip to part way up the length of the jaw, indicating that this material had been present at the start of the experiment. Jaw growth was measured as the length of the non-fluorescent "band" extending from the top of the fluorescent area to the flat shoulder at the aboral end.

Differences among treatments were analyzed separately for each response variable (consumption rate (g of algae consumed · h^{-1} averaged over the experiment), change in test diameter, change in jaw length, change in whole body wet weight, and final gonad dry weight) using one-way ANOVA and a post-hoc Tukey test to compare means (statistical significance was determined at the $p < 0.05$ level). Diet selectivity was studied by examining the rate at which individual species of algae were consumed in mixture treatments with container (individual urchin enclosure) included as a random effect (Gelman & Hill 2006) as consumption rates of individual species of algae in a single container were not independent. A post-hoc comparison of algal species effects was then performed with False Discovery Rate corrected p-values (Benjamini & Hochberg 2000). All statistical models were fit using R version 2.15-3 (R Development Core Team 2012) with the nlme package for mixed models (Pinhero et al. 2012) and the multcomp library for post-hoc analyses (Hothorn et al 2008).

Results

Diet type had a significant effect on all performance measures (Table 1). Sea urchins fed *Chondracanthus, Macrocystis* and mixed diets exhibited the highest test growth, jaw growth, wet weight gain, and gonad weight, with no significant differences between these three diets (Figure 1). Urchins fed *Pterygophora* exhibited significantly lower test growth compared to those fed *Chondracanthus* and *Macrocystis* diets, but had jaw growth and gonad weight that were not statistically different from either of them (Figure 1). Urchins fed *Rhodymenia* exhibited the lowest values of all growth metrics and gonad weight (except that urchins fed *Pterygophora* had slightly lower mean test growth), with values significantly lower than those of urchins fed *Chondracanthus, Macrocystis* and mixed diets, in most cases (Figure 1). Urchins collected from the field as a control group in the middle of the experiment had a gonad weight of 0.20 ± 0.06 g (mean ± SE) which was statistically not detectably different ($p = 0.24$, Welch two-sample t-test) from the gonad weight of experimental urchins fed *Rhodymenia*, the least nutritious diet (Figure 1c).

Within the mixed diet, sea urchins consumed *Macrocystis* at the highest rate, over twice as fast as any other species (Figure 2a, Table 2). When algae were offered alone, however, the consumption rate of *Chondracanthus* and the mixed diet were similar to that of *Macrocystis* (Figure 2b). In contrast, urchins consumed *Pterygophora* and *Rhodymenia* offered singly at the lowest rates.

The four species of algae used in the experiment differed significantly in nutritional value as determined by their C:N ratios ($F_{3,20} = 230.7$, $p < 0.001$, Figure 3). Importantly, we found no relationship between an alga's C:N ratio and food quality as measured by urchin performance ($p > 0.27$ for all correlations between the various measures of urchin performance and algal C:N ratio), with the exception of a correlation between gonad weight and algal C:N ratio (slope = 0.04 ± 0.02 (estimate ± SE), $p = 0.01$). Counter to expectations, the species with the lowest C:N ratio (and thus the highest expected nutritional value) was *Rhodymenia*, which proved to be the least nutritional to urchins in terms of somatic and gonadal growth.

Discussion

We found test growth, wet weight gain, jaw growth, and gonad weight varied significantly among purple sea urchins as a function of diet. Overall, urchins fed monospecific diets of *Chondracanthus, Macrocystis,* and those fed a mixed diet grew significantly faster than those that were fed monospecific diets of *Pterygophora* or *Rhodymenia*, while urchins fed *Rhodymenia* had the lowest gonad weights. Urchins showed a strong preference for the naturally abundant *Macrocystis*, even when other algae were offered alongside. Our results suggest, however, that a diet consisting of other less preferred species of algae can sustain purple sea urchins at equally high levels of fitness at least over the short-term. This feature may be critically important in maintaining the reproductive capacity of purple sea urchins during the peak winter spawning season when *Macrocystis* is least abundant due to intensive wave disturbance (Reed, Rassweiler & Arkema 2008; Reed et al. 2011).

Since no differences in performance were observed among urchins fed *Chondracanthus*, *Macrocystis* (monospecific) and mixed diets, we found little evidence that purple sea urchins fed a mixed diet benefitted over and above those fed a monospecific diet as long as either *Macrocystis* or *Chondracanthus* were present in the mixture. Because our particular mixed diet did not lead to increased performance, there appeared to be no benefit of diet complementarity (as assumed by the balanced diet hypothesis (Pennings, Nadeau & Paul 1993)). Additionally, since consumption was not higher in urchins fed a mixed diet, as could be permitted if species-specific toxins limited consumption of any one species, it does not seem likely that toxin minimization played a large role.

Despite these results, *Macrocystis* was consumed at the highest rate in mixed diets, suggesting that the effects of a mixed diet in the absence of this preferred food might prove different. Understanding urchin performance from algal mixtures in the absence of *Macrocustis* would be useful for understanding urchin dynamics after major kelp removal, as is common following large wave events. In this framework, Byrnes, Cardinale & Reed (2013) found that reduction in the abundance of sessile species by grazing purple sea urchins was positively correlated with species richness in plots where *Macrocystis* had been removed.

The low values for growth and gonad weight observed in purple sea urchins that were fed a monospecific diet of *Rhodymenia* occurred in spite of the fact that this species was often covered with epiphytic invertebrates such as hydroids and encrusting bryozoans, which have been shown to increase urchin somatic and gonad growth (Knip & Scheibling 2007 and references therein). The fact that this alga was absent from the *Rhodymenia* monospeicifc diet and mixed diet for 14% of the total exposure time (due to low availability for collection) most likely did not bias results of performance measurements by much; test growth, jaw growth, change in wet weight, and gonad weight for urchins fed *Rhodymenia* were at least 40% lower than those for *Chondracanthus*, *Macrocystis* (monospecific), and mixed diets each case. Furthermore Leighton (1968) found test growth and gonad index were lower in purple sea urchins fed *Rhodymenia* than those fed either *Macrocystis* or *Pterygophora*. While our results with respect to urchins fed *Rhodymenia* should be interpreted cautiously, they suggest it is likely poor forage for purple sea urchins.

Our findings pertaining to the performance of urchins fed *Pteryoghora* are consistent with those of Leighton (1968)—purple sea urchins fed *Pterygophora* produced relatively large gonads and grew slowly during periods leading up to the peak spawning season. Leighton (1968), however, showed evidence that somatic growth may increase as a proportion of total growth during the time period after spawning, highlighting that the effects of diet may vary with time of year among other factors. Like many organisms urchins display a trade-off in allocating resources to somatic vs. gonadal growth (Lawrence & Lane 1982; Steinberg & van Altena 1992). Ebert (1980) related increased jaw size to lower food availability, suggesting resource allocation toward jaw growth facilitated food gathering ability. Our results suggest purple sea urchins fed a diet of *Pterygophora* may increase the proportion of energy and/or nutrients that they direct to gonad and jaw growth compared to those fed other diets.

C:N ratio, used in our study as a rough measure of algal nitrogen and therefore protein content, was not correlated to any of the performance measures, as *Chondracanthus* and *Macrocystis*, which produced similar urchin performance had dissimilar C:N ratios (12.6 and 8.7, respectively, where the range of C:N values for all species was 7.4 – 15.6), suggesting that additional factors affected urchin performance. Leighton (1968) found that absorption efficiency was higher for purple sea urchins fed *Macrocystis* (70%) than *Pterygophora* (50%) or *Rhodymenia* (34%), and that protein and carbohydrates were absorbed more efficiently with *Macrocystis* than with *Pterygophora*. These results may explain some of the differences that we observed in performance as a function of diet. Concentrations of fatty acids, minerals Khotimchenko, Vaskovsky & Titlyanova 2002) and chemical deterrents (Hall et al. 1973; Crews & Kho-Wiseman 1977; Estes & Steinberg 1988; Iken & Dubois 2006) also vary in other algae that are encountered by purple sea urchins and may play a role in nutritional quality, urchin food preference and consumption rates. Additional work is needed to uncover the relative contributions of different factors that may have led to the differences in consumption and performance that we observed.

Our results focus on the four species of algae that collectively comprised > 75% of the biomass in kelp forests off Santa Barbara (Miller, Harrer & Reed 2012) and elucidate the effects of these algae on performance of purple sea urchins, which may have implications for urchin populations in the wild. First, the ability to switch between diets, namely diets of

Chondracanthus and *Macrocystis* (the urchin's preferred food), with little or no cost to growth and reproduction suggests that *Chondracanthus* could serve as an important alternative food source when *Macrocystis* is disproportionately removed by large waves (Dayton & Tegner 1984; Dayton et al. 1999; Gaylord, Denny & Koehl 2008). Upon the removal of *Macrocystis*, understory algae such as *Chondracanthus* become more abundant (Arkema, Reed & Schroeter 2009; Miller, Reed & Brzezinski 2011) and may serve as a suitable food that can sustain urchin populations and promote high growth and reproduction. *Chondracanthus'* relatively low rate of primary production (Miller, Harrer & Reed 2012), however, indicate it might not be a long-term sustainable food source. Additionally our results suggest that in the context of the four abundant algae we tested, algal assemblage diversity may not be as important as the availability of one or two high quality food sources. We saw little evidence of a diversity effect; in mixed diets urchins mostly consumed *Macrocystis*, and performed no differently than had they consumed *Macrocystis* alone.

Urchin preferences among these algae may also have implications for subtidal community structure, and more work is needed to better understand relative consumption rates of these dominant algae in nature (and the factors affecting these relative consumption rates, such as ambient oceanographic conditions and community interactions). Considering the model of urchin-algal dynamics presented by Harrold & Reed (1985), where following the disappearance of *Macrocystis* urchins shift their behavior from occupying protected cracks and crevices while consuming drift *Macrocystis* to actively grazing the understory on the open substratum, the relative availability of the algae tested here could influence the extent of grazing that occurs after such shifts. Our experiment suggests that algal assemblage composition, along with total abundance and urchin density, all may play a role in shifting urchin dynamics in the wake of environmental perturbations to subtidal systems. More work is needed to understand whether these differences in diet translate to differences in urchin populations at the local and regional scale in pre- and post-disturbance temperate rocky reefs.

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Figure 1(on next page)

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.

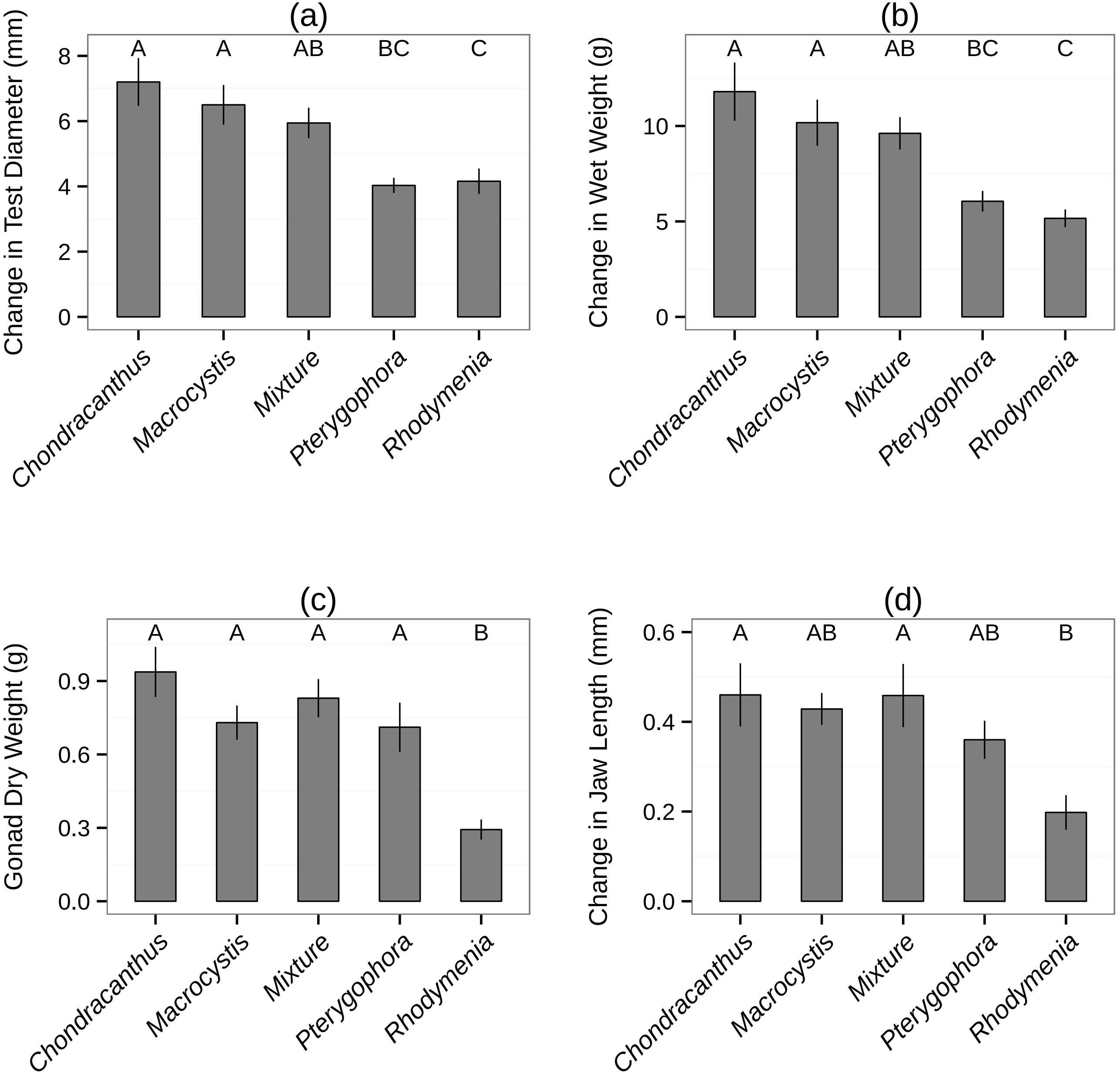
(a)
Change in Test Diameter (mm)
0
2
4
6
8
A
A
AB
BC
C
Chondracanthus
Macrocystis
Mixture
Pterygophora
Rhodymenia
(b)
Change in Wet Weight (g)
0
5
10
A
A
AB
BC
C
Chondracanthus
Macrocystis
Mixture
Pterygophora
Rhodymenia
(c)
Gonad Dry Weight (g)
0.0
0.3
0.6
0.9
A
A
A
A
B
Chondracanthus
Macrocystis
Mixture
Pterygophora
Rhodymenia
(d)
Change in Jaw Length (mm)
0.0
0.2
0.4
0.6
A
AB
A
AB
B
Chondracanthus
Macrocystis
Mixture
Pterygophora
Rhodymenia

Figure 2(on next page)

Consumption Rate

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 on the different species of algae in the mixed species diet. (b) Consumption rate for all diets tested.

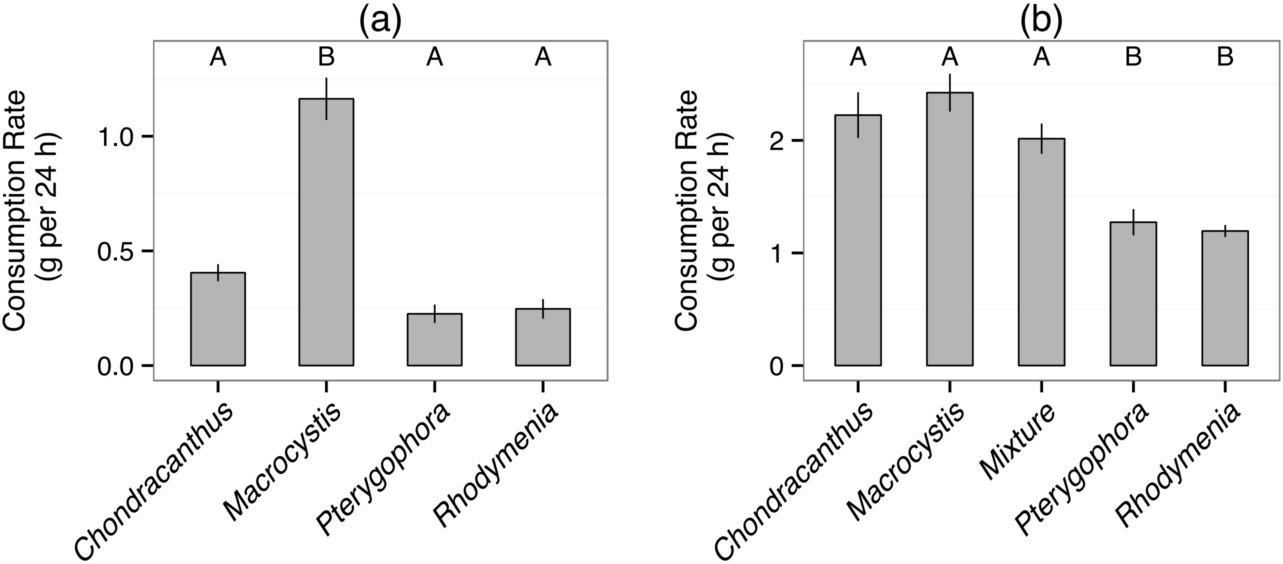
(a)
A
B
A
A
Consumption Rate
(g per 24 h)
1.0
0.5
0.0
Chondracanthus
Macrocystis
Pterygophora
Rhodymenia
(b)
A
A
A
B
B
Consumption Rate
(g per 24 h)
2
1
0
Chondracanthus
Macrocystis
Mixture
Pterygophora
Rhodymenia

Figure 3(on next page)

Algal C:N

Mean carbon:nitrogen ratio (+ 1 SE) of the four algae fed to sea urchins. 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.

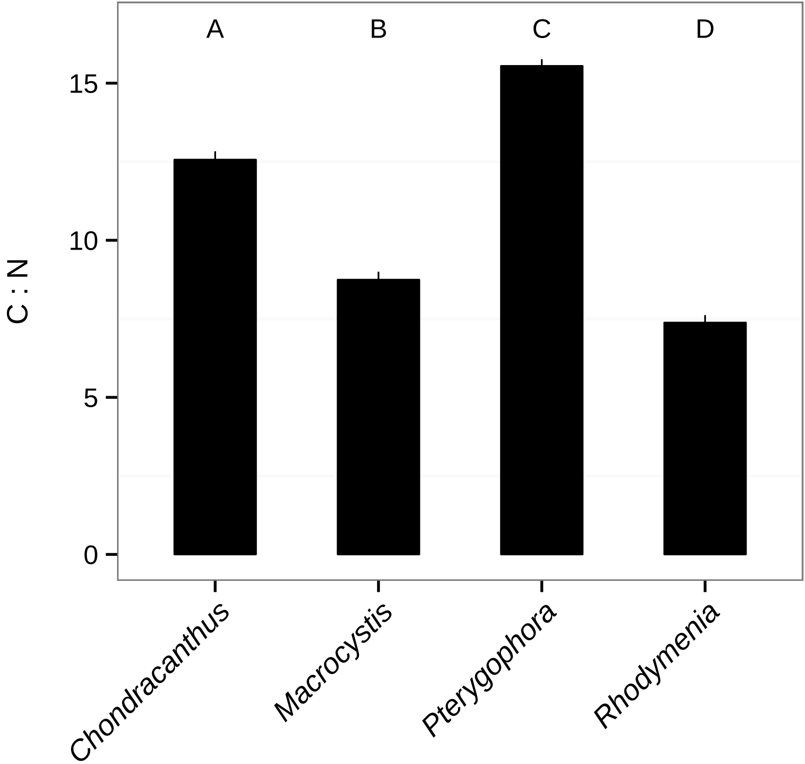
A
B
C
D
15
10
5
0
C : N
Chondracanthus
Macrocystis
Pterygophora
Rhodymenia

Table 1(on next page)

Performance and Consumption Across Diets

F-tables for individual linear models fit with different aspects of urchin performance as response variables and diet treatment 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	224	56.1	7.97	< 0.001
	Residual Error	30	211	7.03		
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	8.79	2.20	15.0	< 0.001
	Residual Error	30	4.38	0.146		

Table 2(on next page)

Consumption Rate within the Mixed Diet

F-table for a linear mixed 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	108	< 0.001
		Standard Deviation			
Random Effects	Container	0.050			
	Residual Error	0.145			