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RESEARCH ARTICLE

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Feeding preferences and the relationships between food choice and assimilation efficiency in the herbivorous marine snail *Lithopoma undosum* (Turbinidae)

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Abstract Preference rankings for 13 macrophytes were established for the subtidal herbivorous snail *Lithopoma undosum* using two-choice laboratory experiments and consumption rates. *L. undosum* did not discriminate among three kelp foods (*Egregia menziesii*, *Eisenia arborea* and *Macrocystis pyrifera*) but ate kelp preferentially and more rapidly over all but *Ulva* spp. among tested macrophytes. Secondary preferences were established for the red alga *Pterocladiella capillacea*, followed by the coralline *Lithothrix aspergillum*, whereas the brown seaweeds *Zonaria farlowii* and *Halidrys dioica* and the seagrass *Phyllospadix torreyi* were the least preferred macrophytes. Fastest consumption rates (1.91 g day^{-1}) were measured in trials consisting only of kelp foods. These results indicate that *L. undosum* exhibits clear feeding preferences even when given less-preferred, non-kelp macrophytes. Using an ash-marker technique, we determined total organic, carbon, and nitrogen assimilation efficiencies (AE%) for six macroalgae used in preference trials. Tested macrophytes were assimilated at different efficiencies but a pattern was not detected between AE (%) and a macrophyte's position in *L. undosum's* preference hierarchy. Highest total organic AEs were found for *P. capillacea* (61.2%) and *H. dioica* (59.4%); lowest AEs were detected for *E. menziesii* (34.9%), a preferred dietary item. Nitrogen was assimilated from red algae with higher efficiencies (74.9–84.3%) than from brown or green algae. These data suggest that the digestive capabilities of *L. undosum* are better suited for assimilating organic material and nitrogen from less-preferred, non-kelp foods. This supports the hypothesis that factors besides nutritional composition and digestive optimization have played a role in the evolution of feeding preferences in *L. undosum* and probably other herbivorous snails associated with northeastern Pacific kelp beds.

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Introduction

Several species of herbivorous macro-invertebrates have been shown to choose certain macrophyte species as foods over others (Leighton 1966; Vadas 1977; Steinberg 1985; McShane et al. 1995; Wakefield and Murray 1998). Macrophyte characteristics such as morphology (Littler and Littler 1980; Padilla 1985) and the presence of deterrent chemicals (Steinberg 1985; Hay and Fenical 1988; Van Alstyne et al. 1999) influence these choices by affecting the edibility and palatability of potential foods. Because an animal's performance is based on obtaining sufficient energy and nutrients, the nutritional components of a food item, in particular its nitrogen content (Mattson 1980; White 1985), also may be important determinants of food choice (Pyke 1984). Most studies (Nicotri 1980; Jensen 1983; McShane et al. 1995; Wakefield and Murray 1998; Arrontes 1999), however, have failed to show a consistent correlation between the nutritional content of consumed macrophytes and their place in a benthic herbivore's dietary preferences.

In the northeastern Pacific and other temperate waters supporting kelp beds, many macro-invertebrate herbivores appear to feed preferentially on kelps over other macrophytes as evidenced by faster rates of kelp consumption (Vadas 1977; Watanabe 1984a) and results of choice experiments (Leighton 1966; Steinberg 1985; Wakefield and Murray 1998). Many molluscan (Schmitt et al. 1983; Watanabe 1984a) and small benthic crustacean (Duffy and Hay 1991, 1994) herbivores have low mobility and suffer high predation rates when removed from macrophyte food resources. This relationship between low mobility and predation has led to the suggestion by several authors (Nicotri 1980; Watanabe 1984a; Duffy and Hay 1991; Wakefield and Murray 1998; Pavia and Herman Carr 1999) that the attraction of small or slow-moving herbivores to particular macrophytes might have evolved primarily because of the benefits a macrophyte provides as habitat and refuge, not because of its nutritional attributes.

Most of our understanding of the relationships between nutritional characteristics of macrophyte foods and the performance of herbivorous macro-invertebrates has been obtained from growth experiments, usually performed on species of commercial value (Leighton and Boolootian 1963; Uki et al. 1986; Stuart and Brown 1994; McBride et al. 1998; Foster et al. 1999a). Much less is known about relationships between macrophyte foods and the efficiency with which they are assimilated and their nutritional constituents made available to meet metabolic, growth, and reproductive demands. Questions remain about whether benthic herbivores possess feeding and digestive processes that compensate for consuming preferred but low quality foods. For example, do herbivores obtain sufficient nutrients from their preferred low quality foods by increasing consumption rates, thereby making more food available for assimilation of nutritional components? Or, alternatively, have benthic herbivores developed unique digestive traits allowing them to assimilate nutrients with higher efficiencies from preferred but lower quality food items?

Lithopoma undosum, the wavy turban snail, is often a conspicuous member of kelp bed communities and occurs in depths of up to 80 m from Point Conception, California, to Isla Ascunción, Baja California, México (McLean 1978; Gotshall 1994). It is one of the largest herbivorous snails in southern California and reaches sizes up to 110 mm in basal shell diameter (McLean 1978). Although *L. undosum* is commonly associated with subtidal kelp, juveniles can be found in the intertidal zone, and both adults and juveniles occur in subtidal and intertidal habitats with little or no kelp biomass (Morris et al. 1980; Myers 1986; Alfaro and Carpenter 1999).

The diet and the feeding ecology of *L. undosum* have been examined in only a few studies. Some gut content (Aguilar Rosas et al. 1990; Halliday 1991) and feeding selectivity (Myers 1986) data suggest that this species is a trophic generalist, which consumes a variety of macrophytes, but other lab studies (Leighton 1966; Halliday 1991) contradict this view and indicate that *L. undosum* feeds preferentially on kelps. These observations, however, have been made in the absence of rigorous food choice experiments.

The purpose of this study was to discover whether *L. undosum* makes distinct choices among macrophyte foods and to analyze how efficiently this snail assimilates its preferred foods. Specifically, we sought to determine a food choice hierarchy for *L. undosum* through a series of two-choice feeding experiments and to examine the relationship between assimilation efficiency (AE) and the position of a food item in this preference hierarchy. We hypothesized that kelps will be consumed preferentially over other potential macrophyte foods available in habitats occupied by this herbivorous snail. We also hypothesized that *L. undosum* will have secondary preferences among these potential macrophyte foods. Lastly, we hypothesized that *L. undosum* will assimilate carbon, nitrogen, and total organic matter with higher efficiency from kelps than from other, less preferred foods.

Materials and methods

Selection of food items

Food choices by *L. undosum* were determined in a series of two-choice feeding experiments using thirteen macrophytes (12 macroalgal species and one seagrass), which varied in morphology and belonged to four taxonomically distinct divisions (Table 1). We selected macrophytes known to be eaten or readily available in habitats frequented by *L. undosum*. *M. pyrifera* was chosen because *L. undosum* often is found feeding on and living amongst this kelp (Leighton 1966; McLean 1978; Morris et al. 1980). Two species of coralline red algae, *Lithothrix aspergillum* and *Bossiella orbigniana*, the brown dictyotaleans *Dictyopteris undulata*, *Dictyota flabellata*, and *Zonaria farlowii*, the fucalean *Halidrys dioica*, the green macroalgae *Ulva* spp. and the seagrass *Phyllospadix torreyi* were chosen for our experiments because electivity values determined by Myers (1986) or gut content data reported by Aguilar Rosas et al. (1990) and Halliday (1991) indicated that *L. undosum* feeds in nature on these macrophytes. The two kelps *Egregia menziesii* and *Eisenia arborea*, and two branched, red seaweeds, *Plocamium cartilagineum* and *Pterocladiella capillacea*, also were used in our food choice experiments because these species often are abundant in habitats occupied by *L. undosum* although none have been reported to be consumed by this snail.

Collection and preparation of *L. undosum* and macrophytes

Using SCUBA, we collected snails before each experiment from different areas at ≤ 7 m depth in Malaga Cove, Palos Verdes, California (33°32′N; 117°47′W). Because food preferences by *L. undosum* may be size-specific (Myers 1986), only snails with a maximum basal diameter between 60 and 70 mm were selected for study. Snails were transported to the laboratory in a cooler and transferred to 322-L refrigerated aquaria kept at 16.0 ± 1.5°C and 33–34‰ salinities.

Snails were starved for 24 h, fed romaine lettuce for 48 h, and then starved again for 48 h before food

Table 1 Descriptions of macrophytes offered to snails in two-choice feeding and assimilation efficiency experiments

Species (order and division)	Type of thallus part used
Macrocystis pyrifera (L.) C. Ag. (Laminariales: Ochrophyta) (kelp)	Pieces of flattened laminae removed from fifth blade from growing frond tip
Eisenia arborea Aresch. (Laminariales: Ochrophyta) (kelp)	Corrugated sections of flattened sporophylls taken from 10 cm from meristematic origin
Egregia menziesii (Turn.) Aresch. (Laminariales: Ochrophyta) (kelp)	Spatulate laminae distributed along central rachis axis
Ulva spp. L. (Ulvales: Chlorophyta)	Pieces of membranous, broadly expanded blades
Pterocladiella capillacea (Gmeln.) Santelices and Hommers. (Gelidiales: Rhodophyta)	Terminal portions of flattened, pinnately branched axes
Plocamium cartilagineum (L.) Dixon (Plocamiales: Rhodophyta)	Terminal portions of flattened pectinately branched axes with tertiary branchlets
Bossiella orbigniana (Dec.) Silva (Corallinales:Rhodophyta)	Calcified, articulated fronds with growing axes
Lithothrix aspergillum Gray (Corallinales: Rhodophyta)	Calcified, articulated fronds with growing axes
Dictyota flabellata (Coll.) S. & G. (Dictyotales: Ochrophyta)	Terminal segments of thin, fan-shaped dichotomous branches
Dictyopteris undulata Holmes (Dictyotales: Ochrophyta)	Terminal segments of thin, fan-shaped dichotomous axes with a terminal midrib
Zonaria farlowii S. and G. (Dictyotales: Ochrophyta)	Terminal segments of fan-shaped apices
Halidrys dioica Gardn. (Fucales: Ochrophyta)	Terminal portions of perennial, basal vegetative branches
Phyllospadix torreyi Wats. (Najadales: Spermatophyta*)*	Terminal portions of leaves

choice experiments. This protocol was used to standardize the condition of snails and minimize the possibility that the recent field diet would influence food choice, and also to ensure that snails would eat during feeding experiments.

Macrophyte foods with apparently healthy thalli were collected from Malaga Cove, Laguna Beach, or Dana Point, California, within 48 h prior to food choice and AE experiments. Actively growing thalli were selected to minimize intra-thallus variation in structural or chemical characteristics. Thalli were transported to the laboratory in a cooler to keep them moist and placed in aquaria at a temperature of 16.0 ± 1.5°C, a salinity of 33–34‰, and kept under low, diffuse light (1–2 W m^{-2}) provided in 12:12 h light–dark cycles.

Food-choice experiments

Differential consumption of macrophytes during two-choice experiments was used to determine food choices by *L. undosum* following procedures described by Peterson and Renaud (1989). Three sets of two-choice experiments were performed. In the first set, three kelps (*M. pyrifera*, *E. arborea*, and *E. menziesii*) were offered, two at a time in different combinations, to determine whether one species of kelp was consistently chosen and consumed over the others. To avoid intra-plant variation that can occur in chemical or morphological characteristics, fronds were collected for experimentation from pre-determined parts of kelp thalli. Flattened laminae were removed from the fifth blade growing from the frond tip of several different individuals of *M. pyrifera* and used in choice trials. Spatulate blades found below the intercalary meristem were used for *E. menziesii*. Lastly, corrugated sections of flattened sporophylls were taken 10 cm from their meristematic origins for *E. arborea*.

In the second set of experiments, we tested whether kelps were chosen over ten other macrophytes, which were either observed to be part of the field diet of *L. undosum* or found in its natural habitat. *E. menziesii* was chosen to represent kelps in these experiments because of its availability in many habitats occupied by *L. undosum* and because we did not detect clear choices among tested kelp species. Lastly, to determine whether a choice hierarchy exists among the non-kelp macrophytes, *L. undosum* was offered six of the earlier used ten non-kelp macrophytes in all possible paired combinations. These six macrophytes were *P. capillacea, L. aspergillum, Z. farlowii, H. dioica, Ulva* spp., and *P. torreyi.* Again, thallus portions used in food choice experiments were kept constant; only the terminal portions of branched axes and fronds were used in our experiments.

All choice trials were conducted in aquaria held under similar conditions as described previously. Snails were placed in enclosed "feeding arenas" made from 4.1 l polyurethane containers with four 60×85 mm rectangular openings in each side to allow for seawater circulation. Nylon window screening (mesh = 2 mm) was used to cover the openings in order to retain food and to keep snails within the feeding arenas. Similar control arenas without snails also were prepared to assess autogenic weight changes in macrophytes during experiments. A Plexiglas sheet (1.5 cm thick) with numerous 5.0 mm diameter holes was placed on top of the arenas to hold them in place and keep them submersed within aquariums. Treatment and control arenas were placed randomly in a single layer in each of four recirculating tanks. Each treatment arena (snail present) contained paired macrophyte samples and a single snail. Control arenas without snails contained similar quantities of up to three species of tested macrophyte foods. Earlier experimental work showed that the autogenic weight changes of two versus three species of algae per control container were not significantly different. An attempt was made in each two-choice experiment to provide equivalent surface areas of the tested macrophyte foods to reduce the probability that *L. undosum* would encounter one species more frequently than another while exploring a feeding arena and thus affect differential feeding results.

Preference data were analyzed in two ways. First the difference in weight loss between the two offered species was calculated for both treatments and controls. Secondly, because of mass differences that can occur between species of similar size with different morphologies, changes in weight were calculated as a percentage of the initial wet weight as described by Peterson and Renaud (1989) and Wakefield and Murray (1998) and recommended by Manly (1993). Only differences in tissue loss expressed as a percentage are reported here because these data produced results highly comparable to those based on mass changes. Data were screened for variance homogeneity using Cochran's test and then subjected to either *t* tests or Welch's corrected *t* tests to determine whether one food was chosen over another following procedures outlined by Peterson and Renaud (1989).

The number of snails choosing one macrophyte food over another also was determined. Choice was based on the mass-based percentage of each macrophyte consumed during two-choice pairings. Total mean consumption rates for all provided macrophyte foods were determined for *L. undosum* during each preference experiment. These consumption rates were reported as the total amount of macrophyte food consumed per snail in grams per day. A one-way ANOVA model was used to test for differences in mean consumption rates among sets of preference trials. Data sets were first examined for homoscedasticity using Cochran's test, followed by attempts to transform the data to meet variance requirements. Because the homoscedasticity criterion could not be met by transformation and variance departures were judged to be large, a randomization test was used in lieu of a one-way ANOVA model to test the null hypothesis of no difference among group feeding rates. As suggested by Manly (1997), random reassignment of the data was repeated 1,000 times for setting α at 0.05. Dunn's multiple range test (MRT) was used following significant randomization test results to determine subsets of means and facilitate data analysis.

Assimilation efficiency experiments

Most of the same brown, green, and red macroalgae used during food choice experiments also were used in assimilation trials. These food items included the brown macroalgae *E. menziesii*, *H. dioica*, *Z. farlowii*, the green macroalgae *Ulva* spp., and two red macroalgae *P. capillacea* and *P. cartilagineum*. These macroalgae were selected to test the hypothesis that AE correlates with preference rankings and to examine assimilation differences between macrophytes belonging to different taxonomic divisions. These efforts were accomplished using an ash-marker technique described and used by Montgomery and Gerking (1980) and Edwards and Horn (1982). This technique is used to estimate AE where the amount of nitrogen, carbon, and total organic material in the food and feces are compared to the amount of ash. Ash is thought to be a good marker for assimilation determination because it is a major component of algae and is assumed to be non-digestable (Montgomery and Gerking 1980; Horn et al. 1995). Although small ions have the potential to be absorbed from the ash leading to under-estimation, these amounts are believed to be small (Montgomery and Gerking 1980) and were considered here to be negligible.

Snails were isolated in feeding arenas and, to reduce the likelihood that previous dietary history influenced assimilation results, were fed a diet of romaine lettuce for 48 h and then starved for 48 h to ensure that all lettuce remains had been egested prior to assimilation trials. Snails were held in arenas and flow-through tanks as described previously and were randomly assigned a single macroalgal food. Snails were allowed to feed ad-libitum for 7–30 days; the food was replaced by freshly collected algal aliquots every 48 h. Feces were collected daily to prevent re-ingestion for a period sufficient to obtain the amount required for fecal analyses. Feces collected within the first 24 h were discarded to ensure material from the gut represented the macroalgae being tested. Aliquots of food and collected feces were blotted to remove salts, dried to a constant weight at 60°C, ground to a powder in a Thomas-Wiley$^{\mathrm{TM}}$ Scientific Mill (algae) or with a mortar and pestle (feces), and weighed to the nearest 0.0001 g. Dried algal and fecal samples ($\sim$0.1 g) were then combusted at 550°C for 4 h, a period determined to provide stable values, to obtain their ash contents. Aliquots of dried food and feces also were sent to the Analytical Lab of the Marine Science Institute at the University of California at Santa Barbara for determination of carbon and nitrogen contents. Total AE was calculated as described by Montgomery and Gerking (1980) using the following equation:

$$\text{Total AE }(\%) = \left[1 - \left(\frac{\%\text{ Ash in food}}{\%\text{ Ash in feces}}\right)\right] \times 100$$

The assimilation efficiencies (AEs) of carbon and nitrogen were similarly calculated where $X = \mathrm{C}$ or N:

$$\mathrm{AE}(\%X) = \left\{1 - \left[\left(\frac{\%\,\text{Ash in Food}}{\%\,\text{Ash in Feces}}\right) \times \left(\frac{\%\,X\text{ in feces}}{\%\,X\text{ in food}}\right)\right]\right\} \times 100$$

Significant differences between mean total organic, carbon, and nitrogen percentage of AE were determined using one-way ANOVAs. Data were examined for variance homogeneity using Cochran's test and transformed where necessary prior to analyses. The total organic AE data did not pass the variance homogeneity test nor could they be transformed to meet variance requirements (Cochran's test results: $P \geq 0.05$). Nevertheless, a one-way ANOVA was executed to test the hypothesis that total AEs differed among tested macrophyte foods because variance departures were considered to be small. Statistically significant subsets of means were determined using Tukey's Multiple Comparisons test procedure following significant ANOVA results to facilitate data interpretation.

Results

Food-choice experiments

Although *L. undosum* did not discriminate among kelp species in two-choice experiments, preferences were exhibited consistently for kelps over other tested macrophytes and for certain non-kelp species over others (Figs. 1, 2, 3). In our first set of experiments (Fig. 1), *L. undosum* feeding did not result in significantly more tissue loss when laminae of *M. pyrifera* were tested against *E. menziesii* (*t* test; $P = 0.53$) or *E. arborea* sporophylls (*t* test; $P = 0.19$). *L. undosum* also did not consume significantly more *E. menziesii* than *E. arborea* (*t* test; $P = 0.72$) when offered only these two kelp foods. The absence of choice among kelp species also was evidenced by the consumption patterns of individual snails. In each of the three kelp trials, consumption preferences in replicate arenas were distributed almost equally between the two tested species: 6 of the 12 snails consumed more *E. menziesii* than *M. pyrifera*, 4 of 6 consumed more *M. pyrifera* than *E. arborea*, and 2 of the 5 consumed more *E. menziesii* than *E. arborea* (Fig. 1). The total mean (±1SE) consumption rate for all kelp foods during this trial was 1.91 ± 0.14 g day^{-1} (Fig. 4).

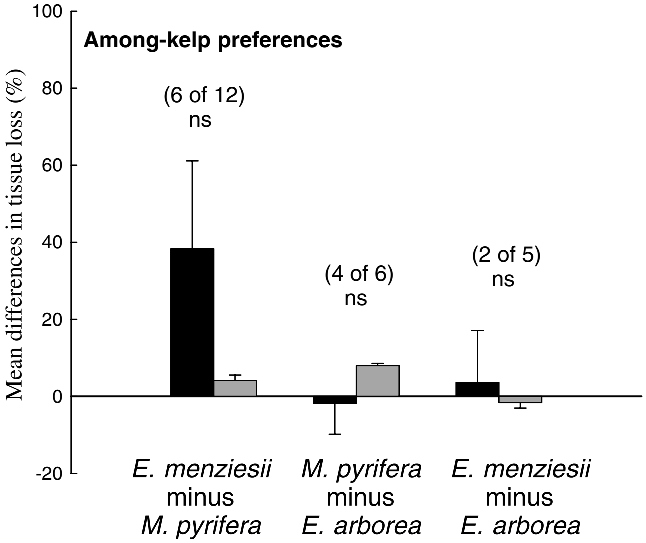

Fig. 1 Results of two-choice feeding experiments among the kelps: *Macrocystis pyrifera*, *Eisenia arborea*, and *Egregia menziesii* when offered to *Lithopoma undosum*. Data are mean (+1 SE) differences in tissue loss as a percentage, when two kelp species were offered together for consumption (*black bars*) and when held as controls in absence of snails (*gray bars*). Results of two-tailed *t* tests or corrected *t* tests for all experiments. *Values above bars* are how many of the snails tested consumed more of the first species listed. *ns* not significant, $P > 0.05$

In the second set of experiments, *L. undosum* exhibited strong feeding preferences for the kelp *E. menziesii* over all other non-kelp foods except for the green algae *Ulva* spp. (Fig. 2). Apart from trials with *Ulva* spp. and the red seaweed *Pterocladiella capillacea*, *L. undosum* consumed almost exclusively *E. menziesii* tissue in all other pair wise comparisons between kelp and non-kelp foods. Moreover, for the eight non-kelp foods besides *Ulva* spp. and *P. capillacea*, snails ate more kelp in experiments in 100 % of the replicate feeding trials. Analyses of two-choice experiments and *L. undosum* feeding patterns indicated a clear preference for kelp over *P. capillacea* (*t* test; $P < 0.01$; 7 of 12 snails chose *E. menziesii* over *P. capillacea*) but no preference for kelp over *Ulva* spp. (*t* test; $P = 0.63$; 5 of 12 snails chose *E. menziesii* over *Ulva* spp.). Despite the presence of less preferred, non-kelp foods, mean (±1 SE) consumption rates by *L. undosum* (1.86 ± 0.14 g d^{-1}) did not differ significantly (Randomization test; Dunn's MRT) from feeding rates calculated for kelp-only feeding trials (Fig. 4).

Lastly, the experimental results showed that *L. undosum* exhibits clear preferences even when comparisons are limited to less-preferred, non-kelp macrophyte foods (Fig. 3a–c). These preferences among the tested macrophytes can be categorized into four hierarchical groups with descending preference based on the combined results of the two-choice experiments, individual snail feeding patterns, and snail consumption rates calculated for tested foods.

In the first group, the two-choice experiments revealed that *L. undosum* ate significantly more *P. capillacea* than each of five other macrophyte species (Fig. 3a). These results were supported by snail choices where in almost every two-choice arena, snails ate more *P. capillacea* than the other offered foods. Mean consumption rates by *L. undosum* when feeding on *P. capillacea* and non-kelp foods in these group 1 trials (0.85 ± 0.19 g day^{-1}), however, were significantly slower (Randomization test, Dunn's MRT) than the rate calculated during trials where kelps were available for consumption in kelp only or in kelp versus non-kelp experiments (Fig. 4).

After *P. capillacea*, *L. undosum* consistently ate significantly more *L. aspergillum* than any of the other four remaining tested macrophytes in the two-choice experiments (Fig. 3b). This preference for *L. aspergillum* during group two trials was supported further by the observation that snails ate more *L. aspergillum* in 100% of these replicated feeding tests. Consumption rates by *L. undosum* in group two experiments (0.85 g day^{-1}) also were significantly slower (Randomization test, Dunn's MRT) than those calculated during the kelp trials but did not vary from values calculated for the group 1 experimental set with *P. capillacea* (Fig. 4).

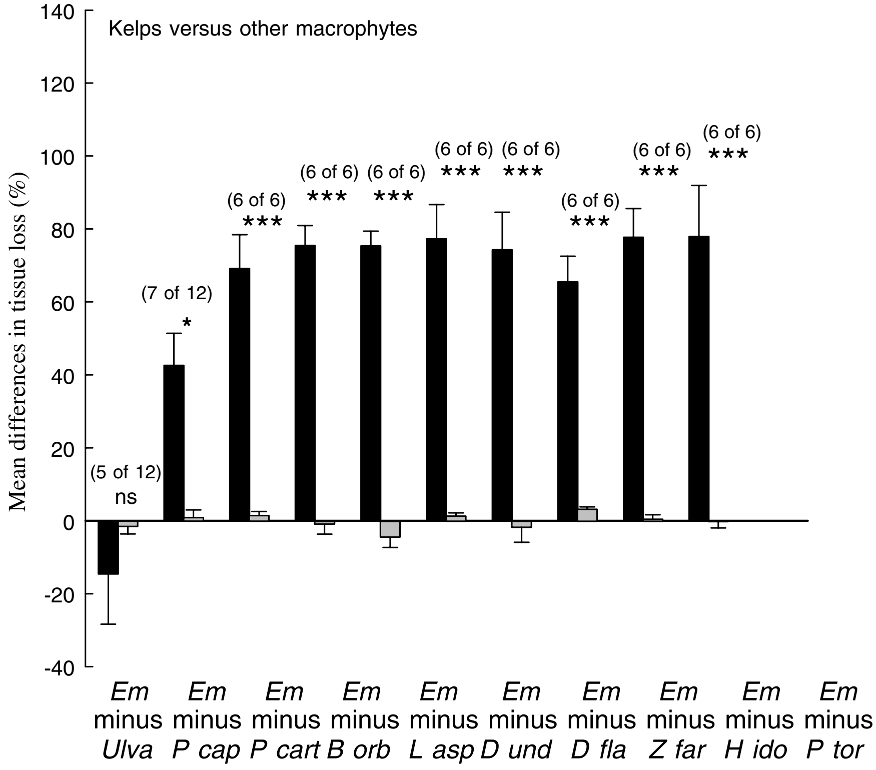

Fig. 2 Results of two-choice experiments for kelp *E. menziesii* versus other macrophytes when offered to *L. undosum*. See Fig. 1 for further details. *ns* not significant, *P* > 0.05; ***P* < 0.01; ****P* < 0.001. Abbreviations: *E m*, *Egregia menziesii*; *P cap*, *Pterocladiella capillacea; P cart*, *Plocamium cartilagineum*; *B orb*, *Bossiella orbigniana*; *L asp*, *Lithothrix aspergillum*; *D und*, *Dictyopteris undulata*; *D fla*, *Dictyota flabellata*; *Z far*, *Zonaria farlowii*; *H dio*, *Halidrys dioica*

Feeding choices remained distinct in most experiments, even with macrophyte foods well down on the food-choice hierarchy exhibited by *L. undosum*. In the third group, *L. undosum*, consumed significantly more *Ulva* spp. than *H. dioica* and *P. torreyi*, but did not show a feeding preference for *Ulva* spp. over *Z. farlowii*

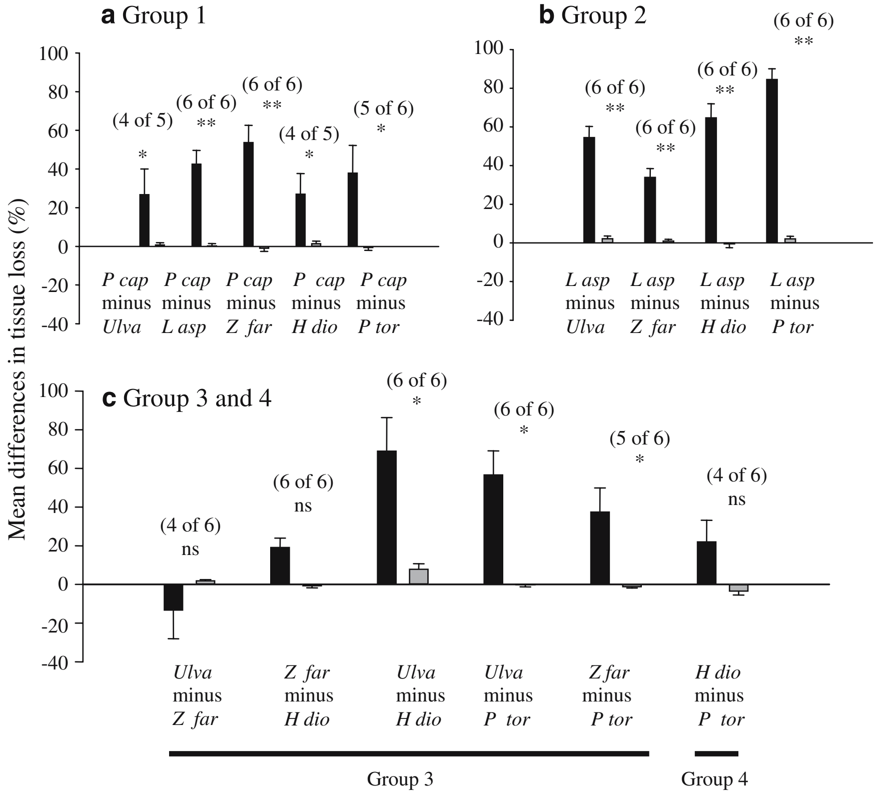

Fig. 3 Results of two-choice experiments between non-kelp versus non-kelp macrophytes when offered in pair wise combination to *L. undosum*. Data are mean (+1 SE) differences in tissue loss expressed as a percentage, when macrophytes were offered together for consumption (*black bars*) and when held as controls in absence of snails (*gray bars*). Results of two-tailed or corrected *t* test for all experiments. *Values above bars* are how many of the snails tested consumed more of the first macrophyte species listed. **a** Group 1, *P. capillacea* preferred over five non-kelp macrophytes, **b** Group 2, *L. aspergillum* preferred over four non-kelp macrophytes, **c** Group 3, *Ulva* spp. and *Z. farlowii* preferred over *H. dioica* and *P. torreyi*. Group 4, *H. dioica* and *P. torreyi* last in preference choices. *ns* not significant, *P* > 0.05; **P* < 0.05; ***P* ≤ 0.01. See Fig. 2 for abbreviations

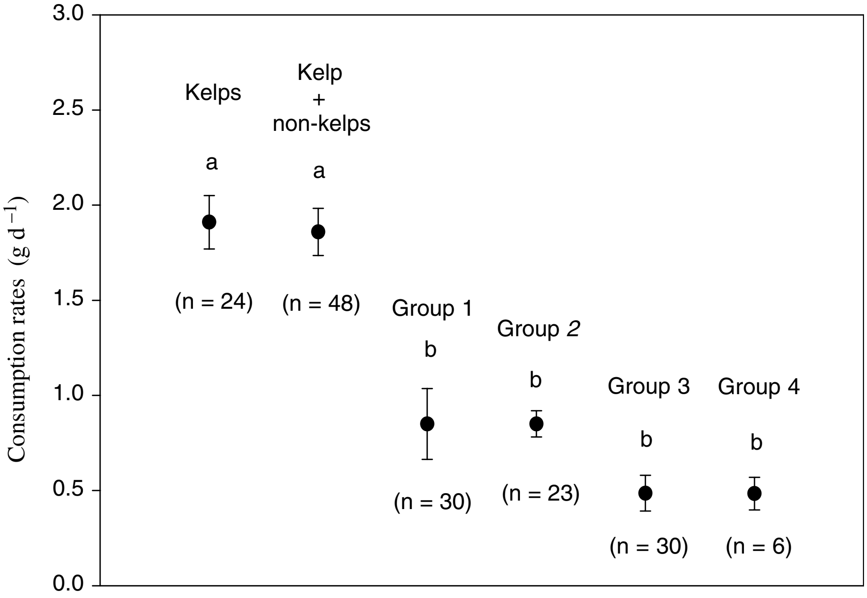

Fig. 4 Consumption rates (g d^{-1}) exhibited by *L. undosum* during kelp and non-kelp two-choice trials. Consumption rates among macrophyte food groups (Group 1 = *Pterocladiella capillacea* and non-kelp macrophytes, Group 2 = *L. aspergillum* and non-kelp macrophytes, Group 3 = *Ulva* spp. and *Z. farlowii*, Group 4 = *Halidrys dioica* and *Phyllospadix torreyi*) differed significantly as determined by randomization test ($F = 18.27$, $P < 0.001$). Values sharing the same letter belong to the same subsets as determined by Dunn's MRT, showing that *L. undosum* consumed macrophyte foods at greater rates with all trials containing kelps

(Fig. 3c). Similarly, *L. undosum* showed a clear preference for *Z. farlowii* over *H. dioica* and *P. torreyi* (Fig. 3c). Hence, when all of the experiments are examined, mixed results were obtained for trials with *Ulva* spp. No preference was shown between *Ulva* spp. and the highly preferred kelp *E. menziesii* and the red alga *P. capillacea* (Figs. 2, 3), but *Ulva* spp. was found to be a less preferred food in trials with *L. aspergillum* and *Z. farlowii* (Figs. 3a–c). In contrast, the results were consistent for placing *Z. farlowii* in the feeding hierarchy. *Z. farlowii* was consumed in statistically greater amounts only when paired with *H. dioica* and *P. torreyi*. Lastly, two choice experiments failed to detect statistically significant differences (*t* test; $P = 0.07$) between *L. undosum* feeding on *H. dioica* and *P. torreyi* (Fig. 3c), the two species that clearly reside at the bottom of the food choice hierarchy. Total macrophyte consumption rates by *L. undosum* were significantly slower (Randomization test, Dunn's MRT) for both group 3 (*Ulva* spp. and *Z. farlowii;* mean ± SE = 0.49 ± 0.09 g day^{-1}) and group 4 (*H. dioica* and *P. torreyi*; mean ± SE = 0.48 ± 0.09 g day^{-1}) trial sets than the feeding rates calculated for the kelp experiments (Fig. 4).

Assimilation efficiency experiments

Tested macrophytes were assimilated at different efficiencies by *L. undosum* (Table 2), but no pattern was found between AE (%) and the place a macrophyte occupied in its feeding preference hierarchy. Total organic AE ranged from 34.8 to 61.2% and varied significantly (ANOVA; $P < 0.001$) among macrophyte species (Table 2). Highest total organic AEs were observed for the red alga *P. capillacea* (61.2%) and the brown alga *H. dioica* (59.4%). The lowest total AE was detected for the kelp *E. menziesii* (34.9%), the most preferred of the examined macrophyte foods. Carbon (59.3–84.3%) and nitrogen (50.0–83.8%) were assimilated at higher efficiencies than total organic matter and AEs differed significantly among macrophyte foods (Table 2). Again, *L. undosum* assimilated carbon (59.3%) and nitrogen (50.0%) from *E. menziesii* with the lowest efficiency. Highest AEs for nitrogen (74.9–84.3%) were observed for the two red macroalgae *P. capillacea* and *P. cartilagineum*. With the exception of *E. menziesii*, *L. undosum* assimilated carbon from all tested macroalgae at similar efficiencies (73.6–84.3%; Table 2).

Discussion

The results of this study support the hypotheses that *L. undosum* consumes kelps preferentially over other macrophytes and that *L. undosum* makes distinct, hierarchical food choices. Results, however, do not support the hypothesis that *L. undosum* assimilates carbon, nitrogen, and total organic matter with higher efficiencies from its preferred macrophyte foods. Despite clear feeding preferences for kelps, *L. undosum* showed lowest AEs for the kelp *E. menziesii* and assimilated nitrogen with highest efficiencies from red macroalgae.

Kelp preferences

Lithopoma undosum and many other benthic invertebrates throughout the northeastern Pacific have feeding preferences for kelp. Working in southern California, Leighton (1966) determined that 11 common kelp forest gastropods, crabs, and urchins preferred *M. pyrifera* over three other non-kelp macroalgae. A preference for kelp by these and other invertebrate herbivores has been attributed to kelp availability (Vadas 1977; Watanabe

Table 2 Percent ash, carbon, and nitrogen in food and feces and percent total organic, carbon (C), and nitrogen (N) assimilation efficiencies (AE) for *Lithopoma undosum* for tested macrophytes

Consumed Macrophyte	Food % Ash	Feces % Ash	Total AE %	Food % C	Feces % C	AE % Carbon	Food % N	Feces % N	AE % Nitrogen
E. menziesii ($n = 13$)	36.2 (0.5)	55.8 (1.3)	34.8 c (1.0)	27.9 (0.3)	17.4 (0.8)	59.3 b (1.9)	2.2 (0.1)	1.7 (0.1)	50.0 c (1.7)
Ulva spp. ($n = 5$)	34.7 (0.3)	70.1 (0.8)	50.4 b (0.6)	34.7 (0.3)	10.6 (0.8)	79.8 a (2.0)	3.1 (0.1)	2.1 (0.2)	65.1 b (3.8)
P. capillacea ($n = 5$)	21.9 (0.7)	56.7 (2.3)	61.2 a (1.2)	21.7 (0.5)	14.4 (1.3)	84.3 a (1.8	3.2 (< 0.1)	1.3 (0.1)	83.8 a (1.4)
P. cartilagineum ($n = 5$)	44.9 (0.6)	70.1 (2.6)	35.6 c (2.9)	35.8 (0.4)	7.6 (0.2)	77.3 a (1.7)	2.8 (< 0.1)	1.1 (0.0)	74.9 ab (1.5)
Z. farlowii ($n = 5$)	32.8 (1.5)	60.4 (1.6)	45.4 b (3.0)	32.0 (0.5)	14.8 (0.8)	73.6 a (3.8)	2.1 (< 0.1)	1.3 (0.1)	64.5 b (4.7)
H. dioica ($n = 5$)	26.8 (0.4)	66.1 (1.3)	59.4 a (0.8)	32.1 (0.7)	12.2 (0.9)	84.1 a (0.9)	1.2 (< 0.1)	1.2 (0.1)	57.5 bc (3.7)
Results of ANOVAS for AE (%)	$df = 5$ MS = 900.9 $F = 47.6$ $P < 0.001$			$df = 5$ MS = 802.3 $F = 24.2$ $P < 0.001$			$df = 5$ MS = 1,048.2 $F = 22.2$ $P < 0.00$		

Data are means (± 1 SE) based on the indicated sample sizes. Tests of differences in AE (%) based on one-way ANOVA followed by Tukey's HSD multiple comparisons test. Values sharing the same letter belong to the same subset of means

1984a), structural (McShane et al. 1995) and chemical (Steinberg 1985; Steinberg and van Altena 1992; Van Alstyne et al. 1999; Toth and Pavia 2002) traits, and to its nutritional composition (Himmelman and Carefoot 1975; Lemire and Himmelman 1996). Invertebrate preferences for kelps also have been attributed to the refuge and habitat value (Watanabe 1984a; Estes and Steinberg 1988; Wakefield and Murray 1998) provided by these canopy-forming seaweeds.

Kelps have broad regional distributions and develop large and persistent stands in temperate waters (Estes and Steinberg 1988; Foster and Schiel 1985). If kelps provide a good food source or other benefits, many macro-invertebrates might have evolved a chemical attraction to kelps to enable location during larval settlement. For example, *Norrisia norrisi*, a kelp bed trochid, appears to locate kelp during settlement, and juveniles can rapidly locate kelps following dislodgement (Schmitt et al. 1983). *L. undosum* settles in coastal, kelp-dominated intertidal and subtidal zones (Alfaro and Carpenter 1999) and it has been observed climbing on or congregating near kelp fronds at night, perhaps a predator avoidance behavior (Halliday 1991).

Kelps are macroalgae with moderate to low structural toughness and weak chemical defenses (Estes and Steinberg 1988; Wakefield and Murray 1998). We found that *L. undosum*, like many other northeastern Pacific benthic invertebrates (Steinberg 1985; Steinberg and van Altena 1992), appeared to avoid feeding on chemically defended macrophytes. Many macrophytes contain secondary chemicals such as terpenes and phlorotannins (Steinberg 1985) or have high structural toughness (Steneck and Watling 1982) that deter herbivory by invertebrates. Myers (1986) observed that *L. undosum* avoided known chemically defended macroalgae (e.g. *Z. farlowii* and *H. dioica*), and in this study *L. undosum* had a lower preference for these same species.

The feeding preference for kelp by *L. undosum* is in accordance with Estes and Steinberg's (1988) hypothesis on the coevolution of kelp, benthic invertebrate consumers, and sea otters. This hypothesis states that kelps are preferred as food by many northeastern Pacific benthic invertebrates because of the once historical abundance of sea otters, which maintained low levels of kelp herbivory. Therefore, kelps are believed to have evolved to invest their energy towards growth and reproduction and not towards the production of chemical herbivore deterrents. The lack of chemical defenses, together with the high growth rate of kelps, makes them an ideal food source for benthic herbivores. Although this is a plausible hypothesis, low levels of deterrent chemicals do not explain preferences for kelps over other macrophytes that similarly lack chemical or structural defenses.

Kelps are not only fast growing and abundant but also may be preferred habitat for some benthic invertebrates because of the refuge capabilities they provide from predation. Isopods with limited mobility prefer algae that are chemically defended (Hay et al. 1988;

Duffy and Hay 1991); thus, these macroalgae provide not only food but also indirectly provide refuge from predators. Slow-moving kelp forest snails, such as *L. undosum*, are limited in their migratory abilities and confined to the substratum where they face strong predation pressures from fishes, octopuses, whelks, crustaceans, sea stars, and sea otters (Schmitt 1981; Fawcett 1984; Watanabe 1984b; Halliday 1991). Unlike any other nearshore predator in cool temperate waters, sea otters consume large quantities of herbivorous benthic invertebrates (Estes and Steinberg 1988). *L. undosum* is possibly an ideal food source for otters because it grows to a large size and is readily available. Sea otter foraging is limited to shallower (20 m average dive depth) depths (Estes and Steinberg 1988), and *L. undosum* (Alfaro and Carpenter 1999) and other potential otter prey, such as sea urchins (Estes and Steinberg 1988), show higher abundances of larger individuals in deeper waters just below their effective foraging depth. These observations suggest that *L. undosum* and other invertebrates might use depth and size as a refuge from predation (Estes and Steinberg 1988; Alfaro and Carpenter 1999), with larger individuals having evolved migratory behaviors resulting in their movement to deeper water to escape otter predation. In contrast, smaller individuals are still able to maintain efficiency at climbing and vertically clinging to kelp. Therefore, smaller gastropods might increase survival by associating with and using kelp as a refuge and readily available food source. Indeed, several species of closely related herbivorous gastropods (e.g., *Tegula* spp. and *N. norrisi*) in the northeastern Pacific are attracted to and show food preferences for kelps (Watanabe 1984b; Wakefield and Murray 1998), and, like *L. undosum*, suffer greater rates of predation when removed from protective kelp fronds (Schmitt et al. 1983; Watanabe 1984b; Schaeffer and Carpenter 1996). In further support of the protective value of kelps, *N. norrisi* is known to migrate from deeper to shallow water on the fronds of *M. pyrifera*, a behavior hypothesized to have evolved to avoid nocturnal benthic predation and daily otter foraging patterns (Lonhart 1996). Although *L. undosum* is rarely seen climbing kelp thalli (Cox, personal observations), Myers (1986) observed daily deep to shallow water migrations of these snails. The migration patterns exhibited by *L. undosum* (Myers 1986) and *N. norrisi* (Lonhart 1996), coupled with increased survival of *Tegula* spp. (Watanabe 1984a), *N. norrisi* (Schmitt et al. 1983), and *L. undosum* (Schaeffer and Carpenter 1996) when associated with kelp fronds, suggest that the ancestor to these northeastern Pacific gastropod families (Hickman and McLean 1990) might also have had a close association with kelp as both a food and a refuge.

Secondary food choices

Determining an organism's secondary food choices facilitates interpretation and enables predictions to be made about natural diets and food selectivity. Yet, hierarchical laboratory determined food preferences rarely have been established for benthic invertebrate herbivores and are known for only a few species including *Strongylocentrotus* spp. (Vadas 1977), *Tegula* spp. (Watanabe 1984a; Steinberg 1985), *Pachygrapsus crassipes* (Barry and Ehret 1993), and *Haliotis rubra* (McShane et al. 1995). We found that *L. undosum* made distinct secondary feeding choices and that the only tested macrophyte that *L. undosum* did not choose in a predictable manner was *Ulva* spp. Species of *Ulva* are difficult to distinguish, and we were unable to determine confidently whether different species were used in our experiments. Some chlorophytes, including *Ulva*, produce chemicals that can deter herbivory (Van Alstyne and Houser 2003), and discrepancies in the results of our food preference trials with *Ulva* might have been caused by variation in palatability, perhaps due to the use of different strains or taxa.

Algal availability and migratory ability can have a large impact on the diets of benthic marine herbivores, particularly those with limited mobility. For example, Barry and Ehret (1993) compared the diets of two mobile fishes to *P. crassipes*, a benthic crab. They found that *P. crassipes* with lower mobility had a limited foraging range and associated these attributes with increased diet breadth. This finding was in contrast to the diets of more mobile fishes, which had narrower diet breadths and were able to search over larger areas for more preferred but less abundant foods. Similar arguments have been made for other benthic invertebrates, including strongylocentrotid urchins (Vadas 1977), brachyuran crabs (Stachowicz and Hay 1999), and gastropods belonging to the genus *Tegula* (Watanabe 1984a).

Despite clear laboratory preferences for kelps, the diet of *L. undosum* in nature appears to be varied (Myers 1986; Aguilar Rosas et al. 1990; Halliday 1991; Alfaro and Carpenter 1999). The laboratory feeding preferences we determined for *L. undosum* were not reflected in the dietary data published by Aguilar Rosas et al. (1990) or Myers (1986), and other northeastern Pacific gastropods have more general and varied diets than suggested by their strong laboratory preferences for kelps (Best 1963; Leighton 1966; Watanabe 1984a). Arguably, laboratory preferences could be considered irrelevant for benthic invertebrate herbivores in a natural setting where predation pressures are strong and preferred seaweeds are scarce or mixed among other potential macrophyte foods. Several studies, however, have emphasized the importance of food preferences in the diets of slower moving organisms, including the land snail *Arianta* (Speiser and Rowell-Rahier 1991), the marine opisthobranch *Aplysia* (Carefoot 1967), and strongylocentrotid urchins (Vadas 1977).

Assimilation efficiency and food choice

The total organic AEs that we obtained for *L. undosum* (35–61%) fell within the wide range of total organic AEs

(39–84%) previously observed for macro-herbivorous marine gastropods (Carefoot 1987). Using the same ash marker method that we employed, Halliday (1991) nevertheless determined that *L. undosum* assimilated kelp with efficiencies ranging between 5 and 70%. Reasons for wide ranging AEs among studies can include difference in methods used in determining assimilation values, the possibility of confounding factors during assimilation experiments (e.g. diet history, temperature, consumer body size, reproductive status, and age), and the type, state, and quality of the food being eaten. Both *T. funebralis* feeding on various marine algae (70% AE; Paine 1971), and the urchins, *S. franciscanus* (48–91%), *S. drobachiensis* (40–84%), and *S. purpuratus* (28–85%) feeding on kelp (Vadas 1977) had higher AEs than we observed for *L. undosum* (29–39%). High AEs of kelp by urchins were attributed to good matches with urchin digestive enzymes (Vadas 1977). Also, *L. undosum* assimilated green (50%), brown (34–59%), and red macroalgae (35–61%) at efficiencies similar to the gastropods *A. punctata* (67%, 45–53%, and 59%, respectively) (Carefoot 1967) and *H. rubra* (44%, 52% and 59%) (McShane et al.1995).

High AEs for herbivores have long been thought to occur on preferred diets (Carefoot 1987), yet our results for *L. undosum* failed to support this hypothesis. Correlations between food preferences and growth (Calow 1975; Carefoot 1987) and preferences and AEs (Carefoot 1970; Vadas 1977; Fleming 1995a) have advanced the idea that invertebrate herbivores process preferred food items more efficiently than less preferred macrophytes. Growing evidence, however, suggests that such a relationship may not exist in herbivorous turbinid and trochid gastropods. Although several kelp forest invertebrates show best growth on preferred foods (Carefoot 1967; Vadas 1977; Fleming 1995b; Lemire and Himmelman 1996), the gastropods *Tegula* spp. (Watanabe 1984a), *Turbo sarmaticus* (Foster et al. 1999a), *H. iris* (Stuart and Brown 1994), and *L. undosum* (Halliday 1991) have been shown to grow equally well or better on mixed algal diets. Although few studies have examined the relationship between growth and AE, the available data not only dispel a relationship between feeding preferences and AE, but also suggest that the consumption of mixed macrophyte diets can compensate for feeding on low quality macrophyte foods (Kitting 1980; Larson et al. 1980; Kennish and Williams 1997; Stachowicz and Hay 1999; Cruz-Rivera and Hay 2001).

Our data suggest that *L. undosum* might be constrained by its digestive abilities, which are better suited to assimilate nitrogen (and hence protein) from red seaweeds compared with more preferred kelps. Higher nitrogen AEs for red macroalgae also have been seen in other mollusks such as *A. punctata* (Carefoot 1967) and *H. rubra* (Fleming 1995a). Mollusks have higher levels of enzyme activity on storage polysaccharides found in red and green compared with brown macroalgae (Foster et al. 1999b). Foster et al. (1999b), however, suggest lack of digestive constraint, by cautioning that mollusks have associated gut bacteria capable of breaking structural carbohydrates and also have the ability to change enzyme production rapidly with their diets.

Like terrestrial plants (Mattson 1980; White 1985), most algae (Montgomery and Gerking 1980; Horn and Neighbors 1984) are very low in nitrogen, and the importance of this nutrient for invertebrate growth (Fleming 1995b; Kennish and Williams 1997; McBride et al. 1998) might have resulted in evolutionary pressures for the development of preferences for nitrogen rich foods and for high nitrogen AEs. Red macroalgae, which store nitrogen in biliprotein pigments, are a better source of nitrogen than most other algae (Edwards and Horn 1982; Horn and Neighbors 1984), and represent good choices for herbivores seeking nitrogen-rich foods. Nitrogen content, however, has not been found to correlate with food choice in other northeastern Pacific herbivorous snails (Steinberg 1985; Wakefield and Murray 1998). In contrast, Australian mollusks, which evolved in a region with no history of otter predation, have been reported (Shepherd and Steinberg 1992; Fleming 1995b) to prefer to feed on more nitrogen-rich red macroalgae. Kelps in Australia have higher levels of phlorotannins, yet invertebrates from this region are less sensitive to these chemical deterrents (Steinberg and van Altena 1992). This finding suggests that hemispherical differences in herbivore preferences for and attractions to kelp might be the result of evolutionary presence of sea otter predation in North American waters (Estes and Steinberg 1988) and their absence in Australian and other southern hemisphere seas. Clearly, more studies are needed to examine the relationship between food choice and mobility and the digestive capabilities of herbivorous mollusks to improve understanding of the evolution of feeding preferences in *L. undosum* and other herbivorous snails.

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References

Aguilar Rosas R, Torres-Moye G, Almanza Heredia A (1990) Qualitative analysis of the marcoalgae diet of the snail, *Astraea undosa* Wood 1828, in Punta Banda Baja California, Mexico. Cienc Mar 16:111–120

Alfaro AC, Carpenter RC (1999) Physical and biological processes influencing zonation patterns of a subtidal population of the marine snail, *Astraea* (*Lithopoma*) *undosa* Wood 1828. J Exp Mar Biol Ecol 240:259–283

Arrontes J (1999) On the evolution of interactions between marine mesoherbivores and algae. Bot Mar 42:137–155

Barry JP, Ehret MJ (1993) Diet, food preference, algal availability for fishes and crabs on intertidal reef communities in southern California. Environ Biol Fishes 37:75–95

Best B (1963) Feeding Activities of *Tegula funebralis*. Veliger 6:42–45

Calow P (1975) The feeding strategies of two freshwater gastropods, *Ancylus fluviatilis* Mull. and *Planorbis contortus* Linn. (Pulmonata), in terms of ingestion rates and absorption efficiencies. Oecologia (Berlin) 20:33–49

Carefoot TH (1967) Growth and nutrition of three species of opisthobranch molluscs. Comp Biochem Physiol 21:627–652

Carefoot TH (1970) A comparison of absorption and utilization of food energy in two species of tropical Aplysia. J Exp Mar Biol Ecol 5:47–62

Carefoot TH (1987) Gastropoda. In: Griffiths. C.L.; Griffiths RJ (ed) Animal energetics. Academic, New York, pp 89–173

Cruz-Rivera E, Hay ME (2001) Macroalgal traits and the feeding and fitness of an herbivorous amphipod: the roles of selectivity, mixing, and compensation. Mar Ecol Prog Ser 218:249–266

Duffy JE, Hay ME (1991) Food and shelter as determinants of food choice by an herbivorous marine amphipod. Ecology 72:1286–1298

Duffy JE, Hay ME (1994) Herbivore resistance to seaweed chemical defense: the roles of mobility and predation risk. Ecology 75:1304–1319

Edwards TW, Horn MH (1982) Assimilation efficiency of a temperate-zone intertidal fish (*Cebidichthys violaceus*) fed diets of macroalgae. Mar Biol 67:247–253

Estes JA, Steinberg PD (1988) Predation, herbivory, and kelp evolution. Paleobiology 14:19–36

Fawcett M (1984) Local and latitudinal variation in predation on a herbivorous marine snail. Ecology 65:1214–1230

Fleming AE (1995a) Digestive efficiency of the Australian abalone *Haliotis rubra* in relation to growth and feed preference. Aquaculture 134:279–293

Fleming AE (1995b) Growth, intake, feed conversion efficiency and chemosensory preference of the Australian abalone, *Haliotis rubra*. Aquaculture 132:297–311

Foster MS, Schiel DR (1985) The ecology of giant kelp forests in California: a community profile. US Fish Wildl Serv Biol Rep 85:1–53

Foster GG, Hodgson AN, Balarin M (1999a) Effect of diet on growth rate and reproductive fitness of *Turbo sarmaticus* (Mollusca: Vestigastropoda: Turbinidae). Mar Biol 134:307–315

Foster GG, Hodgson AN, Boyd CS (1999b) Polysaccharolytic activity of the digestive enzymes of the macroalgal herbivore, *Turbo sarmaticus* (Mollusca: Vestigastropoda: Turbinidae). Comp Biochem Physiol B 122:47–52

Gotshall DW (1994) Guide to marine invertebrates Alaska to Baja. Sea Challengers, Monterey

Halliday EBB (1991) The natural history and feeding ecology of Astraea undosa in a southern California kelp forest. MS. Marine Science, Santa Cruz

Hay ME, Fenical W (1988) Marine plant-herbivore interactions: The ecology of chemical defense. Ann Rev Ecol Syst 19:111–145

Hay ME, Renaud PE, Fenical W (1988) Large mobile versus small sedentary herbivores and their resistance to seaweed chemical defenses. Oecologia 75:246–252

Hickman CS, McLean JH (1990) Systematic revision and supra-generic classification of Trochacean gastropods no.35 science series. Natural History Museum of Los Angeles County, Los Angeles

Himmelman JH, Carefoot TH (1975) Seasonal changes in calorific value of three Pacific coast seaweeds, and their significance to some marine herbivores. J Exp Mar Biol Ecol 18:139–151

Horn MH, Neighbors MA (1984) Protein and nitrogen assimilation as a factor in predicting the seasonal macroalgal diet of the monkeyface prickleback. Trans Am Fish Soc 113:388–396

Horn MH, Mailhoit KF, Fris MB, McClanahan LL (1995) Growth, consumption, assimilation and excretion in the marine herbivorous fish *Cebidichthys violaceus* (Girard) fed natural and high protein diets. J Exp Mar Biol Ecol 190:97–108

Jensen KR (1983) Factors affecting feeding selectivity in herbivorous ascoglossa (Mollusca: Opisthobranchia). J Exp Mar Biol Ecol 66:135–148

Kennish R, Williams GA (1997) Feeding preferences of the herbivorous crab *Grapsus albonlineatus*: the differential influence of algal nutrient content and morphology. Mar Ecol Prog Ser 147:87–95

Kitting CL (1980) Herbivore-plant interactions of individual limpets maintaining a mixed diet of intertidal marine algae. Ecol Monogr 50:527–550

Larson BR, Vadas RL, Keser M (1980) Feeding and nutritional ecology of the sea urchin *Strongylocentrotus drobachiensis* in Maine, USA. Mar Biol 59:49–62

Leighton DL (1966) Studies of food preference in algivorous invertebrates of southern California kelp beds. Pac Sci XX:104–113

Leighton DL, Boolootian RA (1963) Diet and growth in the black abalone, *Haliotis cracherodii*. Ecology 44:227–238

Lemire M, Himmelman JH (1996) Relation of food preference to fitness for the green sea urchin, *Strongylocentrotus droebachiensis*. Mar Biol 127:73–78

Littler MM, Littler DS (1980) The evolution of thallus form and survival strategies in benthic marine macroalgae: field and laboratory tests of a functional form model. Am Nat 116:25–44

Lonhart SI (1996) The vertical distribution and diel migration of *Norrisia norrisi* on Macrocystis pyrifera at Santa Catalina Island. MA Thesis, California State University, Long Beach

Manly BF (1993) Comments on design and analysis of multiple-choice feeding preference experiments. Oecologia 93:149–152

Manly BFJ (1997) Randomization and Monte Carlo methods in biology. 2nd edn. Chapman and Hall, London

Mattson WJ (1980) Herbivory in relation to plant nitrogen content. Ann Rev Ecol Syst 11:119–161

McBride SC, Lawrence JM, Lawrence AL, Mulligan TJ (1998) The effect of protein concentration in prepared feeds on growth, feeding rate, total organic absorption, and gross assimilation efficiency of the sea urchin *Strongylocentrotus franciscanus*. J Shellfish Res 17:1563–1570

McLean JH (1978) Marine shells of southern California. Natural History Museum of Los Angeles County, Los Angeles

McShane PE, Gorfine HK, Knuckey IA (1995) Factors influencing food selection in the abalone *Haliotis rubra* (Mollusca: Gastropoda). J Exp Mar Biol Ecol 176:27–37

Montgomery WL, Gerking SD (1980) Marine macroalgae as foods for fishes: an evaluation of potential food quality. Environ Biol Fishes 5:143–153

Morris RH, Abbott DP, Haderlie EC (1980) Intertidal invertebrates of California. Stanford University Press, Stanford

Myers DJ (1986) Size distribution, movement, and feeding selectivity of subtidal Astraea undosa (Gastropoda: Mollusca) from Santa Catalina Island. MA Thesis, California State University, Fullerton

Nicotri ME (1980) Factors involved in herbivore food preference. J Exp Mar Biol Ecol 42:13–26

Padilla DK (1985) Structural resistance of algae to herbivores, a biomechanical approach. Mar Biol 90:103–109

Paine RT (1971) Energy flow in a natural population of the herbivorous gastropod *Tegula funebralis*. Limnol Oceanogr 16:86–98

Pavia H, Herman Carr PA (1999) Habitat and feeding preferences of crustacean mesoherbivores inhabiting the brown seaweed *Ascophyllum nodosum* (L.) Le Jol. and its epiphytic macroalgae. J Exp Mar Biol Ecol 236:15–32

Peterson CH, Renaud PE (1989) Analysis of feeding preference experiments. Oecologia 80:82–86

Pyke GH (1984) Optimal foraging theory: a critical review. Ann Rev Ecol Syst 15:523–575

Schaeffer TN, Carpenter RC (1996) Patterns of predation on the gastropod Astraea undosa at Santa Catalina Island, CA, 24th edn. In: Woodling S, Allen D, Stancyk S, Williams-Howze R, Fell D, Wethey N, Pentcheff G, Chandler A, Decho A, Coull B (eds) Ann. Ben. Ecol. Meeting, p 73

Schmitt RJ (1981) Contrasting anti-predator defenses of sympatric marine gastropods (Family Trochidae). J Exp Mar Biol Ecol 71:257–270

Schmitt RJ, Osenberg CW, Bercovitch MG (1983) Mechanisms and consequences of the shell fouling in the kelp snail, *Norrisia norrisi* (Sowerby) (Trochidae): indirect effects of octopus drilling. J Exp Mar Biol Ecol 69:267–281

Shepherd SA, Steinberg PD (1992) Food preference of three Australian abalone species with a review of the algal food of abalone. In: Shepherd SA, Tegner MJ, Guzman del Proo SA (eds) Abalone of the world: biology, fisheries and culture. Blackwell Scientific Publications, Oxford, pp 169–199

Speiser B, Rowell-Rahier M (1991) Effects of food availability, nutritional value, and alkaloids on food choice in the generalist herbivore *Arianta arbustorum* (Gastropoda: Helicidae). Oikos 62:306–318

Stachowicz JJ, Hay M (1999) Reduced mobility is associated with compensatory feeding and increased diet breadth of marine crabs. Mar Ecol Prog Ser 188:169–178

Steinberg PD (1985) Feeding preferences of *Tegula funebralis* and chemical defenses of marine brown algae. Ecol Monogr 55:333–349

Steinberg PD, van Altena I (1992) Tolerance of marine invertebrate herbivores to brown algal phlorotannins in temperate Australasia. Ecol Monogr 62:189–222

Steneck RS, Watling L (1982) Feeding capabilities and limitation of herbivorous molluscs: a functional group approach. Mar Biol 68:299–319

Stuart MD, Brown MT (1994) Growth and diet of cultivated blackfoot abalone, *Haliotis iris* (Martyn). Aquaculture 127:329–337

Toth GB, Pavia H (2002) Lack of phlorotannin induction in the kelp *Laminaria hyperborea* in response to grazing by two gastropod herbivores. Mar Biol 140:403–409

Uki N, Sugiura M, Watanabe T (1986) Dietary value of seaweeds occurring on the pacific coast of Tohoku for growth of the abalone *Haliotis discus hannai*. Bull Jpn Soc Sci Fish 52:257–266

Vadas RL (1977) Preferential feeding: an optimization strategy in sea urchins. Ecol Monogr 47:337–371

Van Alstyne KL, Houser LT (2003) Dimethylsulfide release during macroinvertebrate grazing and its role as an activated chemical defense. Mar Ecol Prog Ser 250:175–181

Van Alstyne KL, McCarthy III JJ, Hustead CL, Duggins DO (1999) Geographic variation in polyphenolics levels of northeastern Pacific kelps and rockweeds. Mar Biol 133:371–379

Wakefield RL, Murray SN (1998) Factors influencing food choice by the seaweed-eating marine snail *Norrisia norrisi* (Trochidae). Mar Biol 130:631–642

Watanabe JM (1984a) Food preference, food quality and diets of three herbivorous gastropods (Trochidae: *Tegula*) in a temperate kelp forest habitat. Oecologia 62:47–52

Watanabe JM (1984b) The influence of recruitment, competition, and benthic predation on spatial distributions of three species of kelp forest gastropods (Trochidae: *Tegula*). Ecology 65:920–936

White TCR (1985) When is a herbivore not a herbivore? Oecologia (Berlin) 67:596–597