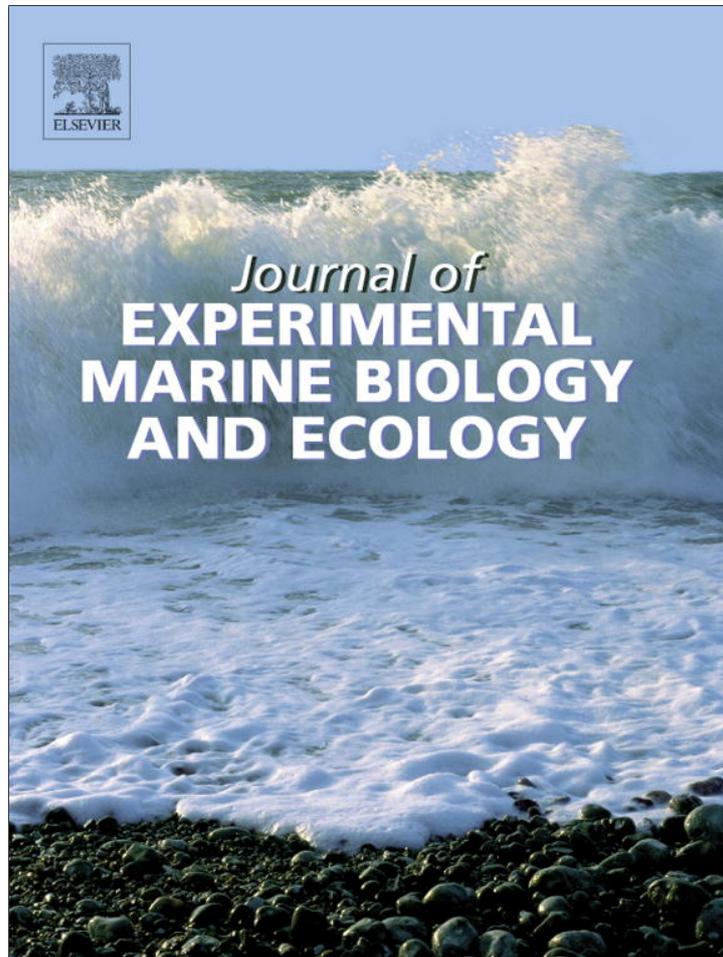


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## Ephemeral macroalgae display spatial variation in relative palatability

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## ABSTRACT

Although geographic variation in algal–herbivore interactions should be common, our appreciation of such variation remains incomplete. For example, feeding choice assays examining variation in palatability of algae typically compare multiple algal species or genera from a single location or a single alga from multiple locations. Unfortunately, most studies have not compared the interaction of herbivores with multiple algae from multiple locations, thus tests of variation of relative palatability are lacking. To examine spatial variation in algal palatability we determined the feeding preferences of the periwinkle snail *Littorina littorea* when offered multiple algal genera at the same time from two regions in choice assays. Multi-choice experiments were repeated throughout the year to examine temporal variation in feeding preferences. Consistent with previous studies, *L. littorea* preferred to feed on ephemeral algae compared to perennial species. Importantly, the relative palatability of the two ephemeral genera, *Ulva* and *Porphyra*, varied greatly between regions and seasons. Under certain conditions, *Ulva* only represented 24% of consumed algal wet mass in choice assays, while under other conditions, *Ulva* was eaten almost exclusively. Preferences for *Ulva* or *Porphyra* were unrelated to differences in morphology. Variation in the relative palatability of algae could influence consumer behavior leading to shifts in algal communities across broad geographic scales.

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## 1. Introduction

Herbivore interactions with plants and algae are spatially dynamic, with variation arising from differences in species composition (Gaines and Lubchenco, 1982), local adaptation (Salgado and Pennings, 2005; Sotka and Hay, 2002), and environmentally-induced plasticity in traits (Bolser and Hay, 1996; Long et al., 2007; Renaud et al., 1990). Such variation can strongly alter the outcomes of plant–herbivore and algal–herbivore interactions, especially when traits influencing palatability change across broad geographic scales. Unfortunately, we lack a complete understanding of this variation because previous studies typically compared the palatability of 1) multiple species from a single location (Jormalainen et al., 2001; Kennish and Williams, 1997; Lubchenco, 1978; Steinberg, 1985) or 2) a single species from multiple locations (Bolser and Hay, 1996; Pennings et al., 2009). Missing are experiments that simultaneously compare the palatability of multiple algae relative to one another from multiple locations or times (Lubchenco and Gaines, 1981). This bias prevents a thorough understanding of the dynamics of herbivore–algae interactions and limits the usefulness of prey palatability categories derived from studies of algae from a single place or time.

The herbivorous snail, *Littorina littorea*, is a dominant structural architect of rocky shores along northern Atlantic coastlines (Lubchenco, 1978). *L. littorea* strongly prefers to feed upon ephemeral algae that typically lack chemical and morphological defenses (e.g. *Ulva* spp. and

*Porphyra* spp.) compared to perennials (e.g. *Fucus vesiculosus* and *Ascophyllum nodosum*; Lubchenco, 1978; Watson and Norton, 1985). However, previous studies have overlooked variation within these broad categories based on life history (e.g. the relative palatability of ephemeral algae). Indeed, the relative palatability of ephemeral algae might be site- or region-specific because environmental conditions display strong heterogeneity across the range of these species and the performance of these ephemeral algae can be sensitive to these environmental factors (Gaines and Lubchenco, 1982).

In this study, we examined feeding preferences of *L. littorea* for algae collected from two regions at three different time periods in the Gulf of Maine to investigate how algal palatability changes in space and time. We focused on changes in the relative palatability of ephemeral algae within the genera *Ulva* and *Porphyra*. We also assessed palatability of homogenized algae to examine if observed patterns in palatability remained after removing morphological differences.

## 2. Materials and methods

## 2.1. Study sites and organisms

To examine spatial variation in the relative palatability of multiple algal genera, we offered *L. littorea* (hereafter *Littorina*) a choice of multiple co-occurring algae collected from two sites separated by 460 km – either Nahant, Massachusetts (42°25′27.34″ N, 70°54′52.16″ W) or Dipper Harbour, New Brunswick, Canada (hereafter DH; 45°16′24.35″ N, 66° 3′50.87″ W) during three collection periods

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(August 2007, March 2008, June 2008). In August 2007, we offered snails a choice of *F. vesiculosus*, *A. nodosum*, *Chondrus crispus* (Nahant assays)/ *Mastocarpus stellatus* (DH assays), *Ulva* spp., and *Porphyra* spp. (hereafter *Fucus*, *Ascophyllum*, *Chondrus*, *Mastocarpus*, *Ulva*, and *Porphyra*; respectively). Because *Chondrus* was rare in DH, we used *Mastocarpus* in place of *Chondrus* in DH assays. *Chondrus* and *Mastocarpus* are both low intertidal red turf algae that are closely related (both belong to the order Gigartinales) and morphologically similar (Villalard-Bohnsack, 2003).

We collected algae from 2 to 3 sites within each region, pooled collections, and transported them in chilled coolers to Nahant. All algae were kept in coolers for 8 h prior to use. Multi-choice assays were conducted the following day by offering Nahant *Littorina* a choice of the five genera collected from a single region. The most striking result of the August assays was a regional difference in the relative palatability of *Ulva* and *Porphyra* (see Results section). Thus, trials performed in March and June (2008) tested differences in palatability between *Ulva* and *Porphyra* only.

## 2.2. Live algae multi-choice feeding assays

For all assays, we measured the decrease in algal wet mass in grazer replicates ( $n = 15\text{--}30$ ) after correcting for autogenic growth in grazer-free controls ( $n = 10$ ). Prior to assays, algae were blotted dry, cut to 0.5 g pieces, and placed in perforated replicate containers ( $10 \times 10 \times 9$  cm). Replicate containers were placed in outdoor, unshaded tanks with flow-through seawater pumped from an adjacent marine cove. Grazer replicates contained 2–4 *Littorina* each (constant number per experiment). Final blotted, wet masses of algae were recorded 2–3 days later. We calculated consumption using the formula  $T_i(C_f/C_i) - T_f$ , where  $T_i$  and  $T_f$  represent algae exposed to grazing, and  $C_i$  and  $C_f$  represent the control algae before (i) and after (f) the trial period (Sotka et al., 2002). Because grazing rates can vary with *Littorina* size, we divided consumption by the final wet *Littorina* mass of all individuals within the corresponding replicate. We converted these to consumption rates by dividing per snail consumption by assay length (consumption = mg algae  $\times$  g snail<sup>-1</sup>  $\times$  day<sup>-1</sup>).

To correct consumption rates for changes in autogenic growth, we used a single correction factor ( $C_f/C_i$ , as above; hereafter control ratio) that averaged autogenic mass changes across control replicates ( $n = 10$ ). We adopted this approach to maximize the number of replicates that contained snails feeding on algae. Such an approach has been criticized because of concerns about artificial suppression of experimental variance (Peterson and Renaud, 1989). However, such a problem “disappears” as the variance among controls decreases (Peterson and Renaud, 1989). Although we saw very little variability in our controls (see Appendix 1), we performed a statistical analysis to examine whether our results would have changed had we calculated consumption with paired grazer and grazer-free replicates. First, we generated new control ratios by randomly resampling our measured control ratios with replacement via bootstrapping in SYSTAT 12 (version 12.02.00). Second, we paired single control ratios with experimental replicates and recalculated consumption rates. Finally, we compared 1) the original measured control ratios to the bootstrapped control ratios and 2) the original measured consumption rates to newly the calculated consumption rates, using two-sample t-tests. No differences were found between our approach and this resampling approach (see Appendix 2).

Mean consumption rates of each algae within each region (multi-choice assay) were compared using the nonparametric Friedman's rank test ( $> 2$  choices, August 2007 multi-species assays; Zar, 1999) or paired t-tests (2 choice assays, March and June 2008 assays; SYSTAT 12, version 12.02.00). Post-hoc analyses of consumption rates were conducted with nonparametric multiple comparisons ( $> 2$  choices). We used a sequential Bonferroni correction (corrected  $\alpha = 1 - (1 - \alpha_{0.05})^{1/k}$ ) to account for the number of comparisons in the March and June 2008 assays ( $k = 4$ , where

$k$  represents the number of comparisons made during the analysis; Rice, 1990).  $P$ -values were only considered significant if less than the corrected  $\alpha$ . Consumption rates of the least preferred algae [*Fucus*, *Ascophyllum*, and *Chondrus* (Nahant)/*Mastocarpus* (DH)] during the August 2007 multi-species trials were summed prior to comparison because they were grazed at low rates, and we were primarily interested in comparing their combined palatability to the palatability of the two most preferred genera, *Ulva* and *Porphyra*.

To examine changes in the relative palatability of *Ulva* and *Porphyra* between sites and time points, we calculated the proportion of total consumption represented by *Ulva* by dividing *Ulva* consumption by the combined consumption of *Ulva* and *Porphyra* for each assay. Thus, this proportion increases with an increasing preference for *Ulva*. If consumption of either *Ulva* or *Porphyra* was negative, it was assumed that it was completely avoided relative to the other genera, and was corrected to 0 before calculating this proportion. From all feeding assays, six replicates out of 144 total replicates displayed negative consumption of all choices. These replicates were excluded from the calculation of proportional consumption. Proportions were compared with a two factor, fixed model ANOVA (SYSTAT 12, version 12.02.00) to test for the effects of region, month, and their interaction on *Littorina* feeding preferences.

## 2.3. Artificial food multi-choice feeding assays

To examine the relative palatability of *Ulva* and *Porphyra* during August 2007 in the absence of algal morphology, we measured grazing on artificial foods containing reconstituted algae using methods adopted from Lindquist and Hay (1996). Artificial foods were prepared by homogenizing freeze-dried, finely-ground algae (5.6% weight: volume) with agar (2.0% w:v). This procedure removes morphological traits while maintaining chemical traits. The algae-agar solution was molded into cubes ( $1 \text{ cm} \times 1 \text{ cm} \times 0.2 \text{ cm}$ ) on fiberglass window screen, and allowed to set for 2–5 min. To avoid desiccation, we immediately placed the samples in seawater until feeding assays began. Preferences were determined using the methods described above in live plant feeding assays, by measuring the mass change of artificial foods (snail treatments,  $n = 25\text{--}29$ ; controls,  $n = 10$ ). Briefly, we 1) offered Nahant *Littorina* a choice of artificial foods made of either *Ulva* or *Porphyra* from the same region, 2) measured grazing after 2 days, and 3) compared final consumption rates of each algal species within each region using paired t-tests.

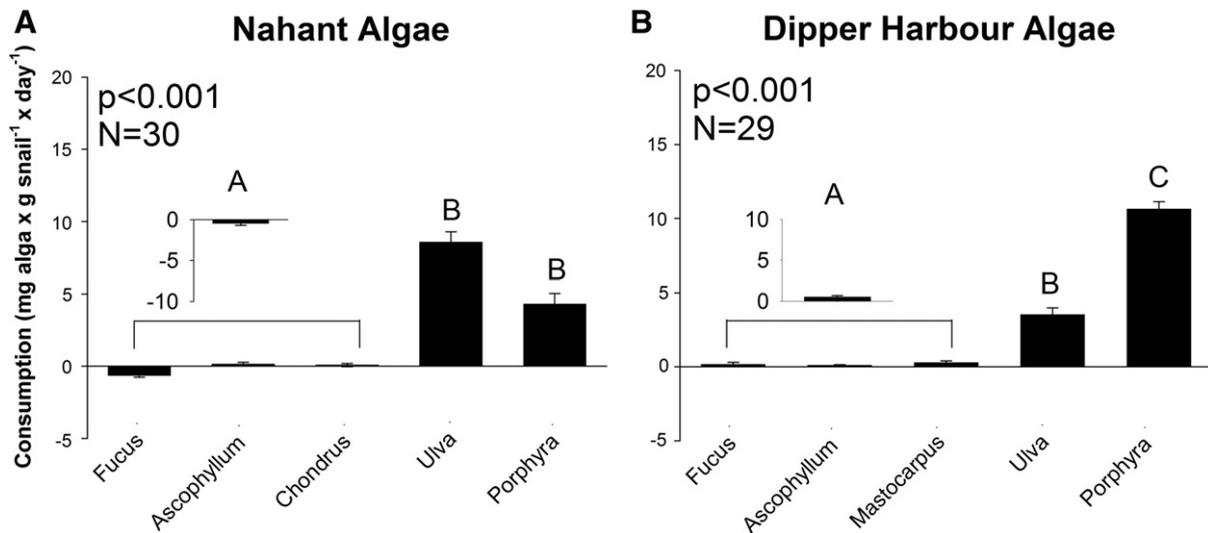
## 3. Results

### 3.1. Spatial variation in algal palatability

Consistent with previous studies (Lubchenco, 1978; Watson and Norton, 1985), *Littorina* preferred ephemeral algae (*Ulva* and *Porphyra*) to perennial algae (*Fucus*, *Ascophyllum*, and *Chondrus/Mastocarpus*) in multi-choice assays (August 2007), regardless of population (Fig. 1; Nahant:  $\chi^2 = 38.067$ ,  $p < 0.001$ , DH:  $\chi^2 = 23.931$ ,  $p < 0.001$ ). Interestingly, the relative palatability of *Ulva* and *Porphyra* changed with algal source. *Littorina* consumed two times more *Ulva* than *Porphyra* from Nahant, but this difference was not significant ( $p > 0.05$ , Fig. 1A). In contrast, *Littorina* consumed three times more *Porphyra* than *Ulva* from DH ( $p < 0.05$ , Fig. 1B). Furthermore, consumption patterns persisted after morphological traits were removed using artificial foods. *Littorina* showed similar preferences for Nahant *Ulva* and *Porphyra* (Fig. 2;  $t_{(24)} = -0.628$ ,  $p = 0.536$ ), while DH *Porphyra* was preferred over *Ulva* (Fig. 2;  $t_{(28)} = -3.872$ ,  $p = 0.001$ ).

### 3.2. Temporal variation in algal palatability

The relative palatability of *Ulva* and *Porphyra* varied temporally at both Nahant and DH. For Nahant algal populations, consumption of



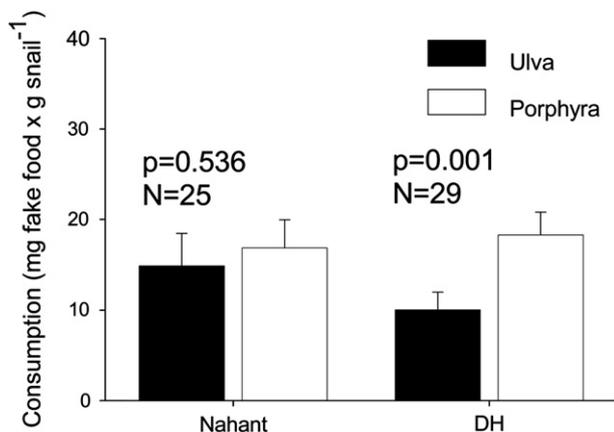
**Fig. 1.** Spatial variation of Nahant *Littorina littorea* consumption of 5 algae (*Fucus vesiculosus*, *Ascophyllum nodosum*, *Chondrus crispus* (Nahant assay), *Mastocarpus stellatus* (DH assay), *Ulva* spp., and *Porphyra* spp.) in multi-choice feeding assays (mean  $\pm$  1 SE) during August 2007. Snails were offered a choice of algae from either Nahant (A) or DH (B) populations. *P*-values indicate significant differences in algal preference as determined with Friedman's rank tests. Letters indicate significant differences ( $p < 0.05$ ) as determined with nonparametric multiple comparisons per algae population. Consumption amounts of the least preferred algae (*F. vesiculosus*, *A. nodosum*, *C. crispus* (Nahant), *M. stellatus* (DH)) were summed and treated as one choice (inset figures) in nonparametric multiple comparisons.

these two algae was similar in choice assays in August (Fig. 1A) and June (Fig. 3C;  $t_{(19)} = -1.763$ ,  $p = 0.094$ ), but a strong preference for *Ulva* appeared in March (Fig. 3A;  $t_{(29)} = 6.178$ ,  $p < 0.001$ ). For DH algal populations, *Porphyra* was preferred over *Ulva* in August (Fig. 1B) and June (Fig. 3D;  $t_{(19)} = -3.189$ ,  $p = 0.005$ ), but they were equally palatable in March (Fig. 3B;  $t_{(14)} = -1.468$ ,  $p = 0.164$ ). Interestingly, the temporal change in palatability occurred at the same time for both regions. Between late summer (August) and early spring (March), the relative palatability of *Ulva* compared to *Porphyra* increased at both locations (Fig. 4).

*Ulva* consumption always represented a greater proportion of the combined consumption of *Ulva* and *Porphyra* in Nahant than in DH (Fig. 4). There was a significant effect of region ( $F_{1,132} = 61.493$ ,  $p < 0.001$ ), month ( $F_{2,132} = 9.338$ ,  $p < 0.001$ ) and their interaction ( $F_{2,132} = 6.046$ ,  $p = 0.003$ ) on the relative palatability of *Ulva* and *Porphyra* (Fig. 4).

#### 4. Discussion

Algal genus, source, and collection period influenced feeding preferences of an ecologically important marine snail. Consistent

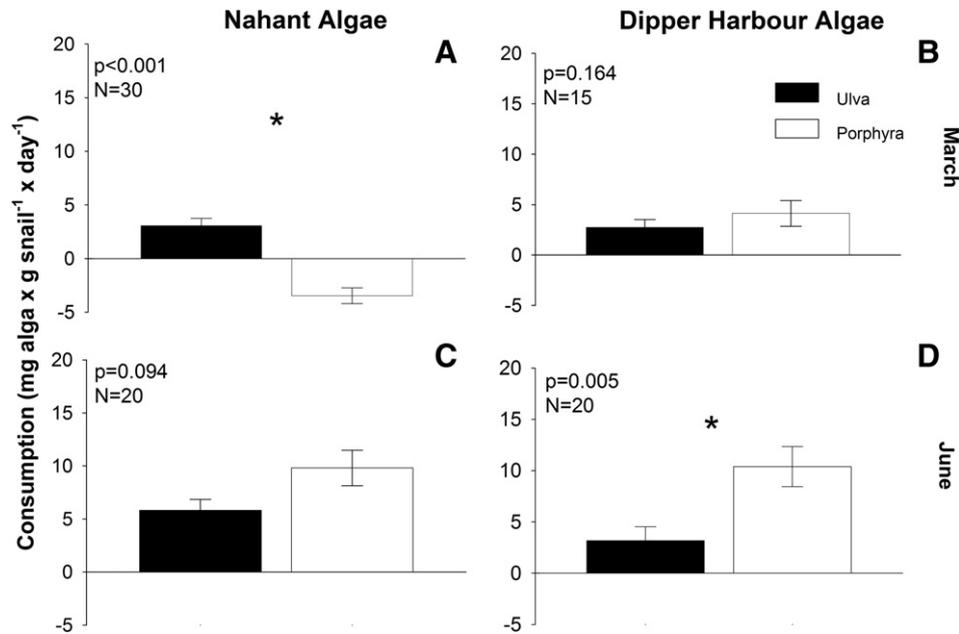


**Fig. 2.** Consumption of artificial foods (mean  $\pm$  1 SE) made from *Ulva* spp. and *Porphyra* spp. from Nahant and DH by Nahant *Littorina littorea* during choice assays. *P*-values indicate significant differences in algal preference as determined with paired *t*-tests.

with previous studies, *Littorina* strongly preferred ephemeral to perennial algae (Lubchenco, 1978; Watson and Norton, 1985). However, the relative palatability of the ephemeral genera, *Ulva* and *Porphyra*, displayed extreme variation in both space and time. For example, the proportion of *Ulva* consumed compared to total consumption of *Ulva* and *Porphyra* varied from 0.24 to 0.89 (Fig. 4). Surprisingly, these data represent one of the only tests of spatial variation in the relative palatability of multiple genera to one another – other studies examining spatial variation in palatability typically focused on variation in a single prey species. In addition, *Porphyra*, typically considered a “palatable” algal genus, was avoided almost entirely in choice assays with Nahant *Ulva* in March (Fig. 3A). This discovery likely would have gone unnoticed had we conducted more typical feeding assays using either multiple algae from a single site or single alga from multiple sites.

Several factors may contribute to geographic variation in algal-herbivore interactions, including interspecific differences (e.g. changes in species composition between sites) and intraspecific differences (either fixed or plastic). Although the morphologies of our *Ulva* and *Porphyra* individuals were consistent with those of *Ulva lactuca* and *Porphyra umbilicalis*, morphological traits may be insufficient for distinguishing cryptic species within these genera in New England. For example, recent studies recommend using molecular techniques to identify *Ulva* and *Porphyra* species (Guidone et al., 2012; Hofmann et al., 2010; Klein et al., 2003). Given our uncertainty of the species composition of these genera within our collections, the spatiotemporal patterns documented here could reflect either intraspecific variation or changes in the species composition within each genus. Regardless of the mechanism, our study identified strong variation in palatability within the ephemeral algae – in some cases an ephemeral alga that was highly preferred relative to perennial algae was avoided entirely when offered with another ephemeral alga.

Chemical content of algal tissues appeared to influence the relative palatability of *Ulva* and *Porphyra*. Spatial patterns in relative palatability persisted after homogenizing tissues and incorporating them into artificial foods, suggesting that morphological differences between *Ulva* and *Porphyra* did not influence relative palatability (Fig. 2). Although *Ulva* is generally considered a palatable algal genus, the hypothesis that chemical defenses are generating these patterns cannot be excluded given recent evidence from the western United States that *Ulva* species can produce chemical feeding deterrents (Van Alstyne, 2008; Van Alstyne et al., 2007).

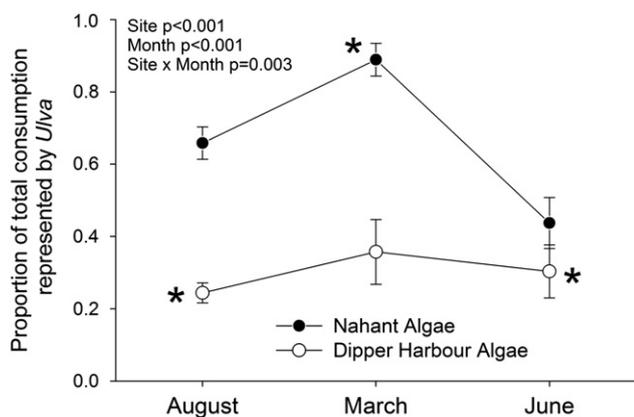


**Fig. 3.** Temporal variation of the consumption of *Ulva* spp. and *Porphyra* spp. by Nahant *Littorina littorea* in two-choice feeding assays (mean ± 1 SE) conducted in March (A,B) and June (C,D) 2008. *P*-values were corrected using sequential Bonferroni adjustments [following Rice (1990)] of uncorrected *P*-values (based on paired *t*-tests). Asterisks (\*) indicate significant differences between preferences for each multi-choice assay.

If the relative palatability of algal genera changes dramatically in time or space, this will limit the usefulness of broad categorizations of palatability (e.g. palatable vs. unpalatable, defended vs. undefended). For example, ontogeny, biogeography, or climate can largely influence plant palatability and physiological responses to herbivory (Pennings et al., 2001; Swihart and Bryant, 2001; Swihart et al., 1994). This can result in highly variable herbivore–plant interactions throughout the range and lifetime of a plant. We observed extreme variation in relative palatability between ephemeral genera – with preferences switching completely between scenarios. For example, had we only conducted our assays in March or August with only Nahant algae, we would have concluded that *Ulva* was more palatable than *Porphyra*. Yet at all other times and places, *Ulva* was either equally or less preferred. Though consumption rates of Nahant *Ulva* and *Porphyra* appeared disparate during August and June assays (i.e. *Ulva* appeared more palatable in August and *Porphyra* more palatable in June), the resulting differences were not significant. However, the observed trends further support strong spatial variation in palatability. While we also observed temporal variability

in snail feeding preferences, this variability may be caused by seasonal changes in herbivores related to shifting resource allocation between reproduction and growth rather than temporal variation in algal traits (Hemmi and Jormalainen, 2004). Clearly, statements about the relative palatability of these genera are context-dependent.

Although these ephemeral algae appear functionally redundant (e.g. they grow rapidly, display a foliose morphology, and are primary successors), changes in their relative palatability could influence marine communities (Lubchenco and Gaines, 1981). Marine grazers are well known for their ability to reduce the abundance of preferred species – sometimes to local extinction (Lubchenco, 1978; Lubchenco and Cubit, 1980; Paine and Vadas, 1969). If these genera differ with respect to ecological roles (e.g. habitat provision, nutrient cycling, or successional position), changes in relative palatability could alter key ecological processes. As an example, an *Ulva* congener utilizes ammonium more effectively than nitrate, but *Porphyra* congeners utilize these nutrients equally well (Bracken and Stachowicz, 2006). Thus, changes in algal palatability could impact local nutrient cycling.



**Fig. 4.** Relative palatability of *Ulva* spp. and *Porphyra* spp. calculated by dividing *Ulva* consumption by the summed consumption of *Ulva* and *Porphyra*. Ratios significantly different from 0.5 indicate a preference for *Ulva* spp. (ratio >0.5) or *Porphyra* spp. (ratio <0.5). Month represents the timing of collections and feeding assays. Asterisks (\*) indicate assays with significant preferences for one of the genera.

### 5. Conclusions

Despite the widely accepted notion that ephemeral algae like *Ulva* and *Porphyra* are equally important to intertidal herbivores like *Littorina*, our observations suggest that this may not always be true. Our study is one of the first to show that the relative palatability of algal genera changes spatially relative to one another. Such variation could influence geographic differences in consumer–prey interactions, leading to differentiation in the structure and function of marine communities.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.jembe.2012.12.009>.

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