INTRODUCTION

Natural selection operates on the intraspecific variation in traits among individuals of a population. Under a particular selective pressure, this variation may confer an advantage to individuals demonstrating a specific form of a trait and may allow those individuals to attain higher fitness. For plant–herbivore interactions, intraspecific variations in both the prey plant and the herbivore consumer can have important consequences for the distribution and abundance of both interacting species. For example, ontogenetic, sexual, and biochemical differences among individuals in plant populations can have strong effects on their susceptibility to herbivores (Karban & Baldwin 1997, Agrawal 2005, Boege & Marquis 2005, Cornelissen & Stiling 2005, Barton & Koricheva 2010). Although fewer numerically, studies on marine and freshwater algae have found similar patterns of intraspecific variation in susceptibility as a function of algal traits and their interaction with environmental variables (Hay 1996, Paul et al. 2001, Vergés et al. 2008, Van Donk et al. 2011). Reciprocally, consumption of the same plant or algal prey species can also vary with herbivore age, feeding history, or sex (Cronin & Hay 1996, Hochuli 2001, Jormalainen et al. 2001).

Much of the work analyzing intraspecific differences in plant susceptibility to herbivory has focused on variations in defensive chemistry, particularly on the role of induction in chemical defense (Hay 1996, Karban & Baldwin 1997, Paul et al. 2001, Agrawal 2005, Amsler 2008, Van Donk et al. 2011). Less is known about how differences in nutritional quality,
structural defenses, or morphology affect herbivore feeding. In marine ecosystems, algae with complex heteromorphic life cycles may experience stage-specific differences in herbivory. In this case, changes related to the life-history of the algae sometimes result in dramatically contrasting body plans that may differ in their susceptibility to natural enemies (Lubchenco & Cubit 1980, Slocum 1980, Vergés et al. 2008). The differences between sporophytes and gametophytes are often large enough that each stage occupies a different niche (but see Thornber et al. 2006) and, thus, will be exposed to herbivores that operate at very different scales or show different feeding modes. A similar scenario occurs for marine invertebrates that release small motile unitary larvae from adults that are large, often modular, and sessile. For these animals, pre- and post-settlement predation likely involve different guilds of predators (Stoner 1990, Maldonado 2006). Yet, for many plants, algae, and sessile invertebrates, noticeable intraspecific variation in morphology need not be related to ontogenetic changes and can be expressed among individuals of the same sex and age as related to genotype or phenotypic plasticity resulting from environmental gradients (Agrawal 2001, Benard 2004, Miner et al. 2005).

The effectiveness of structural defenses for diverse plant and animal species has been documented (Benard 2004, Inbar & Lev-Yadun 2005, Hanley et al. 2007, Ferguson & Davis 2008). However, studies addressing the consequences of intraspecific variation in structure have largely focused on induced defenses of animals (Harvell 1990, Tollrian & Harvell 1999, Benard 2004). Variation in structural susceptibility to herbivores has also been related to induction in plants (Harvell 1990, Hanley et al. 2007), but very few studies have addressed how constitutive structural differences between conspecifics affect herbivore choice, distribution, and nutrient acquisition (Rudgers & Whitney 2006, Wise & Abrahamson 2008, Kawasaki et al. 2009). In part, the lack of studies in this area is related to the rarity of certain morphotypes within natural populations, which constrains the ability to experimentally quantify the susceptibility of those morphologically different plants to grazing pressure.

Cultivated plants and algae can provide useful models for understanding the relation between intraspecific variation in prey traits and susceptibility to consumers without the need of intensive efforts finding, or risking overcollection of, rare phenotypes. Diverse algal strains with specific biochemical and physical traits are now available from breeding efforts on various cultured seaweeds. While many algae in aquaculture are not natural components of the environments in which they are cultivated, a number of cultured seaweeds have become invaders in these novel environments (Schaffelke et al. 2006, Schaffelke & Hewitt 2007, Williams & Smith 2007). During these events local herbivores encounter prey with which they have no evolutionary experience, and the success of an algal species establishing a viable population in this new ecosystem will likely be influenced by the phenotype that has actually escaped into the wild. Thus, measuring intraspecific susceptibility of aquacultured algae to grazers may provide insights into both fundamental ecological mechanisms and allow predictions regarding invasive potential.

In this study, we used 3 cultivated phenotypes (strains) from the agar-producing red seaweed Gracilaria cornea J. Agardh, 1852 and evaluated their susceptibility against 2 herbivores from the Mediterranean. Clearly distinct phenotypes of G. cornea occur spontaneously both in the field (Ferreira et al. 2006) and in cultivation (Friedlander et al. 2001, Friedlander et al. 2008), and thus correspond to natural phenotypic variation for this species. The alga has a broad distribution, with West Atlantic records from the United States to the coast of Brazil, the Caribbean, and eastern Africa (Guiry & Guiry 2012). Although the herbivores used in this study overlap in distribution with the alga over large areas, G. cornea has no known established populations in the Mediterranean. Thus, herbivore responses would not likely be affected by previous experience with any of the algal phenotypes and correspond to perceived characteristics of a novel prey (e.g. an introduced species). Algae in the genus Gracilaria can activate the production of hydrogen peroxide against agar-degrading epiphytic bacteria (Weinberger & Friedlander 2000, Potin 2008, Weinberger et al. 2010), and 1 species is known to induce deterrent eicosanoids upon grazing (Nylander et al. 2011). However, no chemical defenses against herbivores are known to occur in G. cornea (Paul et al. 2001, Amsler 2008), and species in this genus tend to be preferred species for many marine consumers (e.g. Pfister & Hay 1988, Brand-Gardner et al. 1999), particularly after wounding (Diaz et al. 2006). Thus, we hypothesized that herbivore responses would be affected largely by the structural differences among the phenotypes and, potentially, by nutritional differences that may exist among the conspecific algae. We tested the susceptibility of 3 algal phenotypes against 2 common and widely distributed mesograzers: the amphipod Ampithoe ramondi and the crab...
Acanthonyx lunulatus. Using these organisms, the following questions were addressed: (1) Are there differences in palatability among the 3 G. cornea phenotypes? (2) If so, are morphological and nutritional differences among conspecific algae related to their susceptibility to herbivores? (3) Can intraspecific differences in nutrient content of the algae trigger compensatory responses in the mesograzers (e.g. compensatory feeding)?

MATERIALS AND METHODS

The gammaridean amphipod Ampithoe ramondi Audouin, 1826 and the majid crab Acanthonyx lunulatus (Risso, 1816) were collected from the common benthic algae Jania rubens, Padina pavonica, and Ulva lactuca around the intertidal near the Israel Oceanographic and Limnological Research Laboratory in Haifa (32° 49' 0" N, 34° 59' 0" E). A. ramondi is common in the Mediterranean coast of Israel (Fishelson & Haran 1987, Sorbe et al. 2002, Cruz-Rivera & Friedlander 2011) and has a worldwide distribution (Lowry et al. 2012), although reports of this amphipod may include in part misidentified congenic or cryptic species (Myers 2012). A. lunulatus is a small algal-dwelling crab found on algae in the eastern Atlantic, the Azores, and the West Atlantic from Europe to South Africa, as well as on both sides of the Mediterranean (Cruz-Rivera 2001, Cruz-Rivera & Friedlander 2011, Fransen & Türkay 2012). It is known to consume a variety of temperate algae including Mediterranean species of Gracilaria (Cruz-Rivera 2001, Cruz-Rivera & Friedlander 2011).

The red alga Gracilaria cornea (=Hydropuntia cornea [J. Agardh] M. J. Wynne, 1989) was obtained from aquaculture tanks in which different clonal phenotypes had been grown for several years (Friedlander 2008). In these tanks, the thicker coarsely branched red wild strain (‘wild’ hereafter) and a spontaneously occurring thin highly branched red mutant (‘fine’ hereafter) grew together. A third phenotype (strain), green and moderately branching (‘green’ hereafter), was kept in culture separately. Descriptions of the G. cornea phenotypes, and their responses to culturing and environmental conditions are discussed in Levy & Friedlander (1994), Friedlander et al. (2001), and Friedlander (2008). While the terms ‘wild’ and ‘mutant’ are seldom used by ecological geneticists or evolutionary ecologists describing phenotypes, we retain the names that have been used in the works cited above (and others) to refer specifically to these G. cornea strains and other cultivated species. This allows an easier comparison with the aquaculture literature where Gracilaria intraspecific variation has been explicitly assessed the most.

While morphological differences among the 3 algal phenotypes were clearly noticeable and have been previously documented, potential differences in nutritional traits of the algae have not. We compared overall organic content (as a proxy for nutrient content) by quantifying ash-free dry mass (AFDM) in parts from the same algal thalli that were later used in feeding assays with amphipods and crabs (n = 10). To determine wet to dry mass ratios and percentage of ash, algal pieces were first dried with absorbent paper and weighed. These were then dried at 60°C for about 4 d, reweighed, and burned in a furnace at 450°C for at least 8 h to obtain ash masses. Most studies in animal nutrition present nutrient data as proportions of dry mass. However, animals in nature encounter foods that may contain broadly different water content. High water content in a diet can affect nutrient acquisition and assimilation for the consumer (Cruz-Rivera & Hay 2001, Lavoie & Oberhauser 2004). Therefore, ash and AFDM contents herein were analyzed as percents of dry mass (which allows comparisons with other published works) and wet mass (which is how herbivores encounter algae).

To assess the susceptibility of Gracilaria cornea phenotypes to marine herbivores, 2 types of feeding assays with Ampithoe ramondi and Acanthonyx lunulatus were conducted. In multiple-choice experiments, G. cornea pieces of all 3 phenotypes were simultaneously offered to either amphipods or crabs. In no-choice experiments, animals were confined to feeding on only 1 of the 3 phenotypes. Treatment replicates for both types of experiments were run in small plastic containers to which fresh seawater, grazers, and algae had been added. Controls for autogenic changes in algal mass (Peterson & Renaud 1989) were interspersed among treatments and had similar masses of algae in fresh seawater, but no grazers. Replicates in which animals consumed no food were eliminated from the analyses. Only healthy-looking thalli (without bleached areas that may constitute microbial infection; Friedlander 2008) were used in the assays to avoid confounding structural or nutritional differences in phenotype susceptibility with changes in palatability related to an immune response of Gracilaria or other activated mechanisms (Weinberger & Friedlander 2000, Potin 2008, Weinberger et al. 2010, Nylund et al. 2011).

During multiple-choice assays, pieces of the 3 algal phenotypes (ca. 80 to 120 mg for amphipods and 150 to 200 mg for crabs, as per differences in animal size)
were placed in each of the replicate containers. Three adult *Ampithoe ramondi* or a single crab were added to treatment containers (n = 10 for amphipods and n = 12 for crabs) and allowed to feed for a maximum of 3 d. The same number of containers served as controls for autogenic changes in algal mass (Peterson & Renaud 1989). Upon termination of this multiple-choice assay, animals were removed and remaining algal pieces were weighed. Consumption (mg eaten/individual consumer/day) was calculated after correcting for mass changes unrelated to consumer feeding using the formula \( (H_t - C_t) / C_t \) – \( H_i \), where \( H_t \) and \( H_i \) were the initial and final algal masses of the pieces exposed to herbivores and \( C_t \) and \( C_i \) were the initial and final masses of the paired controls for autogenic changes (Peterson & Renaud 1989, Cronin & Hay 1996).

Because herbivores may increase their feeding rates to compensate for low food quality (compensatory feeding), we also measured consumption by *Ampithoe ramondi* and *Acanthonyx lunulatus* when constrained to feed on only 1 of the 3 *Gracilaria cornea* phenotypes. Pieces of each algal phenotype (ca. 70 to 100 mg for amphipods and 150 to 200 mg for crabs, as per differences in size) were placed with 2 adult *A. ramondi* or 1 *A. lunulatus* in single replicate containers (n = 7 for amphipods and n = 9 for crabs). Animals were allowed to feed for up to 3 d. Equal numbers of controls for autogenic changes in algal mass were run simultaneously. After allowing animals to feed, algal pieces were weighed again and consumption was calculated as explained above for the multiple-choice assays.

Differences in organic content and feeding rates from no-choice experiments were analyzed using 1-way ANOVA, followed by Tukey-Kramer post hoc tests. When F-tests detected heterogeneity in variances, logarithmic transformations were used. In all cases, transformations attained homoscedasticity. Because multiple-choice experiments offered all the phenotypes simultaneously to grazers, consumption of any alga was not independent of the consumption of other choices. Thus, data from these assays were analyzed using the non-parametric Friedman’s test followed by pair-wise post hoc comparisons (Conover 1980). For these multiple-choice assays, we also analyzed the relative contribution of each of the 3 algal phenotypes to overall consumption for each mesograzer in order to discern differences in these patterns. This was accomplished by calculating the percentage of the total amount consumed in each replicate that was comprised by each phenotype. These percentages (relative consumption in amphipods versus crabs) were then compared for each phenotype using unpaired t-tests.

To assess the possibility of compensatory feeding as a function of algal organic content, we compared the feeding rates of each herbivore, on each algal phenotype, against the %AFDM per wet mass contents of the algae. This approximation of organic content in a food is clearly a coarse measurement of food quality and does not preclude the possibility that consumers may be cueing on specific nutrients that covary with total organic mass. However, AFDM has been demonstrated to have considerable predictive power explaining feeding rates of marine crustaceans within the same families (Ampithoidae and Majidae, respectively) as those used here (Stachowicz & Hay 1999, Cruz-Rivera & Hay 2001, Sotka & Hay 2002). Regression lines and 95% confidence intervals were calculated by plotting the feeding rates in individual replicates versus the organic content of the algae used in those replicates. This was possible because AFDM values were quantified in algal subsamples that were matched to each treatment replicate.

### RESULTS

Significant differences in composition (measured as water, dry mass, and ash contents) were found among the 3 *Gracilaria cornea* phenotypes (p ≤ 0.001 for all analyses, 1-way ANOVA; Table 1). This led to concomitant significant differences in AFDM when calculated as ratios of wet or dry mass (p < 0.001 for both analyses, 1-way ANOVA). The wild phenotype

<table>
<thead>
<tr>
<th></th>
<th>Fine</th>
<th>Green</th>
<th>Wild</th>
<th>p</th>
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<tbody>
<tr>
<td>Water</td>
<td>81.41 ± 0.14A</td>
<td>88.92 ± 0.09B</td>
<td>78.38 ± 0.31C</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Dry mass</td>
<td>18.59 ± 0.14A</td>
<td>11.08 ± 0.09B</td>
<td>21.62 ± 0.31C</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Ash (WM)</td>
<td>5.41 ± 0.02A</td>
<td>5.72 ± 0.02B</td>
<td>5.32 ± 0.12A</td>
<td>0.001</td>
</tr>
<tr>
<td>Ash (DM)</td>
<td>29.13 ± 0.30A</td>
<td>51.65 ± 0.41B</td>
<td>24.66 ± 0.73C</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>AFDM (WM)</td>
<td>13.18 ± 0.15A</td>
<td>5.36 ± 0.08B</td>
<td>16.30 ± 0.30C</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>AFDM (DM)</td>
<td>70.67 ± 0.30A</td>
<td>48.35 ± 0.41B</td>
<td>75.34 ± 0.73C</td>
<td>&lt;0.001</td>
</tr>
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had the highest organic content (AFDM), followed by the fine and green phenotypes, and all were statistically different among themselves (p < 0.05, Tukey-Kramer tests). The wild phenotype contained the highest percentage of dry mass (lowest percent of water per wet mass), coupled with the lowest concentration of ash of all 3 phenotypes (Table 1). Differences in AFDM by wet mass between the 3 phenotypes were more pronounced, but the overall pattern was similar whether organic content was expressed as a percentage of dry or wet mass, with all 3 phenotypes being significantly different from each other.

When presented with pieces of all 3 Gracilaria cornea phenotypes, both amphipods and crabs consumed significantly more of the fine phenotype than of either of the other 2 phenotypes (p < 0.001, Friedman’s test; Fig. 1). Consumption of the green phenotype was intermediate, but significantly higher than consumption of the wild phenotype for both mesograzers. While overall patterns were similar (shown as mean mg consumed animal⁻¹ d⁻¹ in Fig. 1), the magnitude of the differences in relative consumption of the 3 G. cornea phenotypes differed between consumers. When amounts eaten of each phenotype were converted to percentages of total consumption per individual replicate, the fine phenotype comprised about 63% of overall consumption by amphipods and close to 80% of overall crab consumption. The green phenotype accounted for 34% of total consumption in amphipods, but 16% in crabs, and the wild phenotype accounted for 2 and 4% of consumption in amphipods and crabs, respectively. These differences in relative consumption between amphipods and crabs were not significant for either the fine (p = 0.079, unpaired t-test) or the wild (p = 0.484, unpaired t-test) phenotypes. However, there was a significant difference in the relative contribution of the green phenotype to overall food choice, with amphipods consuming relatively more of this phenotype than crabs (p = 0.014, unpaired t-test).

In contrast to the patterns found in the multiple-choice experiments, Ampithoe ramondi confined with only 1 of the 3 algal phenotypes showed significantly higher feeding rates on the green than on either of the other 2 phenotypes (p < 0.001, 1-way ANOVA; Fig. 2). Post hoc analyses showed that consumption of each phenotype was significantly different from that

Fig. 1. Gracilaria cornea. Feeding by the amphipod Ampithoe ramondi (upper panel) and the majid crab Acanthonyx lunulatus (lower panel) on 3 phenotypes offered simultaneously (food choice). Bars represent means ± 1 SE. Analyses and significant groupings are from non-parametric Friedman’s tests followed by pair-wise comparisons

![Graph showing feeding rates of Ampithoe ramondi and Acanthonyx lunulatus on three Gracilaria cornea phenotypes](image1)

Fig. 2. Gracilaria cornea. Feeding by amphipods (upper panel) and crabs (lower panel) confined with 1 of 3 phenotypes (no-choice). Bars represent means ± 1 SE. Analyses and significant groupings are from 1-way ANOVA followed by Tukey-Kramer tests.
of the other 2 phenotypes. Under no-choice conditions, amphipod feeding rates were approximately 56% higher on the green than on the fine phenotype. Amphipods also consumed approximately 43% more of the fine phenotype than of the wild one (Fig. 2). Feeding rates under no-choice conditions for *Acanthonyx lunulatus* on the 3 algal phenotypes also showed significant differences (p = 0.045, 1-way ANOVA; Fig. 2). However, crabs consumed on average considerably more of the fine phenotype and similar amounts of both green and wild phenotypes in this experiment. Post hoc analyses revealed only a significant difference between crab feeding rates on the fine versus the wild phenotype, likely due to the high variance in consumption on both the fine and green phenotypes (Fig. 2).

When feeding rates for each herbivore replicate were related to the organic content of the algal pieces they were offered, contrasting patterns emerged. Amphipod feeding rates were strongly and inversely related to the organic content of the algae per wet mass (AFDM/WM) (p < 0.001, R² = 0.83; Fig. 3). This relation was also found when AFDM/DM was used, but it was slightly weaker (p < 0.001, R² = 0.81). Thus, individuals feeding on algae with lower organic content consumed more tissue than individuals feeding on algae with higher AFDM/WM per unit of time (i.e. compensatory feeding). In contrast, crabs showed no relation between feeding rates and algal AFDM/WM (p = 0.868, R² = 0.01; Fig. 3) or AFDM/DM (p = 0.554, R² = 0.02). It should be noted that, although using organic content per dry mass might lead to significant correlations, the animals studied here would seldom encounter algae as dry items. Thus, using AFDM/WM is a more ecologically realistic approach (Cruz-Rivera & Hay 2001).

**DISCUSSION**

Feeding preference and feeding rates of consumers differed strongly as a function of algal phenotype (Figs. 1 & 2), thus demonstrating significant intraspecific variation in susceptibility of an algal species to herbivory. Intraspecific variation in plant and animal traits has been invoked as an important determinant of direct and indirect species interactions, community assemblage, and ecosystem-level processes including invasion dynamics (Janzen 1979, Agrawal 2001, Albert et al. 2011, Violle et al. 2012).

Although less information is available for algae than for vascular plants, studies in marine systems have shown that differences in palatability can be marked between individuals of different populations (Bolser & Hay 1996, Taylor et al. 2003) or between individuals of the same population exposed to different environmental regimes (Renaud et al. 1990, Cronin & Hay 1996), life stages or sexes of the same species (Lubchenco & Cubit 1980, Slocum 1980, Thornber et al. 2006, Vergés et al. 2008), or morphotypes of the same microalga (Long & Hay 2006). Previous history of attack can also alter susceptibility of individuals when induced chemical defenses make those plants (Karban & Baldwin 1997) or algae (Toth & Pavia 2007, Van Donk et al. 2011) less palatable to natural enemies. In fact, the majority of studies documenting intraspecific variation in plant or algal susceptibility to grazing has focused on how biotic or abiotic factors induce or constrain the expression of...
chemical defenses (Hay 1996, Karban & Baldwin 1997, Paul et al. 2001, Agrawal 2005, Toth & Pavia 2007, Van Donk et al. 2011). For animals, induction of defenses has been well documented and can also lead to large differences in susceptibility to predators (Harvell 1990, Tollrian & Harvell 1999).

From this perspective, our data are uncommon in that we focused on constitutive, rather than induced traits, for a macroalga that is not known to produce defensive secondary metabolites against herbivores. Algae in this genus can produce hydrogen peroxide as an induced immune response against bacteria (Weinberger & Friedlander 2000, Potin 2008, Weinberger et al. 2010) and, in 1 species, induced eicosanoids have been shown to serve as chemical defenses against isopods (Nylund et al. 2011). However, no studies to date have addressed phenotypic defenses against isopods (Nylund et al. 2011). How- ever, no studies to date have addressed phenotypic variation of these activated mechanisms in Gracilaria; thus, their involvement in explaining our results for G. cornea, albeit intriguing, remain speculative.

In contrast with chemical defenses, the role of intraspecific differences in nutrient content modifying prey palatability is understood less well. The ash content of the 3 phenotypes used here, and concomitantly AFDM, differed significantly (Table 1). Previous studies have reported ash contents of Gracilaria cornea of between 24 and 39% dry mass (Robledo & Freile Pelegrín 1997, Orduña-Rojas et al. 2002). Our samples had ash contents of ca. 25, 29, and 52% dry mass for the wild, fine, and green phenotypes, respectively. Thus, our data overlap with previous ranges reported, but expand the intraspecific range of nutritional values for this seaweed.

Nutrient enrichment experiments on macroalgae (Boyer et al. 2004), phytoplankton (Meunier et al. 2012), and seagrasses (Goecker et al. 2005), and some studies on the effects of desiccation on intertidal algae (Renaud et al. 1990) have found that intraspecific differences in nutrient content can influence consumer food choice. In terrestrial systems intraspecific differences in foliar nutrients have also been linked to differences in herbivore choice, feeding rates, dispersal potential, and fitness (e.g. Lavoie & Oberhauser 2004, Huberty & Denno 2006, Chen et al. 2008). Studies have also linked organic content to differences in marine herbivore feeding rates when various algal species are compared (Stachowicz & Hay 1999, Cruz-Rivera & Hay 2001, Satka & Hay 2002). However, to our knowledge, intraspecific differences in nutritional quality of macroalgae have not been previously shown to mediate compensatory feeding as was observed for amphipods in this study (Figs. 2 & 3). Differences in organic content of the algae explained approximately 83% of the variance in feeding rates for the amphipods, but had no relation to crab consumption rates (Fig. 3). Terrestrial herbivores such as monarch butterflies Danaus plexippus are known to consume more when feeding on host plants that have been manipulated for low foliar nitrogen (Lavoie & Oberhauser 2004). However, for this and many studies using live foods, the effects of intraspecific differences in nutrients versus changes in secondary chemistry are difficult to disentangle.

In our experiments, the relative susceptibility of the algal phenotypes differed strongly when animals were provided the ability to choose among them. The fine phenotype was consumed significantly more by both grazers than any of the other phenotypes (Fig. 1). Nutrients alone could not explain these differences, and it is likely that structural differences acted primarily or in concert with nutritional quality.

In a previous study, Cruz-Rivera & Friedlander (2011) exposed 3 species of Gracilaria to the same species of amphipods and crabs used here. In choice experiments, it was found that thinner, finely branched, species (G. lemaneiformis and G. conferta) were consistently preferred to the coarse G. cornea wild type by both consumers. The authors hypothesized that the size of the chelae in Acanthonyx lunulatus hindered the manipulation of the thick fronds of G. cornea (wild). A similar phenomenon could be operating here, with the fine phenotype being the easiest to manipulate, and the intermediate to coarse green phenotype, in turn, being easier than the coarsely branched wild phenotype. In contrast, the mouth parts of the amphipods could readily slice through the thalli of different Gracilaria species (Cruz-Rivera & Friedlander 2011). For these amphipods, nutritional quality could be a stronger determinant of feeding behavior on algae that can be readily processed when alternatives are not present.

Nonetheless, concluding that structure was unimportant for amphipods would be misleading. Amphipods preferred significantly the finely branched phenotype in multiple-choice assays, despite the fact that this phenotype had lower AFDM than the wild type (Table 1). It is known that some amphipod species cue on the structural complexity of algae while selecting habitat (Hacker & Steneck 1990). Thus, Ampithoe ramondi could have been attracted to the higher complexity of the finely branching red strain, while its capacity for compensatory feeding would allow this amphipod to cope with the lower nutrient content of this phenotype. Other species in this amphipod genus are known to efficiently offset the fitness costs of feeding on lower quality diets through
compensatory feeding (Cruz-Rivera & Hay 2000, 2001).

The role of intraspecific differences in structure explaining variation in consumer–prey interactions is better understood for animals that can induce defensive structures such as spines or thicker shells upon attack (Harvell 1990, Tollrian & Harvell 1999). In some microalgae, nutrient limitation or grazing can induce morphological changes in cells and the production of thicker cell walls. These changes result in cells that are less susceptible to micrograzer digestion and cause significant losses in fitness to the consumers (reviewed in Van Donk et al. 2011). Morphology also influences ingestion of microalgae that grow as colonies or as individual cells (Long & Hay 2006, Van Donk et al. 2011). For macroalgae, reproductive tissues of Mazzaella flaccida that were more structurally complex were preferred by snails in food-choice assays, but when the same tissues were homogenized to maintain constant nutritional and chemical traits, this preference disappeared (Thornber et al. 2006). A few studies on plant–insect interactions have also demonstrated the importance of intraspecific differences in constitutive morphology mediating susceptibility to insects (Rudgers & Whitney 2006, Wise & Abrahamson 2008, Kawasaki et al. 2009).

Artificial selection has yielded a diversity of plant varieties and hybrids that can be readily grown and used for addressing fundamental questions in ecology. On the applied side, our findings are relevant to the selection of algae for aquaculture, such as Gracilaria, which is harvested for the production of agar (Buschmann et al. 2001, Friedlander 2008). Under culture conditions, small invertebrate consumers often reach high densities, resulting in losses in biomass production (Buschmann et al. 2001, Friedlander 2008). Selection of specific phenotypes that are herbivore resistant could ameliorate these problems.

From an ecological standpoint, this study adds to our knowledge of intraspecific variation in plant–herbivore interactions by focusing on phenotypic differences in nutritional quality and structure as algal traits affecting consumer feeding behavior. Our data suggest that, for communities in which these species overlap, the coarser phenotypes may be less susceptible to herbivores and could be more common than the finely branched phenotype. However, no field data on herbivory are available for Gracilaria cornea in its natural range, and, by focusing only on mesograzers, the community-wide effects of larger herbivores (e.g. fishes and urchins) on populations of this alga remain untested. Given that a number of agarophytes, including Gracilaria species, have now been established as important invaders around the world (Schaffelke et al. 2006, Schaffelke & Hewitt 2007, Williams & Smith 2007), the study of relations between phenotype and grazing susceptibility for aquacultured algae increases our potential to understand and predict biological invasions.

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