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FOOD AND SHELTER AS DETERMINANTS OF FOOD CHOICE BY AN HERBIVOROUS MARINE AMPHIPOD[1]

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Abstract. Because food and habitat are closely linked for small herbivores that live on plants, food choice in the field may be constrained by the need to choose plants that provide safe living sites. We investigated the importance of food value and refuge value in determining the plant utilization patterns of the herbivorous marine amphipod *Ampithoe longimana*. When offered a choice of five common seaweeds, this amphipod fed most readily on *Dictyota* and *Hypnea* and less readily on *Sargassum, Chondria,* and *Calonitophyllum.* Rates of feeding on the different seaweeds were unrelated to seaweed gross morphology, toughness, nitrogen, or protein content. When cultured on each of these seaweeds in the laboratory, amphipod survivorship was high on *Dictyota* (82%), intermediate (35 and 18%, respectively) on *Sargassum* and *Hypnea,* and low (0%) on the other seaweeds. Survivorship on the different diets was strongly correlated ($r = 0.930$) with algal protein content; however, neither protein content nor amphipod performance on the different diets was significantly related to feeding rates on those diets. Additionally, amphipods from the three seaweed species that produced some survivors did not differ in growth rate, fecundity, egg size, or age at first ovulation. Variance in survivorship, and related measures, among sibling groups of amphipods suggested that this amphipod population possessed heritable variation for performance on the different seaweed species.

In the field, abundance of *A. longimana* on the different species of algae was more clearly related to the preference of omnivorous fishes for these algae than to feeding rates of the amphipods when given those algae in the laboratory. *A. longimana* was more abundant on *Dictyota* and *Sargassum* (both unpalatable to omnivorous fishes), than on *Hypnea, Chondria,* and *Calonitophyllum* (all of which are palatable to fishes). During the season when omnivorous fishes were abundant, density of *A. longimana* increased on *Dictyota,* which is chemically defended from fishes, but decreased or remained unchanged on the seaweeds that are more palatable to fishes. Competition with other amphipods as a group did not appear to explain the distribution of *A. longimana* among seaweeds, since there were no negative correlations between *A. longimana* abundance and total amphipod abundance in any month. The lack of any consistent relationship between host-plant use in the field and either feeding preference or diet value, as measured by survivorship and reproduction, suggests that host-plant use by *A. longimana* may be strongly constrained by requirements for shelter from predation.

Key words: amphipods; Ampithoe longimana; Dictyota; *fitness; food choice; plant–herbivore interactions; predation refuge.*

INTRODUCTION

Food selection by animals is influenced both by food quality and by environmental constraints on feeding (Morse 1980, Lubchenco and Gaines 1981). In particular, the threat of predation has an important impact on habitat use and foraging in a variety of animals, often causing foragers to choose foods or foraging sites of lower quality in order to avoid predators (Sih 1982, Werner et al. 1983, Power 1984, Damman 1987, Holbrook and Schmitt 1988, Holomuzki and Short 1988). For phytophagous insects and small marine herbivores (mesograzers) that live on the plants they consume, food and habitat are closely tied, and the refuge value of a plant may be as important as its food value, or more so, in determining patterns of plant use (Price et al. 1980, Bernays and Graham 1988, Hay et al. 1989, 1990, Hay 1990).

Previous studies found that the herbivorous marine amphipod *Ampithoe longimana* fed preferentially on the brown seaweed *Dictyota dichotoma,* which was unpalatable to sympatric fishes (Hay et al. 1987, 1988*b*), and that, during seasons when predators of amphipods were abundant, other amphipod species declined precipitously, but *A. longimana* persisted on *Dictyota* (Duffy 1989). Moreover, the diterpene metabolites pachydictyol A and dictyol E, produced by *Dictyota,* deterred feeding by local omnivorous fishes but did not affect feeding by *A. longimana* at natural concentrations (Hay et al. 1987, 1988*b*). This and several similar examples (reviewed by Hay 1990) suggest that predation by fishes has driven many small grazing invertebrates to feed

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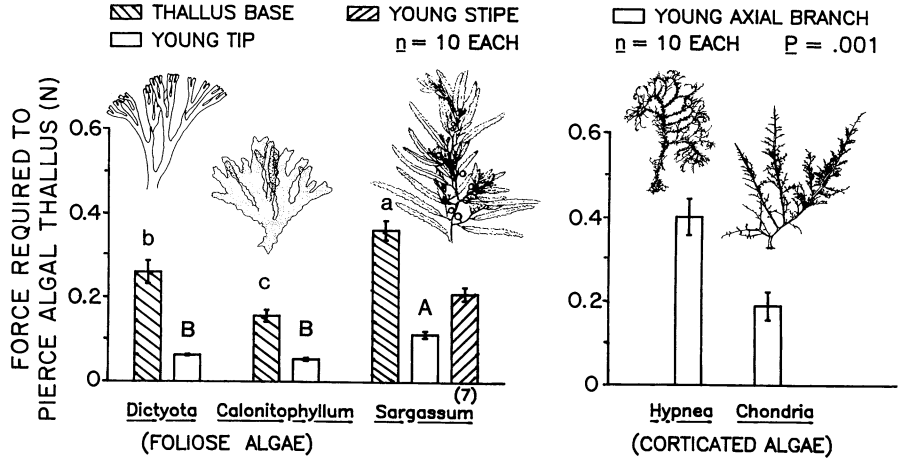

FIG. 1. Physical resistance (toughness) of five seaweeds to a piercing force perpendicular to the thallus surface. Bars represent means ± 1 SE. For the three flat-bladed species at left, toughness varied significantly with species ($P < .0001$) and thallus region (i.e., bases vs. tips, $P < .0001$) with no significant interaction ($P = .117$, two-way ANOVA). Letters in the graph at left show the results of separate ANOVAs, each followed by a Student-Newman-Keuls multiple-comparison test (on log-transformed data), for bases or tips. Species with bars marked by the same capital letter do not differ significantly ($P > .05$) in toughness of tips; lowercase letters distinguish species that differ significantly ($P < .05$) in toughness of basal tissue. The P value for the comparison between *Hypnea* and *Chondria* is from a t test. $n = 10$ for all samples except *Sargassum* stipes, for which $n = 7$.

and live on seaweeds that are chemically defended from, and thus not often visited by, fishes. However, previous studies have not addressed food value as an alternative hypothesis for plant choice by these grazers.

In this study, we examined feeding and fitness (survivorship, growth, and fecundity) of *Ampithoe longimana* on a suite of seaweeds in relation to their morphology, toughness, nutritional value, and palatability to omnivorous fishes. We asked the following questions: (1) How do amphipod feeding rates on different seaweed species relate to plant morphology, toughness, nitrogen content, protein content, and availability of alternative foods? (2) What are the consequences for amphipod growth and reproduction of eating different seaweeds, and are these fitness-related differences reflected in food choice? (3) Do field distributions of *A. longimana* among plants reflect food value and/or refuge value of the plants?

METHODS

The organisms

The herbivorous amphipod *Ampithoe longimana* is common in marine and estuarine habitats along the east coast of North America (Bousfield 1973). It lives in tubes that it constructs on plants and other substrates. We examined amphipod feeding on five species of seaweeds spanning a range of morphology and attractiveness to *Ampithoe longimana*. Seaweeds fell into several of the morphological categories, termed functional form groups, that Littler and Littler (1980) and Steneck and Watling (1982) suggest should differ in their physical resistance to grazing. The brown seaweed *Dictyota dichotoma* and the red seaweed *Calonitophyllum medium* are both flat-bladed (foliose) plants (Fig. 1) only a few cell layers thick. The cylindrical, branching red algae *Hypnea musciformis* and *Chondria dasyphylla* (corticated macrophytes) also form a morphologically similar pair (Fig. 1). The brown seaweed *Sargassum filipendula* is morphologically complex, bearing flattened fronds attached to a tough stipe (Fig. 1), and does not fit easily into any one functional form group. We concentrated on the fronds of this species because they comprise the greatest fraction of the plant's surface area, and thus its most productive photosynthetic tissue. Although functional form models predict that herbivores would graze foliose algae more easily than corticated macrophytes (Steneck and Watling 1982), previous work suggested considerable variance among species within each group in susceptibility to grazing by *A. longimana* (Duffy 1989). By comparing nutritional characteristics of, and amphipod responses to, algae in each of these morphological pairs and across morphological types, we hoped to separate the role of plant morphology from other factors in influencing amphipod food choice.

Amphipod feeding assays

To assess feeding preferences of amphipods among the five algae, we conducted both choice and no-choice feeding assays. We used ≈15 plants of each species, minimizing intraspecific variance in algal food quality between the assays by using cuttings from each plant in both choice and no-choice assays, and by conducting them simultaneously. Remaining portions of these same plants were used (1) for determining protein and nitrogen concentrations of each species, and (2) in an-

other choice assay in which plants were finely ground and incorporated into agar pellets (see description of agar assay in this section, below).

Amphipods were collected from algae in a shallow area of Bogue Sound, North Carolina, and held in buckets with seawater and algae for a few hours before the assays began. In the choice assay, amphipods were simultaneously offered approximately equal masses (85–114 mg) of each of the five seaweeds. One preweighed piece of each species was placed in a 10 cm diameter bowl filled with 150 mL of seawater, and 10 *Ampithoe longimana* were added to the bowl (i.e., ≈2 amphipods/100 mg algae). Fourteen replicate bowls received amphipods, and 11 bowls containing algae, but no amphipods, were used to estimate changes in algal mass due to factors other than herbivory. Assays were run at room temperature with ≈9 h of overhead fluorescent lighting per day. This was intended to approximate the lighting regime in the field. After 67 h, including two light/dark cycles, algae remaining in the bowls were blotted dry and weighed.

In the no-choice assay, 5 cm diameter cups were filled with 50 mL of seawater, and each received two *A. longimana* and only a single species of algae (85–122 mg). As in the choice assay, this resulted in a density of ≈2 amphipods/100 mg algae. For each algal species 15 replicate cups received amphipods and 10 control cups received no amphipods. Environmental conditions and source of amphipods were the same as for the choice assay. Amphipods were allowed to feed for 69 h before algae were removed and weighed.

In an attempt to experimentally remove the effect of plant physical structure on feeding, each seaweed species was freeze-dried, ground to a fine powder in a Wiley mill fitted with a 180-μm mesh sieve, and incorporated into physically identical agar pellets. The pellets were offered to amphipods in a feeding assay. This method was imperfect in that freeze-drying the plants may have resulted in several undesired changes, such as removing volatile compounds and coagulating proteins. Freeze-drying was used only after initial attempts to incorporate fresh algae were unsuccessful. The fresh algae could not be ground finely, and the consistency of the agar pellets differed considerably between algal species.

The agar assay used cuttings from the same plants used in the feeding assays described above in this section. All cuttings from a given species of plant were combined together and mixed thoroughly; this mixture was intended to achieve the mean chemical composition for that species. For each algal species, agar (0.36 g) was mixed into 20 mL of distilled water and brought to a boil. When this mixture had cooled to 55°C, the dried algal powder (0.72 g) was stirred in, and the mixture was poured into a 50 mm diameter Petri dish and allowed to gel. Dried algae added to the agar at 55°C retained their color; when added at higher temperatures some species were discolored, possibly indicating thermal degradation. Pellets were made by coring the cooled gel with a cork borer, and one preweighed pellet (61–117 mg) of each algal species was placed in a 5 cm diameter plastic cup with 50 mL of seawater and 10 *A. longimana.* Thus all five species were simultaneously available to the amphipods. The amphipods were allowed to feed for 46 h, after which remaining portions of each pellet were removed and weighed. Eighteen replicate cups received amphipods; seven cups received pellets but no amphipods and served as controls.

Measurement of plant toughness

To estimate the physical resistance of each seaweed species to being bitten (toughness), we measured the force required to pierce the thallus with a penetrometer consisting of an insect pin held point down in a narrow vertical sleeve, and supporting a light plastic cup in which a mass could be placed. The plant was clamped in place below the pin, and dry sand was added to the cup a few milligrams at a time until the pin pierced completely through the algal tissue. The sand in the cup was then weighed and added to the mass of the pin and cup to determine the force required to pierce the thallus. Measurements were made on 10 plants of each species. For the flat-bladed species *Dictyota, Calonitophyllum,* and *Sargassum,* we made measurements on both young tips (within 1 cm of the distal end of a young frond) and basal portions (the oldest unfouled region of the plant). For *Sargassum,* we also measured toughness of distal stipe tissue (within 4 cm of the plant's apex). For *Chondria* and *Hypnea,* the most distal parts of the plant were too thin for these measurements so we measured young axial branches where they were 1–1.5 mm wide.

Measurement of plant protein and nitrogen content

Protein concentrations in each algal species were measured colorimetrically with Coomassie Brilliant Blue (Bradford 1976). Although unreliable for absolute quantification of unknown proteins, this method is useful for establishing relative values, as was our purpose here (Davis 1988). Coomassie Blue is also considerably less susceptible than the commonly used Lowry method to interference by many substances likely to be present in whole tissue preparations (Davis 1988).

We measured protein concentration in samples of the same plants used in the feeding assays (collected in August 1988), except for *Calonitophyllum,* of which insufficient tissue remained after feeding assays for protein determination. Protein was also measured in samples of all five species collected in November 1987. Because all cuttings from a given seaweed species collected on the same date were combined and mixed (see description of agar pellet assay in *Methods: Amphipod feeding assays*), samples taken from any one of these mixtures estimate its mean protein concentration; however, variance among samples does not estimate variance among individual plants since plants were

pooled. Samples (6.27–6.83 mg each, $n = 4$ for each species) of the powdered dry tissue prepared for the agar pellet assay were further ground in 1.0 mL of 1 mol/L NaOH and incubated in microcentrifuge tubes for 18–21 h. Following incubation, samples were centrifuged until all visible particulate material had settled (at least 5 min), and 100 μL of the supernatant was added to 5 mL of protein-binding reagent (acidified Coomassie Brilliant Blue G-250; Bradford 1976). After the dye-binding reaction had proceeded for 8–25 min (Kochert 1978), absorbance at 595 nm was read on a Bausch and Lomb Spectronic 2000 spectrophotometer. Absorbance values were converted to protein concentrations using a regression derived from a bovine serum albumin standard.

Total nitrogen content of each algal species was measured by combustion. Samples (7.65–14.40 mg each, $n = 4$ for each species) from the same freeze-dried, ground plants (collected in August 1988) used in the feeding assays and protein determinations were combusted in a Carlo Erba 1500 CNS analyzer using acetanilide as a standard.

Amphipod cultures

To examine the consequences of different algal diets for amphipod fitness, we raised *Ampithoe longimana* from birth to sexual maturity on each of the five seaweed species. Ovigerous female amphipods were collected from algae at Lennoxville Point, near Beaufort, North Carolina, USA (34°42′ N, 76°41′ W). The amphipods were placed individually in 5 cm diameter plastic cups with small pieces of mixed algae and ≈50 mL of seawater, and held until newborn amphipods left the mother's brood pouch. Within 48 h of leaving the brood pouch, each juvenile amphipod was placed in a separate cup with a small (<100 mg) piece of 1 of the 5 seaweed species and ≈50 mL of seawater. Forty individual amphipods, consisting of 8 siblings from each of 5 mothers (i.e., 5 families), were started on each seaweed species. Another 40 amphipods (8 siblings from each of 5 mothers) were placed in individual cups without algae and served as controls. Different families were used for each seaweed species (i.e., amphipods on different diets were unrelated). To avoid trapping the very small juvenile amphipods in the surface tension of the water, the seawater in the cups was not aerated.

Amphipods were examined every other day for evidence of feeding and death. Food was added as needed, and food and water were changed every 10–15 d. After the first female in these assays produced eggs, amphipods were examined every day. Females were preserved on the day of their first ovulation, and the eggs were counted. We haphazardly picked five eggs from each female and measured each along its longest dimension; all eggs were measured if the clutch contained fewer than five eggs. Individual females were considered replicates for analysis of egg size, using the mean size of eggs in a female's clutch as the datum for the analysis. Males were preserved at age 36 d. Survivorship was calculated by subtracting only natural deaths from the initial cohort; thus it was assumed that ovulating females, which were preserved at first ovulation, would have survived to the end of the experiment (day 36). For comparing sizes of the amphipods, we measured the distance from the base of the first antenna to the posterodorsal edge of the third body segment (hereafter called "anterior length") with an ocular micrometer. Because amphipods flex their bodies to varying degrees when preserved, total length was difficult to measure. Anterior length appeared to be relatively insensitive to differences in body flexion.

Field sampling of amphipods

To assess distribution of amphipods among the five seaweed species, plants and their associated faunas were sampled monthly at Radio Island jetty near Morehead City, North Carolina, USA (34°42′ N, 76°41′ W) from May through September 1988. On each date we sampled five plants of each species; in most cases these were whole individual thalli but in some cases (mostly large *Sargassum* plants) only the distal portion of a plant was collected. Plants were pulled from the substrate at depths of 0.5–1.5 m and immediately (within a few seconds) sealed underwater in individual plastic bags. We attempted to collect plants that were relatively free of epiphytes. Samples were preserved in formalin, and associated animals were removed by repeatedly washing the plant with tapwater and pouring the water through a 163-μm mesh sieve. In most cases, all amphipods retained by the sieve were counted and identified to species. For *Sargassum* samples collected in May, high amphipod densities necessitated subsampling. In these cases, all amphipods were removed from the plant as above, and suspended in 300 mL of tapwater. A subsample (7–10% of the original) was then removed with a Stempel pipette and sorted. The sorted subsamples contained 401–944 amphipods each. Each plant was weighed after being spun in a salad spinner to remove excess water. Amphipod densities are expressed as a function of plant wet mass.

Statistical analysis

For comparing means of three or more treatments (except in the feeding choice assay, see *Results*), we used ANOVA, followed by the Student-Newman-Keuls (SNK) test, after checking for heteroscedasticity with Cochran's test. When Cochran's test found that variances were significantly different, we transformed the data by $\log x$, or by $\sqrt{x}$ in the case of amphipod abundance data from field samples. In the few cases where transformation failed to achieve homogeneous variances, we proceeded with ANOVA on the transformed data despite persistent variance heterogeneity, since ANOVA is considered very robust to variance heterogeneity (Scheffé 1959, Underwood 1981). Use of rank

TABLE 1. Results of feeding assays with the amphipod *Ampithoe longimana*. Amphipods were offered five species of seaweeds either simultaneously (choice assay), singly (no-choice assay), or simultaneously after seaweeds were freeze-dried, finely ground, and suspended in agar pellets (agar assay).

Assay / Alga	Algal mass change (mg)		P*
	Amphipods	No amphipods	
Choice assay	(n = 14)	(n = 11)	
Dictyota dichotoma	−43.2 ± 6.5	−1.9 ± 0.8	<.0001(†)
Hypnea musciformis	−37.4 ± 4.5	1.1 ± 0.8	<.0001(†)
Sargassum filipendula	−1.1 ± 1.6	5.5 ± 1.3	.006
Chondria dasyphylla	−9.4 ± 2.0	−3.4 ± 1.1	.016(†)
Calonitophyllum medium	−13.6 ± 2.2	−10.5 ± 1.9	.309
No-choice assay	(n = 15)	(n = 10)	
Dictyota dichotoma	−23.9 ± 4.4	−3.3 ± 1.7	.0004(†)
Hypnea musciformis	−27.7 ± 2.5	−4.7 ± 3.2	<.0001
Sargassum filipendula	−11.2 ± 1.6	−1.0 ± 1.8	.0004
Chondria dasyphylla	−20.2 ± 3.9	−5.5 ± 2.0	.003(†)
Calonitophyllum medium	−16.2 ± 2.2	−14.4 ± 2.0	.576
Agar assay	(n = 18)	(n = 7)	
Dictyota dichotoma	−51.3 ± 3.0	−3.3 ± 0.8	<.0001(†)
Hypnea musciformis	−32.6 ± 1.8	−5.0 ± 0.9	<.0001(†)
Sargassum filipendula	−37.8 ± 2.5	−3.6 ± 0.8	<.0001(†)
Chondria dasyphylla	−34.0 ± 2.9	−1.7 ± 0.9	<.0001(†)
Calonitophyllum medium	−29.7 ± 2.9	−2.0 ± 1.1	<.0001(†)

* Significance of grazing on each species was determined by comparing mass change of the seaweed in the presence vs. absence of amphipods using t tests, or t tests for unequal variance (SAS 1985) in cases marked by (†).

tests such as Kruskal-Wallis was rejected because these assume equal variances as well (Underwood 1981).

RESULTS

Amphipod feeding preferences

Ampithoe longimana fed on all seaweeds except *Calonitophyllum* (Table 1). When given a choice of seaweeds, *A. longimana* consumed primarily *Dictyota* and *Hypnea*; grazing on the other three species was minimal (Fig. 2A). These apparent feeding preferences were obscured in the absence of choice (Fig. 2B). We did not analyze differences in feeding rate among algal species in these assays because their designs were incompatible with the assumptions of ANOVA (Peterson and Renaud 1989).

To assess whether availability of alternative foods affected feeding rates, we compared grazing losses of each alga between the two assays. This involved a separate two-way ANOVA for each algal species with factors being "assay" (choice vs. no-choice) and "amphipods" (present vs. absent). A significant interaction term indicated that grazing rate (i.e., the difference between amphipod and no-amphipod treatments) differed between the two assays. Significant interaction terms were found only for *Hypnea* (P = .021), with a trend (P = .100) toward significance for *Dictyota*, implying that these two species were grazed more in the choice assay, where the total number of amphipods per replicate was higher (n = 10), and the amphipods were often seen to aggregate on *Hypnea* and *Dictyota*, than in the no-choice assay (Fig. 2A, B). Feeding rates in the choice and no-choice assays were similar for the other three species ($P \geq .267$ for interaction terms).

There was no correspondence between amphipod feeding preference and functional form groups of algae. Of the two foliose species, *Dictyota* was heavily grazed while *Calonitophyllum* was not eaten (Table 1, Fig. 2A). Of the corticated species, *Hypnea* was highly preferred in the choice test while *Chondria* was little grazed (Table 1, Fig. 2A). When freeze-dried algae were ground and suspended in agar pellets, *A. longimana* preferred *Dictyota* pellets over all others (Fig. 2C). Because choice tests cannot be analyzed by ANOVA (see Peterson and Renaud 1989), we analyzed the agar assay as follows. An ANOVA on the amphipod-free control replicates (n = 7 for each algal species) showed no significant difference in mass change of control pellets among the five species (P = .108) so controls were ignored in further analysis. In each replicate exposed to amphipods, mass changes of the five pellets were ranked, the frequency of being ranked highest was computed for each algal species, and these frequencies were analyzed with G tests (see Hay et al. 1988*a*, Peterson and Renaud 1989). *Dictyota* was preferred significantly more often than the other four species ($P < .05$); there were no significant differences among the latter ($P > .05$; Fig. 2C).

Plant toughness

Physical resistance of the two foliose seaweeds, *Dictyota* and *Calonitophyllum*, and the morphologically complex *Sargassum*, varied as much among different regions of individual thalli as among different species (Fig. 1). There were highly significant differences in toughness, both among the three species ($P < .0001$) and between thallus regions (i.e., base vs. tip, $P <$

.0001), with no significant interaction between species and thallus region ($P = .117$, two-way ANOVA on log-transformed data). Separate one-way ANOVAs, followed by SNK, for the two thallus regions showed that young tips of *Dictyota* and *Calonitophyllum* were equally resistant to piercing force while those of *Sargassum* were significantly tougher ($P < .05$). Resistance of basal tissue was highest in *Sargassum,* intermediate in *Dictyota,* and lowest in *Calonitophyllum* ($P < .05$; Fig. 1).

The two corticated seaweeds, *Hypnea* and *Chondria,* are generally thicker than the flattened species (J. E. Duffy, *personal observation*), and their cylindrical axes appeared to stretch somewhat more when pressure was applied to the penetrometer. Because this stretching might have influenced the estimate of thallus toughness for *Hypnea* and *Chondria,* they were analyzed separately from the other three species. *Hypnea* was significantly more resistant to piercing force than *Chondria* ($P = .001$, t test; Fig. 1).

There was no significant correlation between toughness (using values for thallus base in *Dictyota, Calonitophyllum,* and *Sargassum*) and estimated amount eaten in the choice assay ($r = 0.501$, $P = .390$). However, amphipod feeding preferences may have been influenced by some aspect of algal physical structure that was changed by drying and grinding the plants for the agar assay, since the amounts of each species eaten in the choice assay vs. the agar assay were not significantly correlated ($r = 0.480$, $P = .414$).

Plant protein and nitrogen content

In samples of the plants collected in August 1988 and used in feeding assays, protein concentration was highest in *Sargassum* and *Dictyota,* intermediate in *Hypnea,* and lowest in *Chondria* (ANOVA followed by SNK tests; Fig. 3). Insufficient material was available for measuring *Calonitophyllum.* Surprisingly, total nitrogen concentrations in samples from the same plants were inversely related to protein concentration ($r = -0.96$, $P < .05$): nitrogen was highest in *Chondria* and *Hypnea,* intermediate in *Dictyota,* and lowest in *Sargassum* (ANOVA followed by SNK tests on log-transformed data; Fig. 3). Samples of the same four algae plus *Calonitophyllum,* all collected in November 1987, showed a similar rank order in protein content except that *Dictyota* was significantly higher than *Sargassum.* Protein content of *Calonitophyllum* was similar to that of *Hypnea* (Fig. 3). Using data from these November 1987 samples, there was no significant correlation between algal protein content and feeding rate in the choice assay ($r = 0.427$, $P = .474$).

Dietary effects on amphipod fitness

Survivorship of *Ampithoe longimana* differed greatly among algal diets (Fig. 4). Number of survivors dropped precipitously between days 3 and 7 on all diets (in-

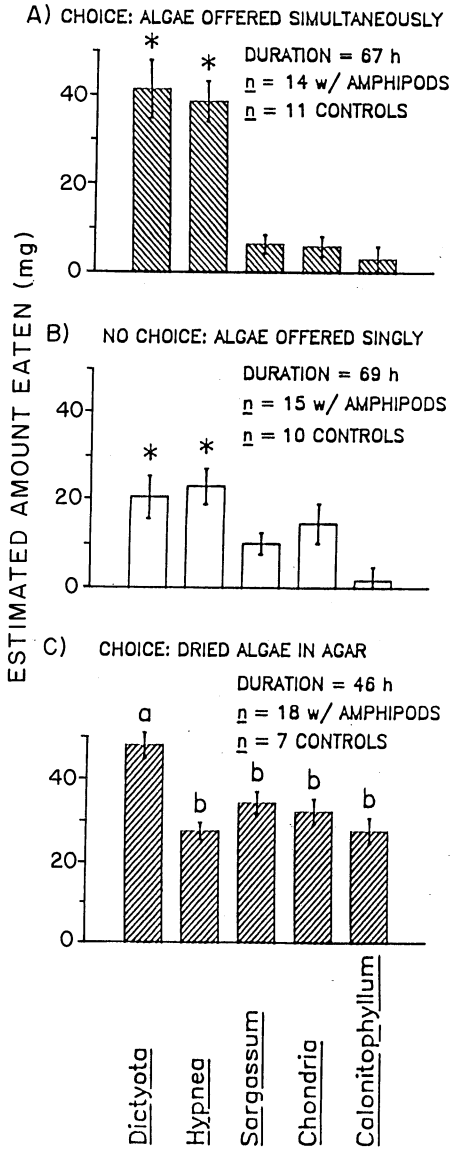

FIG. 2. Estimated grazing by the amphipod *Ampithoe longimana* on five seaweed species when seaweeds were offered (A) simultaneously, (B) singly, or (C) simultaneously as physically identical pellets produced by suspending freeze-dried, finely ground algae in agar. All foods were available in excess. Bars represent means ± 1 SE. Estimated amount eaten equals mean mass change in replicates with amphipods minus mean mass change in control replicates without amphipods (see Table 1); SE of this estimate is calculated as the SE of the difference between two means (Zar 1974). * indicates a significant ($P = .021$ for *Hypnea*) or nearly significant ($P = .100$ for *Dictyota*) difference in grazing between the choice and no-choice assays (parts A and B, respectively) for that species, as determined by a separate two-way ANOVA for each algal species (see *Results: Amphipod feeding preferences* for details). Species with the same letter in (C) do not differ significantly in their frequency of being ranked highest in grazing loss ($P > .05$, G tests).

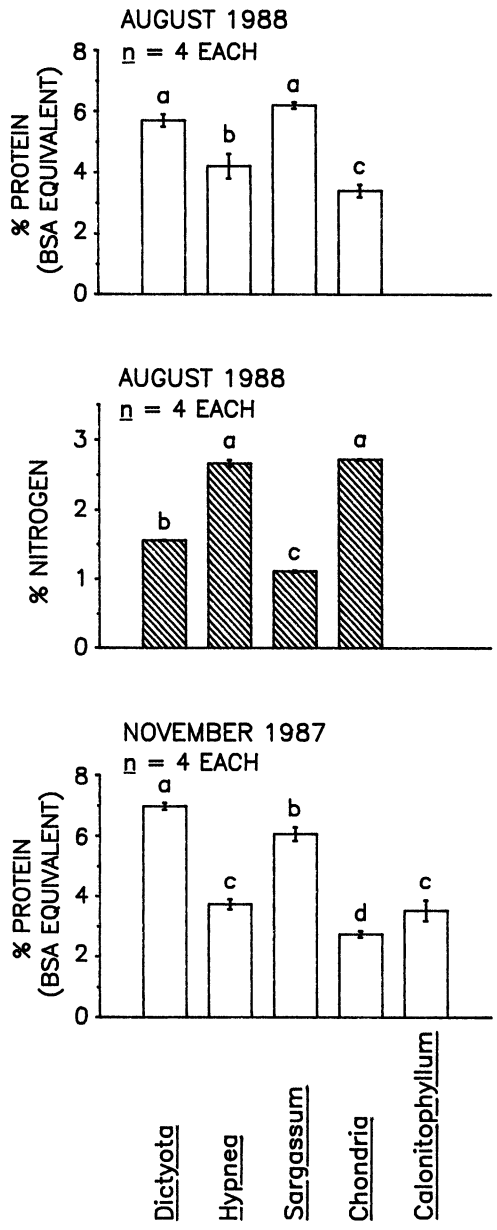

FIG. 3. Protein (as bovine serum albumin equivalent) and total nitrogen concentrations in five seaweeds. August 1988 samples were taken from the same plants used in feeding assays (Fig. 2) after all plants of a given species were pooled and mixed thoroughly. Thus variance in these measurements reflects variance inherent in sample preparation and analysis rather than variance among individual plants. Insufficient *Calonitophyllum* remained after the August 1988 feeding assays for these measurements. Material for the November 1987 samples was also pooled and mixed for each species. Data were analyzed by ANOVA and SNK on raw (protein) or log-transformed (nitrogen) data. Symbols as in Fig. 1.

cluding no food) except *Dictyota* and *Sargassum*; on day 7, number of survivors on these two species was significantly higher ($P < .05$) than on all other species, and there were no significant differences among these other species (G tests). Survival to adulthood was significantly higher (82%) on *Dictyota* than on any other species ($P < .05$, G tests). Survival on *Sargassum* (35%) and *Hypnea* (18%) was intermediate, significantly lower than on *Dictyota,* but significantly higher than on the other diets. No amphipods survived to adulthood on *Calonitophyllum, Chondria,* or in the absence of food (Fig. 4). Age at death of amphipods on *Chondria* (mean ± 1 SE = 6.4 ± 0.5 d) or *Calonitophyllum* (5.5 ± 0.3 d) did not differ significantly from amphipods without access to food (5.3 ± 0.2 d, $P = .144$, ANOVA on log-transformed data). Few individuals in the *Calonitophyllum* and *Chondria* treatments produced feces during the first few days; it is therefore likely that these animals starved. On the other three diets, feces were visible when cultures were first checked (day 3).

Algal protein content, measured in samples from November 1987, was strongly correlated with amphipod survivorship both at day 7 ($r = 0.972$, $P = .006$) and at adulthood ($r = 0.930$, $P = .022$).

Other than survivorship, none of the fitness components we measured differed significantly among surviving amphipods on the three algal diets that produced survivors (Fig. 5). These included growth rate ($P = .576$, ANOVA on log-transformed data), age at first ovulation ($P = .322$, ANOVA), number of eggs per female ($P = .793$, ANOVA), and mean size of eggs ($P = .194$, ANOVA; Fig. 5). There was no correlation between feeding rate in the choice assay and survivorship on the five seaweeds ($r = 0.663$, $P = .226$).

Survival among the five families (groups of siblings) of *A. longimana* raised on *Dictyota* was uniformly high ($P > .900$, G test); it was uniformly low among families on *Hypnea* ($P > .750$, G test, Table 2). There were, however, significant differences in survival among families raised on *Sargassum* ($.050 > P > .025$, G test), and significant differences in age at death among fam-

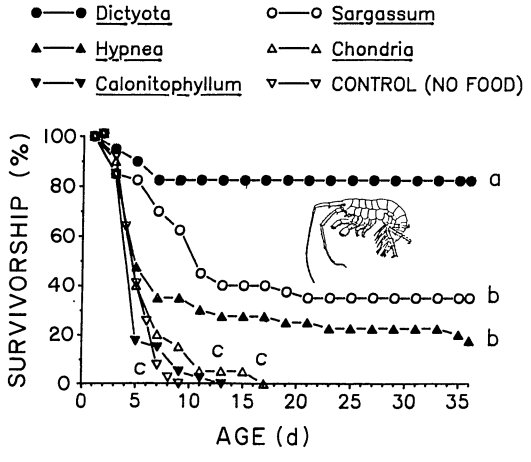

FIG. 4. Survivorship of *Ampithoe longimana* on five algal diets. Forty newborn (<48 h old) amphipods, each in a separate container, were initiated on each diet. Identical letters at the end of survivorship curves indicate that numbers of survivors on day 36 did not differ significantly ($\alpha = 0.05$, G tests) among those diets.

ilies raised on *Hypnea* ($P < .001$, ANOVA on log-transformed data). For those diets that produced no survivors, there were significant differences in age at death among families raised on *Calonitophyllum* ($P = .011$, ANOVA on log-transformed data) but not on *Chondria* ($P = .871$, ANOVA) or in the absence of food ($P = .261$, ANOVA). Growth rate differed significantly among amphipod families raised on *Dictyota* ($P = .008$, ANOVA), but not on *Sargassum* ($P = .770$, ANOVA). There were no significant differences in age at first ovulation, number of eggs per female, or mean egg size among families raised on *Dictyota* or *Sargassum* (Table 2).

Amphipod distribution and seasonality in the field

Abundance of *Ampithoe longimana* differed considerably among the five seaweed species (Fig. 6). To address the hypothesis that *A. longimana* preferentially associates with seaweeds that are low-preference foods for omnivorous fishes, the five algae were divided into a group of species that are low-preference foods for fishes (*Dictyota* or *Sargassum*) and a group of species preferentially eaten by fishes (*Hypnea, Chondria,* and *Calonitophyllum*; see Hay et al. 1987, 1988*b*). Similarly, the five monthly collections were lumped into an "early summer" group (May and June), when fish are relatively small (Adams 1976, Nelson 1979) and are just beginning to feed on amphipods (Stoner 1980), and a "late summer" group (July, August, and September), when fish are larger and feed on algae and amphipods, and predation pressure on amphipods appears much higher. *A. longimana* was significantly more abundant ($P < .0001$) on the group of species that are low-preference for fishes, and there was a strong trend ($P = .051$) toward greater abundance in late summer, with no significant interaction ($P = .818$) between algal group and time period (two-way ANOVA on square root transformed data). Separate one-way ANOVAs followed by SNK tests for each month revealed that *A. longimana* abundance was significantly ($P < .05$) greater on *Sargassum* than on all other species in May and July, and significantly greater on *Dictyota* than on all other species in August (Fig. 6). In September, there was a nonsignificant ($P = .110$) trend toward greater abundance of *A. longimana* on *Dictyota* than on other species. In June, there were no significant differences among algal species (Fig. 6).

In contrast to the pattern for *A. longimana,* total abundance of amphipods (i.e., all species combined; Fig. 6) did not differ significantly between algae that were high-preference vs. low-preference foods for fishes ($P = .846$) and significantly decreased between early and late summer ($P < .0001$), also with no significant alga vs. time interaction ($P = .322$, two-way ANOVA on square root transformed data). In June, total abundance of amphipods was higher on *Sargassum* and *Hypnea* than on other species, and in September, total abundance was higher on *Chondria* than on *Dictyota*

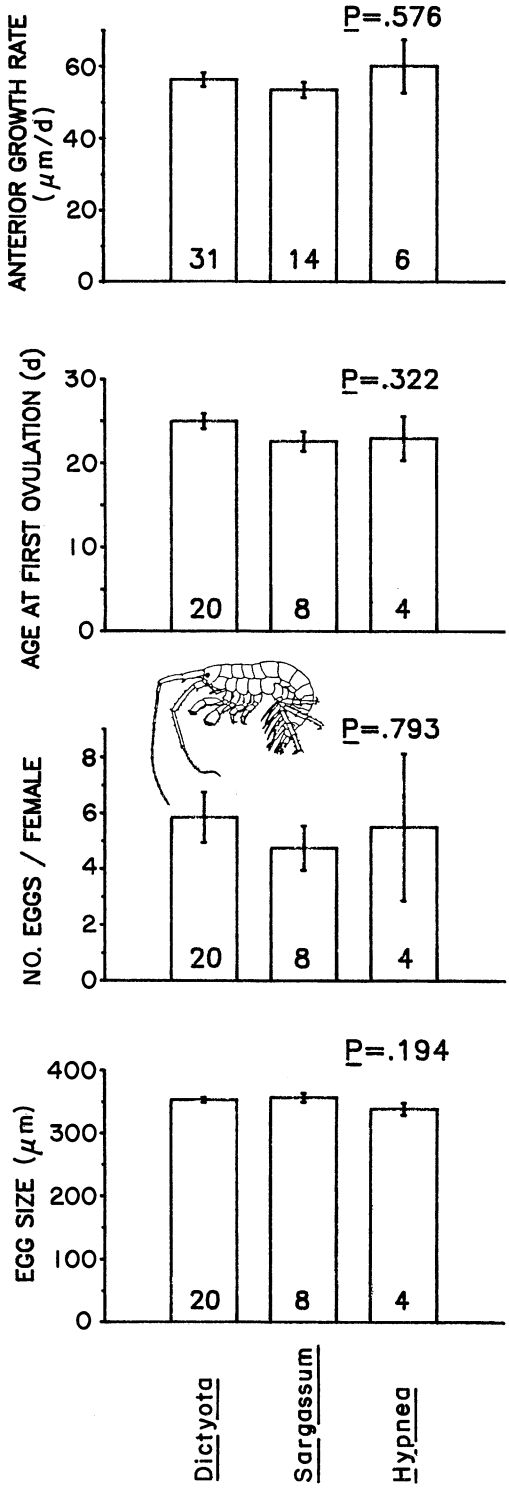

FIG. 5. Fitness components of *Ampithoe longimana* on the three algal diets that produced surviving adults. Anterior growth rate = anterior length (head plus first three body segments)/age in days. Numbers at the base of each bar are sample sizes. *P* values are from ANOVAs.

TABLE 2. Tests of among-family differences in fitness components for *Ampithoe longimana* raised on each of five algal diets.* The initial cohort of 40 amphipods on each diet consisted of eight siblings from each of five mothers (i.e., five families). Amphipods on different diets were unrelated.

Diet alga Fitness component	Test statistic	P
Dictyota dichotoma (20♀, 11♂ survivors)		
Survivorship (5 families)	$G = 1.02$	>.900
Growth rate (5 families)	$F = 4.46$‡	.008
Age at first ovulation (5 families)	$F = 2.35$	.101
Number of eggs/female (5 families)	$F = 0.99$	.441
Egg size (5 families)	$F = 1.17$	.365
Sargassum filipendula (8♀, 6♂ survivors)		
Survivorship (5 families)	$G = 10.54$	$.05 > P > .025$
Age at death (5 families)	$F = 0.80$	.541
Growth rate (5 families)	$F = 0.38$	.770
Age at first ovulation (3 families)	$F = 0.03$	.971
Number of eggs/female (3 families)	$F = 0.20$	.827
Egg size (2 families)	$t = 2.18$	.117
Hypnea musciformis (4♀, 3♂ survivors)		
Survivorship (5 families)	$G = 1.89$	>.750
Age at death (5 families)	$F = 8.89$†	<.001
Chondria dasyphylla (0♀, 0♂ survivors)		
Age at death (5 families)	$F = 0.31$	.871
Calonitophyllum medium (0♀, 0♂ survivors)		
Age at death (5 families)	$F = 3.82$†	.011
Controls (no food) (0♀, 0♂ survivors)		
Age at death (5 families)	$F = 1.38$	.261

* Only *Dictyota* and *Sargassum* produced enough survivors for analyses of components other than survivorship and age at death. Number of families included in each analysis is listed in parentheses after the fitness components; analyses other than survivorship included all families that produced more than one survivor (or female survivor for the fecundity-related components).

‡ Indicates that log transformation failed to reduce variance heterogeneity, so ANOVA was run on untransformed data.

† Indicates that data were log transformed.

($P < .05$, ANOVA and SNK; Fig. 6). There were no significant differences in total amphipod abundance among algal species in May, July, or August (Fig. 6). *A. longimana* comprised a relatively small proportion of total amphipods; abundant species were *Caprella penantis, Jassa falcata, Ericthonius brasiliensis,* and *Stenothoe* sp., which together made up 93% of total amphipods.

There were no significant negative correlations between *A. longimana* abundance per sample and total amphipod abundance per sample in any month ($P \geq .296$ for each of the 5 mo). This suggests that direct competition with other amphipods as a group is unlikely to explain observed differences in *A. longimana* abundance among algal species.

DISCUSSION

Several factors have been hypothesized or demonstrated to affect food choice in marine herbivores. These include seaweed secondary chemistry (Hay and Fenical 1988), protein concentration (Horn and Neighbors 1984), toughness or physical resistance (Littler and Littler 1980, Steneck and Watling 1982, Steneck 1983), gross morphology (Hay 1981, Steneck and Watling 1982, Steneck 1986), and the herbivore's susceptibility to predation when feeding on specific seaweeds (Hay 1990). Because food and habitat can be tightly coupled for small herbivores such as certain insects and small marine invertebrates that live on the plants they consume, the value of a plant as refuge from physical stresses and predation may be especially important in the evolution of host-plant use in these animals (Price et al. 1980, Strong et al. 1984, Hay et al. 1987, 1989, 1990, Bernays and Graham 1988, Hay 1990).

In this study we found that the amphipod *Ampithoe longimana* was most abundant on two brown seaweeds, *Dictyota dichotoma* and *Sargassum filipendula,* which have previously been shown or suggested to provide especially effective refuge from fish predation (Hay et al. 1987, 1988*b*, Holmlund et al. 1990). Although *A. longimana* fed on *Hypnea* as readily as on *Dictyota,* and fed preferentially on *Hypnea* over *Sargassum* (Fig. 2), *A. longimana* rarely occurred on *Hypnea* in the field. *Hypnea* is a preferred food of local omnivorous fishes (Hay et al. 1987, 1988*b*), and amphipods on *Hypnea* appear to be at greater risk of predation than those on seaweeds that are less palatable to fishes (Holmlund et al. 1990). The lack of any consistent relationship between host-plant use (Fig. 6) and either feeding preference (Fig. 2) or diet value for survivorship and re-

production (Figs. 4 and 5) suggests that host-plant use by *A. longimana* may be strongly constrained by requirements for shelter from predation.

Food value of plants

Dictyota was the preferred food of *A. longimana* in this study (Fig. 2A) and in others (Hay et al. 1987, Duffy 1989). Chemistry may be a proximate reason for this preference since *A. longimana* grazed *Dictyota* preferentially in the agar pellet assay (Fig. 2C), where physical consistency of the five diets was identical. Protein also may have affected *A. longimana*'s preference for *Dictyota,* since this alga and *Sargassum* had the highest protein contents of the five species (Fig. 3). In long-term feeding assays, the survivorship of *A. longimana* was also higher on *Dictyota* than on any other species tested (Fig. 4).

Plant toughness and morphology have traditionally been considered important in limiting the ability of small herbivores such as amphipods to feed on macroalgae (Brawley and Adey 1981, Steneck 1983), though several amphipods eat large seaweeds, sometimes in preference to microalgae (Duffy 1990). We used several approaches to assess the importance of seaweed physical structure in amphipod feeding. The reduced feeding selectivity in the agar pellet assay may indicate that some aspect of plant physical structure affected amphipod feeding. However, the results of this assay are difficult to interpret in light of the chemical changes likely to have been caused by freeze-drying. More importantly, feeding rates were unrelated to plant toughness or gross morphology. In fact, toughness varied little among seaweed species that spanned three functional form groups, and there was as much or more variation in toughness among regions of a single thallus as among similar regions in different species (Fig. 1).

The penetrometer we used to estimate plant toughness has a larger point, and may impinge on the plant more vertically, than an amphipod mandible. Such differences could produce misleading results (Padilla 1985). However, for algae with flattened thalli such as *Dictyota, Calonitophyllum,* and the fronds of *Sargassum,* amphipods usually begin grazing at the edge of the thallus such that the mandibles appear to impinge on the thallus surface at a high angle. Thus the vertical orientation of the pin in the penetrometer may reasonably approximate the action of an amphipod mandible on such plants. For the cylindrical axes of *Hypnea* and *Chondria,* the angle is probably further from perpendicular and our penetrometer may be less accurate. However, this seems unlikely to change the relative toughness of the latter two species, which are morphologically similar.

Regardless of the accuracy of the toughness data, our results demonstrate that the morphological classes of algae suggested by some workers to differ in physical resistance to grazing do not differ in susceptibility to grazing by amphipods. This result is somewhat unexpected; because of their small size, amphipod mouthparts might be expected to be weaker than those of larger herbivores, and thus especially sensitive to the physical structure of their algal food.

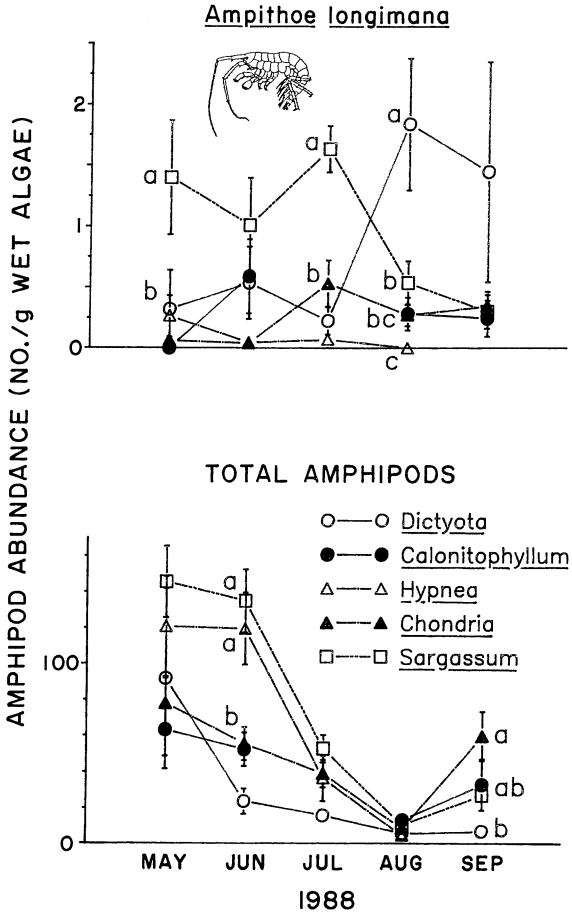

FIG. 6. Abundances of *Ampithoe longimana* and of total amphipods (all species combined) on five species of seaweeds at Radio Island Jetty, North Carolina, USA during summer 1988. Each symbol represents the mean ± 1 SE of five plants (except *Hypnea* in July, $n = 3$). Means of zero (i.e., symbols on the x axis) indicate that the plant was sampled and no *A. longimana* were present; absence of a symbol in a given month means that the plant was not present and thus not sampled (e.g., *Calonitophyllum* in July). Means with the same letter in a given month do not differ significantly ($P > .05$, ANOVA with SNK on square root transformed data); a letter above a group of closely spaced means (e.g., b in May, top graph) indicates that these means are not significantly different from one another. Absence of letters indicates no significant difference among seaweed species during that month (ANOVA). For further statistical analysis of these data, see *Results: Amphipod distribution and seasonality in the field.*

Usable nitrogenous compounds (proteins, amino acids, and their derivatives) are the limiting nutrient for many herbivores (Mattson 1980, White 1984). In this study, as in previous ones (Carefoot 1967, Nicotri 1980, Robertson and Lucas 1983), nitrogen content was unrelated to food preference, presumably because crude nitrogen content is not closely related to protein con-

centration in algae (Fig. 3; Horn and Neighbors 1984). We are unaware of any other study showing an inverse correlation between protein and nitrogen. Since protein is higher, and nitrogen lower, in the two brown algae (*Dictyota* and *Sargassum*) than in the two red algae studied (*Hypnea* and *Chondria*; Fig. 3), the inverse correlation may be an artifact of different allocation of nitrogen to protein and nonprotein compounds in these two taxonomic groups and the small number of species measured. It is unclear what form the nonprotein nitrogen takes in these plants.

Protein content was strongly correlated with amphipod survivorship, especially during the 1st wk of life, in accordance with White's (1985) suggestion that availability of nitrogenous compounds is especially critical during the early life of herbivores. Surprisingly, despite the apparent importance of protein to amphipod fitness, food choice was rather weakly related to nutritional value of the plants, as determined by protein content. More importantly, feeding preferences bore little relationship to survivorship of amphipods raised on each species. Similarly, for reasons that remain obscure, many phytophagous insects normally accept (i.e., oviposit on) a narrower range of plants than those on which they are capable of growing (Thompson 1988).

Because our culture data do not distinguish between differences in feeding rates vs. physiological differences in development when feeding on different plants, we cannot determine with certainty the cause of survivorship differences. However, the strong correlations of amphipod survivorship with algal protein content suggest that protein availability is important for this herbivore. Amphipods fed *Calonitophyllum* and *Chondria* probably starved since few of these individuals produced feces. Amphipods on the other three diets did in fact feed and, at least for *Hypnea* and *Dictyota,* it is unlikely that survivorship differences result from different feeding rates, since these seaweeds were eaten at similar rates in feeding assays (Fig. 2).

The nutritional quality of a plant depends not only on how closely its nutrient composition matches a herbivore's needs, but also on how secondary metabolites interfere with its digestion or physiology (Rosenthal and Janzen 1979, Robbins et al. 1987, Bernays et al. 1989). The high survivorship of *Ampithoe longimana* on *Dictyota* (Fig. 4) suggests that pachydictyol A and related secondary metabolites produced by *Dictyota* in North Carolina (Hay et al. 1987) have no strong detrimental effects on *A. longimana.*

Refuge value of plants

Seaweeds provide habitat as well as food for small herbivorous invertebrates. Just as plant species differ in food value, they also differ in longevity (and thus habitat stability for phytal fauna), provision of living space (Hacker and Steneck 1990), and protection from predators (Stoner 1982, Coull and Wells 1983, Edgar 1983, Hay et al. 1989, 1990, Holmlund et al. 1990). Since predation is often the most important factor regulating densities of phytal invertebrates (Van Dolah 1978, Young and Young 1978, Nelson 1979, Leber 1985), refuge from predation is likely to be an important selective force affecting host-plant use by these animals.

In our field samples, *Ampithoe longimana* was significantly more abundant on *Sargassum* than on all other species in May and July, and more abundant on *Dictyota* than on all other species in August (with a similar trend in September; Fig. 6). The most obvious characteristics separating these two species from the other three are that *Dictyota* and *Sargassum* are both brown algae that are low-preference foods for common omnivorous fishes in this area (Hay et al. 1987, 1988*b*).

Field and laboratory experiments have shown that several small grazing invertebrates experience reduced predation when on seaweeds that are low-preference foods for fishes, and both feeding and host-plant recognition may be cued directly by algal secondary metabolites that deter feeding by fishes (Hay et al. 1989, 1990, Hay 1990). *A. longimana*'s high abundance on chemically defended *Dictyota* in late summer suggests a similar explanation for its preferential feeding on this seaweed (Fig. 2; Hay et al. 1987). *A. longimana* increased in abundance on *Dictyota* between July and September, when omnivorous fishes are extremely abundant (Adams 1976). During this period, abundance of *A. longimana* on the other species declined or remained the same, and total abundance of all amphipod species dropped sharply on most algae (Fig. 6). Similar seasonal increases in the relative abundance of *A. longimana* on unpalatable plants vs. plants that are palatable to fishes have been described from other algae and other sites (Duffy 1989, Holmlund et al. 1990). Refuge from predation may also explain the higher density of *A. longimana* on *Sargassum* in May and July, as *Sargassum* is intermediate in refuge value among a suite of algae in this system (Holmlund et al. 1990). The proximate mechanism producing differences in abundance of phytal animals among plant species or stands of different plant density is often habitat selection, rather than predation (Choat and Kingett 1982, Leber 1985, Bell and Westoby 1986, Gotceitas and Colgan 1989, Hacker and Steneck 1990). However, predation is likely to be the ultimate selection pressure for choice of safe habitats, as well as for positive responses to secondary metabolites (Hay et al. 1989, 1990).

In addition to selection exerted by predators, evolutionary changes in host-plant use require genetic variance in the herbivore population. Our results (Table 2) suggest that heritable variation exists in this amphipod population for the ability to survive and grow on certain seaweed species. Among-family variance in amphipod survivorship, or the related measure age at death, was significant for all diets other than *Dictyota,* which produced uniformly high survival, and *Chon-*

dria, which produced no survivors. Although it is not possible to rule out the influence of nongenetic maternal effects in producing these differences, these may be unlikely since all mothers were collected from the same site and held under identical conditions in the laboratory. Selection by predators for amphipod association with safe plants (Holmlund et al. 1990), coupled with significant genetic variance for *A. longimana* performance on different plants, suggest that predator-driven changes in host-plant use are evolutionarily feasible in this system.

Explanations other than predator avoidance for the seasonal shifts in field distributions of *A. longimana* are less compelling. Relative abundances of *A. longimana* among seaweed species were not a simple function of food preference; *Chondria* and *Hypnea* are low- and high-preference foods, respectively, for *A. longimana* (Fig. 2), but both supported relatively low numbers of *A. longimana.* Significantly, these are both preferred foods for fishes (Hay et al. 1987, 1988*b*). Plant morphology alone is also unlikely to produce the patterns in Fig. 6 since *Dictyota* harbored significantly more *A. longimana* than did the morphologically similar *Calonitophyllum.* Finally, competition for space between *A. longimana* and all other amphipods as a group does not appear to explain these patterns since there were no significant negative correlations between densities of *A. longimana* and total amphipods for any alga.

The correspondence between *Ampithoe longimana*'s feeding preference for *Dictyota* (Fig. 2), its high survivorship on this diet (Fig. 4), and its persistence on *Dictyota* in the field during seasonal periods of high fish predation (Fig. 6), suggest that feeding preference in this amphipod reflects fitness consequences of both eating and associating with *Dictyota.* In light of these data, the question arises why this amphipod has not specialized on *Dictyota,* as several small tropical invertebrates have specialized on chemically defended seaweeds (Hay et al. 1989, 1990, Hay 1990). The most obvious possibility is that *Dictyota* is a summer annual at this site. Such resources cannot continuously support populations of amphipods, which lack the capability for seasonal diapause found in many temperate insects (Chapman 1982) that specialize on annual plants. Seasonal variation in the physical environment, algal community structure, and predation pressure may interfere with the evolution of specialized feeding associations in temperate marine systems such as this.

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Literature Cited

Adams, S. M. 1976. The ecology of eelgrass, *Zostera marina* (L.), fish communities. I. Structural analysis. Journal of Experimental Marine Biology and Ecology **22**:269–291.

Bell, J. D., and M. Westoby. 1986. Abundance of macrofauna in dense seagrass is due to habitat preference, not predation. Oecologia (Berlin) **68**:205–209.

Bernays, E. A., G. Cooper Driver, and M. Bilgener. 1989. Herbivores and plant tannins. Advances in Ecological Research **19**:263–302.

Bernays, E., and M. Graham. 1988. On the evolution of host specificity in phytophagous arthropods. Ecology **69**: 886–892.

Bousfield, E. L. 1973. Shallow-water gammaridean Amphipoda of New England. Cornell University Press, Ithaca, New York, USA.

Bradford, M. M. 1976. A rapid and sensitive method for the quantification of microgram quantities of protein utilizing the principle of protein-dye binding. Analytical Biochemistry **72**:248–254.

Brawley, S. H., and W. H. Adey. 1981. The effect of micrograzers on algal community structure in a coral reef microcosm. Marine Biology **61**:167–177.

Carefoot, T. H. 1967. Growth and nutrition of *Aplysia punctata* feeding on a variety of marine algae. Journal of the Marine Biological Association of the United Kingdom **47**: 565–589.

Chapman, R. F. 1982. The insects: structure and function. Third edition. Harvard University Press, Cambridge, Massachusetts, USA.

Choat, J. H., and P. D. Kingett. 1982. The influence of fish predation on the abundance cycles of an algal turf invertebrate fauna. Oecologia (Berlin) **54**:88–95.

Coull, B. C., and J. B. J. Wells. 1983. Refuges from fish predation: experiments with phytal meiofauna from the New Zealand rocky intertidal. Ecology **64**:1599–1609.

Damman, H. 1987. Leaf quality and enemy avoidance by the larvae of a pyralid moth. Ecology **68**:88–97.

Davis, E. M. 1988. Protein assays: a review of common techniques. American Biotechnology Laboratory **6**:28–37.

Duffy, J. E. 1989. Ecology and evolution of herbivory by marine amphipods. Dissertation. University of North Carolina at Chapel Hill, Chapel Hill, North Carolina, USA.

———. 1990. Amphipods on seaweeds: partners or pests? Oecologia (Berlin) **83**:267–276.

Edgar, G. J. 1983. The ecology of south-east Tasmanian phytal animal communities. IV. Factors affecting the distribution of ampithoid amphipods among algae. Journal of Experimental Marine Biology and Ecology **70**:205–225.

Gotceitas, V., and P. Colgan. 1989. Predator foraging success and habitat complexity: quantitative test of the threshold hypothesis. Oecologia (Berlin) **80**:158–166.

Hacker, S. D., and R. S. Steneck. 1990. Habitat architecture and the abundance and body-size-dependent habitat selection of a phytal amphipod. Ecology **71**:2269–2285.

Hay, M. E. 1981. The functional morphology of turf-forming seaweeds: persistence in stressful marine habitats. Ecology **62**:739–750.

———. 1990. Seaweed chemical defenses: their role in the evolution of feeding specialization and in mediating complex interactions. *In* V. J. Paul, editor. Ecological roles for marine secondary metabolites. Explorations in chemical ecology series. Comstock, Ithaca, New York, USA, *in press.*

Hay, M. E., J. E. Duffy, and W. Fenical. 1990. Host-plant specialization decreases predation on a marine amphipod: an herbivore in plant's clothing. Ecology **71**:733–743.

Hay, M. E., J. E. Duffy, W. Fenical, and K. Gustafson. 1988*a*. Chemical defense in the seaweed *Dictyopteris delicatula*: differential effects against reef fishes and amphipods. Marine Ecology Progress Series **48**:185–192.

Hay, M. E., J. E. Duffy, C. A. Pfister, and W. Fenical. 1987. Chemical defense against different marine herbivores: are amphipods insect equivalents? Ecology **68**:1567–1580.

Hay, M. E., and W. Fenical. 1988. Marine plant–herbivore interactions: the ecology of chemical defense. Annual Review of Ecology and Systematics **19**:111–145.

Hay, M. E., J. R. Pawlik, J. E. Duffy, and W. Fenical. 1989. Seaweed-herbivore-predator interactions: host-plant specialization reduces predation on small herbivores. Oecologia (Berlin) **81**:418–427.

Hay, M. E., P. E. Renaud, and W. Fenical. 1988*b*. Large mobile versus small sedentary herbivores and their resistance to seaweed chemical defenses. Oecologia (Berlin) **75**: 246–252.

Holbrook, S. J., and R. J. Schmitt. 1988. The combined effects of predation risk and food reward on patch selection. Ecology **69**:125–134.

Holmlund, M. B., C. H. Peterson, and M. E. Hay. 1990. Does algal morphology affect amphipod susceptibility to fish predation? Journal of Experimental Marine Biology and Ecology **139**:65–83.

Holomuzki, J. R., and T. M. Short. 1988. Habitat use and fish avoidance behaviors by the stream-dwelling isopod *Lirceus fontinalis*. Oikos **52**:79–86.

Horn, M. H., and M. A. Neighbors. 1984. Protein and nitrogen assimilation as a factor in predicting the seasonal macroalgal diet of the monkeyface prickleback. Transactions of the American Fisheries Society **113**:388–396.

Kochert, G. 1978. Protein determination by dye binding. Pages 91–93 *in* J. A. Hellebust and J. S. Craigie, editors. Handbook of phycological methods. Physiological and biological methods. Cambridge University Press, Cambridge, England.

Leber, K. M. 1985. The influence of predatory decapods, refuge, and microhabitat selection on seagrass communities. Ecology **66**:1951–1964.

Littler, M. M., and D. S. Littler. 1980. The evolution of thallus form and survival strategies in benthic marine macroalgae: field and laboratory tests of a functional form model. American Naturalist **116**:25–44.

Lubchenco, J., and S. D. Gaines. 1981. A unified approach to marine plant-herbivore interactions. I. Populations and communities. Annual Review of Ecology and Systematics **12**:405–437.

Mattson, W. J. 1980. Herbivory in relation to plant nitrogen. Annual Review of Ecology and Systematics **11**:119–161.

Morse, D. H. 1980. Behavioral mechanisms in ecology. Harvard University Press, Cambridge, Massachusetts, USA.

Nelson, W. G. 1979. An analysis of structural pattern in an eelgrass (*Zostera marina* L.) amphipod community. Journal of Experimental Marine Biology and Ecology **39**:231–264.

Nicotri, M. E. 1980. Factors involved in herbivore food preference. Journal of Experimental Marine Biology and Ecology **42**:13–26.

Padilla, D. K. 1985. Structural resistance of algae to herbivores: a biomechanical approach. Marine Biology **90**:103–109.

Peterson, C. H., and P. E. Renaud. 1989. Analysis of feeding preference experiments. Oecologia (Berlin) **80**:82–86.

Power, M. E. 1984. Depth distribution of armored catfish: predator-induced resource avoidance? Ecology **65**:523–528.

Price, P. W., C. E. Bouton, P. Gross, B. A. McPherson, J. N. Thompson, and A. E. Weiss. 1980. Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. Annual Review of Ecology and Systematics **11**:41–65.

Robbins, C. T., T. A. Hanley, A. E. Hagerman, O. Hjelford, D. L. Baker, C. C. Schwartz, and W. W. Mautz. 1987. Role of tannins in defending plants against ruminants: reduction in protein availability. Ecology **68**:98–107.

Robertson, A. I., and J. S. Lucas. 1983. Food choice, feeding rates, and the turnover of macrophyte biomass by a surf-zone inhabiting amphipod. Journal of Experimental Marine Biology and Ecology **72**:99–124.

Rosenthal, G. A., and D. H. Janzen. 1979. Herbivores: their interaction with secondary plant metabolites. Academic Press, New York, New York, USA.

SAS. 1985. SAS user's guide: statistics. Version 5 edition. SAS Institute, Cary, North Carolina, USA.

Scheffé, H. 1959. The analysis of variance. J. Wiley & Sons, New York, New York, USA.

Sih, A. 1982. Foraging strategies and the avoidance of predation by an aquatic insect, *Notonecta hoffmanni*. Ecology **63**:786–796.

Steneck, R. S. 1983. Escalating herbivory and resulting adaptive trends in calcareous algal crusts. Paleobiology **9**: 44–61.

———. 1986. The ecology of coralline algal crusts: convergent patterns and adaptive strategies. Annual Review of Ecology and Systematics **17**:273–303.

Steneck, R. S., and L. Watling. 1982. Feeding capabilities and limitations of herbivorous molluscs: a functional group approach. Marine Biology **68**:299–319.

Stoner, A. W. 1980. Feeding ecology of *Lagodon rhomboides* (Pisces: Sparidae): variation and functional response. Fishery Bulletin **78**:337–352.

———. 1982. The influence of benthic macrophytes on the foraging behavior of pinfish, *Lagodon rhomboides* (Linnaeus). Journal of Experimental Marine Biology and Ecology **58**:271–284.

Strong, D. R., J. H. Lawton, and R. Southwood. 1984. Insects on plants: community patterns and mechanisms. Harvard University Press, Cambridge, Massachusetts, USA.

Thompson, J. N. 1988. Evolutionary ecology of the relationship between oviposition preference and performance of offspring in phytophagous insects. Entomologia Experimentalis et Applicata **47**:3–14.

Underwood, A. J. 1981. Techniques of analysis of variance in experimental marine biology and ecology. Oceanography and Marine Biology Annual Review **19**:513–605.

Van Dolah, R. F. 1978. Factors regulating the distribution and population dynamics of the amphipod *Gammarus palustris* in an intertidal salt marsh community. Ecological Monographs **48**:191–217.

Werner, E. E., J. F. Gilliam, D. J. Hall, and G. G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology **64**:1540–1548.

White, T. C. R. 1984. The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. Oecologia (Berlin) **63**:90–105.

———. 1985. When is a herbivore not a herbivore? Oecologia (Berlin) **67**:596–597.

Young, D. K., and M. W. Young. 1978. Regulation of species densities of seagrass-associated macrobenthos: a field experimental study of predation. Journal of Marine Research **36**:569–593.

Zar, J. H. 1974. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, New Jersey, USA.