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FACTORS INVOLVED IN HERBIVORE FOOD PREFERENCE[1]

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Abstract: Herbivore food preference can be measured either in terms of attractiveness or of edibility; these quantities are not necessarily correlated. The isopod *Idotea baltica* (Pallas) is attracted to large, tough, branched algae (perennials) while the amphipod *Ampithoe valida* (Smith) is attracted to softer, filamentous or bladed algae (ephemerals). Attractiveness for *Ampithoe* is related to the nutritive value of the algae; this is not so for *Idotea*, which responds more to algal morphology and availability. *Idotea's* mobility, possible susceptibility to fish predation, and preference for moderate wave exposures may select for a primary response to algae as habitat rather than as food source.

INTRODUCTION

Herbivore food preferences are of considerable theoretical and practical interest to ecologists. Preference determines the quantity and quality of food ingested by a grazer and hence affects its physiological condition and fitness (Hsiao & Fraenkel, 1968). Herbivore preference also interacts with plant competitive abilities, life histories, and physical tolerances to determine the impact of a grazer on the plant community (Lubchenco, 1978). Frequently, herbivore effects on plant distributions, biomass, and diversity are dramatic (Huffaker & Kennett, 1959; Harper, 1969; Paine & Vadas, 1969a; Mann & Breen, 1972; Janzen, 1973; Mattson & Addy, 1975; McNaughton, 1976; Snyder & Janke, 1976). Furthermore, the relationship between plants and herbivores is not static; each may effect evolutionary change in the other (Ehrlich & Raven, 1964; Dethier, 1970; Dolinger *et al.*, 1973; Freeland & Janzen, 1974; Gilbert, 1975; Benson *et al.*, 1976; Edmunds & Alstad, 1978).

Two distinct components of food preference are commonly recognized: one relating to the selection of a potential prey item (attractiveness), and the other relating to the rate at which that prey is ingested (edibility). Attractiveness is measured by methods that permit herbivores to choose between several possible foods. This may involve chemoreception over some distance (Vadas, 1977) or it may involve direct chemical and tactile sampling of plants (Himmelman & Carefoot, 1975; Lawrence, 1975; Lubchenco, 1978). Methods dealing with edibility assume that, under equivalent hunger conditions, herbivores consume preferred items faster (Leighton & Boolootian, 1963; Carefoot, 1967); edibility will reflect not only the speed with which a given item satisfies the physiological needs of a herbivore, but also the ease

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with which that item is handled and ingested. In the literature, attractiveness and edibility have sometimes been used interchangeably; however, it is clear that they are distinct and measure different aspects of preference (Lawrence, 1975).

Preference may be influenced by factors not relating directly to nutritional qualities of the plant. For instance, small aquatic herbivores that live nestled among algal fronds may utilize an alga as habitat as well as food source. The amount of protection offered from predators or the amount of shelter from wave action are important habitat characteristics (Colman, 1940; Wieser, 1952; Nagle, 1968) and might influence herbivore choice as much as the food value of the plant. The predictability of plant presence in space and time is also important and, in evolutionary terms, may affect herbivore preferences (Paine & Vadas, 1969a; Feeny, 1976).

Preference has been studied in a number of marine herbivores. Investigators generally have concentrated on sea urchins (extensively reviewed by Lawrence, 1975; Vadas, 1977), molluscs (Leighton & Boolootian, 1963; Dahl, 1964; Leighton, 1966; Carefoot, 1967; Himmelman & Carefoot, 1975; Nicotri, 1977a; Lubchenco, 1978), and fish (Tsuda & Bryan, 1973; Vine, 1974; Ogden, 1976; Ogden & Lobel, 1978). There is some information available about the diets of nonplanktonic herbivorous crustaceans (Ravanko, 1969; Jones, 1971; Carefoot, 1973), but, in general, preferences of this group are poorly known. This is unfortunate since such crustaceans are common and often quite abundant. This study was designed to examine the food preferences of two of these crustaceans, the isopod *Idotea baltica* (Pallas) and the amphipod *Ampithoe valida* (Smith). After factors that influence both components of preference have been investigated, results of this study are compared with preferences of the periwinkle *Littorina littorea*, an extremely common and abundant marine gastropod studied by Lubchenco (1978). Since the distribution of *Littorina* broadly overlaps that of *Idotea* and *Ampithoe* and all three grazers could potentially be using the same plants, it is of interest to compare the similarity of food preferences.

Idotea baltica is an active isopod found among seaweeds in intertidal and very shallow subtidal zones throughout temperate latitudes (Naylor, 1955a). It is herbivorous (Naylor, 1955b; Ravanko, 1969) and is an extremely abundant potential pest in a polyspecies aquaculture system at Woods Hole Oceanographic Institution, Cape Cod, Massachusetts (Ryther *et al.*, 1975; Nicotri, 1977b). It is also an opportunistic scavenger (Sywula, 1964) and is cannabalistic at high densities. It grows fast, up to 2 mm/week, depending on available food, and may reach sizes of 3 cm (Nicotri, 1977b).

Ampithoe valida is a sedentary tube-dwelling amphipod, rarely leaving its tube except under duress (Skutch, 1926). It may reach very high local densities (Bousfield, 1973) and often does so in the aquaculture system at Woods Hole (Nicotri, 1977b). Since movement is limited and the alga chosen becomes both habitat and food source, initial settlement is quite important. However, under adverse conditions, individuals can and do move and are capable of swimming rapidly for short periods.

Growth averages about 1 mm/week under conditions of optimal food availability; maximal body length is about 1.8 cm (Nicotri, 1977b).

MATERIALS AND METHODS

Eighteen species of marine plants naturally encountered by *Idotea* and *Ampithoe*, representing a variety of taxonomic and morphological groups, were examined (Table I). Fifteen species were collected from natural field populations near Woods Hole, Mass.; the remaining three (*Hypnea*, *Gracilaria*, and *Neoagardhiella*) were taken from mass outdoor cultures maintained at the Environmental Systems Laboratory, Woods Hole Oceanographic Institution. Only macroalgae free of attached epiphytes were used; although small amounts of epiphytic diatoms and microalgae

TABLE I

Morphological, taxonomic, and life history classification of marine plants: P, perennial; A, annual, with long season of abundance; E, ephemeral (annual, with short season).

Morphology	Clorophyceae (green algae)	Phaeophyceae (brown algae)	Rhodophyceae (red algae)	Angiosperm (flowering plant)
Firm, branched	*Codium fragile* (Suringar) Hariot (P)	*Ascophyllum nodosum* (Linnaeus) LeJolis(P) *Fucus vesiculosus* Linnaeus (P) *Sargassum filipendula* C. Agardh (P)	*Chondrus crispus* Stackhouse (P) *Corallina officinalis* Linnaeus (P) *Gracilaria foliifera* (Forsskal) Borgesen (A) *Neoagardhiella baileyi* (Harvey ex Kutzing) Wynne and Taylor (A)	*Zostera marina* Linnaeus (P)
Soft, branched	*Spongomorpha lanosa* (Roth) Kutzing (E)		*Ceramium rubrum* (Hudson) C. Agardh (A) *Dictyosiphon feoniculaceus* (Hudson) Greville (E) *Hypnea musciformis* (Wulfen) Lamouroux (A)	
Soft, flat sheet	*Ulva lactuca* Linnaeus (A)	*Petalonia fascia* (O. F. Muller) Kuntze (E)	*Porphyra* sp. (E)	
Soft, tubular sheet	*Enteromorpha linza* (Linnaeus) J. Agardh (A)	*Scytosiphon lomentaria* (Lyngbye) J. Agardh (E)		

may have been present, effort was made to minimize variation due to this source (plants obviously fouled by diatoms were not used).

Intraspecific variability was minimized by using freshly collected plants in good physiological condition and by sampling over a restricted seasonal span (spring); however, due to the number of tests run, work continued from February through July. As a result, some seasonal variation in plant quality may be present in the data.

Several algal characteristics relevant to herbivore nutrition were examined. Samples were oven-dried at 50 °C for 48 h to determine water content and then combusted at 450 °C for 5 h to determine ash-free dry weight. Other dried samples were subjected to analysis on a Perkin-Elmer 240 elemental analyzer to estimate percent composition of nitrogen. Caloric contents have been measured by Paine & Vadas (1969b) and by Carefoot (1973) for west coast representatives of many of the east coast algae used in this study; these 'literature' values have been used here, but should be viewed cautiously in this context. In the absence of other data, these values should be adequate as first approximations.

The contribution that an alga makes to the nutrition of a grazer is dependent both on the absolute content of the 'substance' being considered (i.e. organic matter, calories, etc.) and on the rate at which that alga is ingested. Grazing rates were obtained from a set of experiments in which isopods were given access to only one plant species at a time. Pre-weighed amounts of each alga were placed in separate containers in a water table (at 20 °C) and five large isopods were added to each container; three replicates per alga were run. After five days, isopods were removed and the algae reweighed. Grazing rates were then calculated after correction for weight changes in ungrazed controls.

An attractiveness hierarchy was constructed using a 5-l testing chamber which was divided into five interconnecting compartments. Equal weights of two species of algae were added alternately to the four corner compartments and 40 adult isopods were released into the central (empty) space. Isopods actively explored the whole chamber and moved freely from one section to another; after 1–3 h, exploratory behavior markedly declined. Access between compartments was then closed and the number of isopods in each section was recorded. This procedure was repeated with a fresh batch of animals and with algae rotated between compartments (to correct for possible differences between them). The total number of individuals choosing each alga for all comparisons involving that alga was then summed and divided by the total number of isopods involved in that set of experiments to arrive at an attractiveness index. Thus, higher scores indicate greater attractiveness.

The testing procedure was the same for *Ampithoe* as the grazer. Since *Ampithoe* tends to cling to surfaces, it had difficulty moving between compartments; therefore, an unpartitioned testing chamber was used. Only 16 plant species were compared, because *Hypnea* and *Dictyosiphon* were no longer available.

An experiment was devised to test the hypothesis that isopods respond to plant morphology rather than to qualities affecting food value. Plastic plants of two types were used; one was highly branched with small leaves (rose type) and the other was a whorled, monocot type. The attractiveness of these plastic plants was tested against two attractive and two unattractive live species in the manner already described.

An edibility hierarchy was determined for *Idotea* but, due to time constraints, not for *Ampithoe*. Grazing rates were obtained as earlier described, except that here algae were offered in pair-wise combinations rather than singly. To determine a hierarchy, the mean grazing rate was calculated over all combinations involving each alga.

Grazer growth rates were determined by rearing juveniles of both crustacean species on various kinds of algae at 20 °C. For each alga, 20 juveniles of each grazer were individually reared and changes in total body length were measured weekly; fresh algae, in excess of consumption needs, were supplied weekly.

RESULTS

ALGAL CHARACTERISTICS

Table II details some characteristics of algae that seem relevant to questions of preference. The percent dry matter and, better yet, percent organic matter give an

TABLE II

Nutritional characteristics of marine plants; three replicates of each species were averaged; percentage calculations: % H_2O, (wet weight of algae – dry weight)/wet weight; % organic matter, ash-free dry weight/wet weight; % N, weight N/dry weight alga; caloric content, calories/mg dry weight.

Alga	% Dry matter		% Organic matter		% N		Caloric content*	
	%	Rank	%	Rank	%	Rank	Calories	Rank
Codium	7.4	18	3.9	18	1.38	14	2.62	9
Enteromorpha	13.9	14	11.5	10	1.87	9	3.69	4
Spongomorpha	19.7	6.5	9.3	13	1.86	10	3.08	8
Ulva	16.3	9	13.2	7	1.71	11.5	4.52	2
Ascophylum	26.1	2	20.2	1	2.03	8		–
Fucus	21.8	5	16.8	4	3.67	4	3.43	5
Petalonia	18.6	8	14.7	6	2.71	6		
Sargassum	15.1	10	11.1	11	1.17	16		–
Scytosiphon	19.7	6.5	16.5	5	3.09	5	3.37	7
Ceramium	11.1	16	7.8	16	1.71	11.5	3.39	6
Chondrus	24.7	3	18.8	2	2.51	7	–	–
Corallina	58.7	1	11.9	9	1.36	15	0.86	10
Dictyosiphon	11.7	15	8.5	14	–	–	–	–
Gracilaria	14.1	12	9.5	12	3.72	3	–	–
Hypnea	15.0	11	8.2	15	–	–	–	–
Neoagardhiella	9.8	17	6.0	17	4.19	2	–	–
Porphyra	14.0	13	12.2	8	4.73	1	4.61	1
Zostera	24.4	4	18.0	3	1.69	13	4.48	3

* Data from Paine & Vadas (1969b) and Carefoot (1973).

indication of the amount of solid or organic material 'per bite' available to grazers. This is highest for species like *Ascophyllum* and *Chondrus* and lowest for *Neoagardhiella* and *Codium*. *Corallina* has a misleadingly high dry matter content due to its calcified nature.

The quality of organic material will vary depending on its chemical composition. Nitrogen and caloric contents could be assumed to be important parameters that vary significantly from alga to alga, but not necessarily in similar directions. For instance, *Ulva* and *Zostera* have relatively high caloric contents, but relatively low N contents.

Grazing rates for *Idotea* on individual species of algae are given in Table III.

TABLE III

Grazing rates on individual species of algae for *Idotea baltica*.

	Wet weight eaten		Organic intake		Caloric intake	
Alga	$mg \cdot day^{-1} \cdot ind.^{-1}$	Rank	mg organic matter eaten $\cdot day^{-1} \cdot ind.^{-1}$	Rank	$cal \cdot day^{-1} \cdot ind^{-1}$	Rank
Codium	8.1	1	3.1	7.5	15.7	5
Enteromorpha	3.3	4.5	3.8	4	20.6	4
Spongomorpha	3.8	3	3.5	6	22.7	2
Ulva	2.9	7	3.8	4	21.4	3
Ascophyllum	0.8	14.5	1.6	10	–	–
Fucus	0.9	12	1.5	11.5	6.7	8
Petalonia	3.3	4.5	4.9	2	–	–
Sargassum	2.8	8	3.1	7.5	–	–
Scytosiphon	2.3	9	3.8	4	15.2	6
Ceramium	0.2	17.5	0.2	15.5	0.8	9
Chondrus	0.8	14.5	1.5	11.5	–	–
Corallina	0.8	14.5	0.1	17.5	0.4	10
Dictyosiphon	3.1	6	0.3	14	–	–
Gracilaria	0.8	14.5	0.8	13	–	–
Hypnea	1.8	10	0.2	15.5	–	–
Neoagardhiella	0.2	17.5	0.1	17.5	–	–
Porphyra	5.9	2	7.2	1	38.1	1
Zostera	1.1	11	2.0	9	12.1	7

The amount of organic matter ingested per unit time was calculated by multiplying grazing rates by organic content. In a similar manner, caloric intakes were obtained. Again, a wide range of values is evident for both organic and caloric intakes; species with soft bodied blades like *Porphyra*, *Ulva*, and *Enteromorpha* have high yields and tough substantial plants like *Fucus* and *Corallina* have low yields. However, it should be remembered that each alga's contribution to herbivore nutrition will be further modified by differences in assimilation efficiency (Lowe & Lawrence, 1976; Vadas, 1977).

ATTRACTIVENESS

Table IV shows the attractiveness hierarchies constructed for *Idotea* and *Ampithoe*. Attractive species occur in all taxonomic groups, reflecting the generalized nature of their diets. Morphologically robust species are preferred by *Idotea* to those with softer filaments and blades, which are favored by *Ampithoe*.

TABLE IV

Preferences and growth rates for *Idotea* and *Ampithoe*.

	Idotea						*Ampithoe*			
	Attractiveness		Edibility		Growth		Attractiveness		Growth	
Alga	%*	Rank	mg/ind./day	Rank	mm/week	Rank	%*	Rank	mm/week	Rank
Codium	59.2	1	44.6	1	0.9	9	25.8	16	0.4	12.5
Enteromorpha	39.4	17	18.0	5	1.1	7	41.1	5	0.6	9
Spongomorpha	53.3	6	18.3	4			39.5	6	0.6	9
Ulva	44.3	13	7.1	13	0.8	10	46.9	2	0.9	4
Ascophyllum	54.8	4	16.4	7	0.3	15	28.5	14	0.7	7
Fucus	55.5	3	10.7	10	1.6	3	33.0	12	0.4	12.5
Petalonia	44.1	14	17.7	6	1.7	2	35.8	10	0.9	4
Sargassum	55.9	2	26.2	2	1.4	4	39.4	7	0.9	4
Scytosiphon	49.0	10	20.1	3	1.8	1	30.1	13	1.0	2
Ceramium	40.7	16	8.7	11	0.6	11.5	43.3	4	0.8	6
Chondrus	50.3	9	11.3	9	1.2	6	36.2	9	0.3	14.5
Corallina	54.6	5	2.4	16	0.6	11.5	35.3	11	–	–
Dictyosiphon	46.3	12	–	–	0.1	17	–	–	–	–
Gracilaria	50.6	8	11.9	8	1.0	8	46.2	3	0.6	9
Hypnea	47.1	11	–	–	0.4	13	–	–	–	–
Neoagardhiella	41.4	15	4.5	14	0.3	15	38.5	8	0.5	11
Porphyra	39.0	18	7.4	12	1.3	5	52.7	1	1.1	1
Zostera	52.7	7	4.2	15	0.3	15	27.7	15	0.3	14.5

* % = number of individuals selecting a species per total number of individuals run.

Since the algae most attractive to *Idotea* are large, tough plants, it could be that isopods are responding, at least proximately, to algal morphology rather than food value. Table V gives the results of a set of experiments testing live algae against plastic plants having morphologies hypothesized to be attractive. Isopods sometimes choose the real plant and sometimes do not discriminate between live and plastic plants. Plastic plants are significantly preferred to unattractive live species. This is evidence that attractiveness is measuring factors not related to feeding.

When attractiveness is examined in relation to algal life history type (using the Kruskal–Wallis one-way analysis of variance), it is seen that *Idotea* strongly prefers perennials over either annuals or ephemerals (Table VI). *Ampithoe*, however, prefers annuals and ephemerals to perennials.

Spearman rank correlation coefficients were calculated to assess the relation between attractiveness and various other characteristics of the algae (Table VII). For

TABLE V

The comparative attractiveness of natural and artifical plants: plastic plants (rose and monocot) were tested against attractive algal species (*Codium* and *Fucus*) and against unattractive algae (*Porphyra*, *Ceramium*); the number of isopods on each plant is shown; 2 trials are summed; *, χ^2 significant at $P < 0.05$.

	Rose	Alga	χ^2	Monocot	Alga	χ^2
Codium	34	42	0.84	20	60	20.00*
Fucus	38	40	0.05	26	54	9.8*
Porphyra	74	4	62.82*	72	8	51.20*
Ceramium	58	18	21.05*	46	19	11.22*

TABLE VI

Preference as a function of algal life history: means for each life history type are calculated from Table IV and compared by Kruskal–Wallis one-way analysis of variance.

	Perennials	Annuals	Ephemerals	
Mean attractiveness (*Idotea*)	54.7	43.9	46.9	$P < 0.01$
Mean attractiveness (*Ampithoe*)	32.3	43.2	39.5	$P < 0.05$
Mean edibility (*Idotea*)	16.5	10.0	15.9	$P < 0.20$

TABLE VII

Spearman rank correlation coefficients: *, values significant at $P < 0.05$; numbers in parentheses = N.

	Idotea			*Ampithoe*	
	Attractiveness	Edibility	Growth	Attractiveness	Growth
Algal organic content	0.15(18)	−0.22(16)	0.29(17)	−0.40(16)	−0.04(15)
% N	−0.48(16)*	−0.12(16)	0.30(15)	0.31(16)	0.16(15)
Caloric content	−0.67(10)*	−0.35(10)	0.15(9)	0.48(10)	0.32(9)
Organic intake	−0.15(18)	0.43(16)*	0.61(17)*	–	–
Caloric intake	−0.41(10)	0.25(10)	0.38(9)	–	–
Edibility	0.32(16)	–	–	–	–
Growth	0.03(17)	0.54(15)*	–	0.47(15)*	–

Idotea, organic content shows no relation to attractiveness, and % N and caloric content show significant negative correlations with attractiveness. For *Ampithoe*, none of these quantities correlate significantly. In contrast with the findings by Himmelman & Carefoot (1975) using chitons, attractiveness does not correlate with either organic or caloric intake. This means that these isopods and amphipods are not choosing to locate themselves in algae that return the most nutritional yield to them.

EDIBILITY

Mean grazing rates calculated from experiments where algae were offered in pair-wise combinations (edibility, Table IV) are greater than rates observed when each species was offered individually (Table III). Similar observations were made by Lowe (1974, cited by Lawrence, 1975) for sea-urchin grazing. Other studies have found the converse, that algae offered singly are consumed faster than when offered in combination (Leighton, 1971; Vadas, 1977). Although it is uncertain why different trends have been observed, it is clear that experimental design will affect the results obtained.

A variety of taxonomic and morphological types are highly edible, with both tough, robust species and soft, filamentous or bladed ones being highly consumed. A Kruskal–Wallis one-way analysis of variance (Table VI) confirms that no significant differences in edibility exist among means for perennials, annuals, or ephemerals, in contrast to the significant differences observed in attractiveness.

Edibility does not correlate well with attractiveness (Table VII). This is further evidence that isopods are not attracted to algae solely by food considerations.

Edibility does not correlate well with organic content, % N, caloric content, or caloric intake (Table VII). In agreement with these data, Paine & Vadas (1969b) and Carefoot (1973) found that preference in a variety of marine herbivores bears little relation to caloric content. Calories may not be a meaningful measure of food value since many of the carbohydrates of an alga are structural and indigestible by grazers (Lawrence, 1975). Westoby (1974) commented that palatability may or may not be related to plant nutritional value.

The relation between edibility and organic intake is significant ($P < 0.05$) and indicates that animals graze faster on foods from which they get more organic material. This makes sense evolutionarily, for selection should favor eating more of those foods that produce highest yields.

GROWTH

For *Idotea*, growth varied from a low of 0.3 mm/week on *Zostera* or *Neoagardhiella* to 1.8 mm/week on *Scytosiphon* (Table IV). There is no correlation between growth and attractiveness, or between growth and organic content, % N, caloric content, or caloric intake (Table VII). However, growth does show a significant correlation with edibility and organic intake. These data again support the hypothesis that isopods are not choosing algae on the basis of food value.

For *Ampithoe*, the only significant correlation is that between growth and attractiveness; this suggests that *Ampithoe* preferences are more related to the food value of the algae than are those of *Idotea*.

Discussion

Much of the literature concerning terrestrial herbivore food preference centers on the presence of a number of secondary plant compounds thought to deter grazing (Dethier, 1954; Fraenkel, 1969; Feeny, 1970; Jones, 1973; Rhoades & Cates, 1976). It is becoming clear that chemical defense is employed by a number of marine algae, although much remains to be learned in this area. Tannins occur in *Fucus*, *Sargassum*, and *Ascophyllum* (Conover & Sieburth, 1965; Sieburth, 1969). A number of halogenated compounds are widespread, especially in red algae (Fenical, 1975); some of these have been hypothesized to be anti-microbial (Hornsey & Hilde, 1974), but could play an anti-herbivore role as well. A wide variety of other toxic chemicals are known in algae and presumably function against herbivores (Ogden & Lobel, 1978). Herbivores may be differentially susceptible to such chemicals, depending on the possession of alternate metabolic pathways or detoxification capacities (Freeland & Janzen, 1974). Very little information of this nature is available for marine herbivores. I have no data on the extent to which algal chemical defense affects isopod or amphipod grazing.

Cates & Orians (1975) have argued that early successional (or "r-selected") plants gain a measure of protection from herbivores by being unpredictable in space and time. Therefore, such plants devote less energy to anti-herbivore chemical defenses and, hence, should be preferred by generalist herbivores to later successional ("K-selected") species. Slug grazing supports this predicted pattern. Here, although attractiveness ratings by *Ampithoe* are in accord with the prediction, those for *Idotea* follow an opposite trend (Table VI). Edibility, for *Idotea*, shows no relation to successional state. These observations also support the contention that isopods choose algae for qualities largely unrelated to feeding.

The robust algae favored by *Idotea* are all perennial and available throughout the year. There is some evidence that predictability of the resource is important in determining preference. Paine & Vadas (1969b) concluded that for a variety of marine herbivores highly preferred algae tend to be those perennials (or those without strong seasonal components) forming a predictable, dependably available resource. Feeny (1976) has reached similar conclusions for terrestrial insects, while Otte (1975) and Futuyma (1976) have used this argument to explain grasshopper and lepidopteran preferences respectively.

There are several other reasons why there could be strong selection for *Idotea* to prefer robust algae. The morphology of these plants provides secure surfaces for small herbivores to grip. *Idotea* is most common in areas of moderate to heavy wave action (Sywula, 1964; Lubchenco, pers. obs.). There could be strong selective pressure to choose seaweeds that provide secure clinging sites under surf-swept conditions.

Tough, branched algae may also offer refuge from predators, especially fish. Because isopods may make up an important part of the diets of some fish (Larsen, 1936), selection could be strong for isopods to seek shelter in algae that offer hiding places. Brower (1958) has proposed that some insect plant preferences may similarly be selected for by bird predation. Likewise, *Ampithoe* preferences may be a compromise, taking into account a plant's food value, suitability for tube-building, protection, etc.

COMPARISON OF PREFERENCES OF THREE MARINE HERBIVORES

Because the attractiveness of various algal species to *Littorina littorea* has been measured in a manner very similar to that used here (Lubchenco, 1978), some interesting comparisons are posible (Table VIII). Preferences of *Littorina* and

TABLE VIII

Preferences (based on attractiveness) of three herbivores: H, highly preferred (approximately upper 1/3 of plants tested); M, medium preference ranking; L, low ranking (lower 1/3 of species tested).

	Idotea baltica	*Ampithoe valida*	*Littorina littorea**
Codium	H	L	–
Enteromorpha	L	H	H
Spongomorpha	H	M	H
Ulva	L	H	H
Ascophyllum	H	L	L
Fucus	H	M	L
Petalonia	L	M	H
Sargassum	H	M	–
Scytosiphon	M	L	H
Ceramium	L	H	H
Chondrus	M	M	L
Corallina	H	M	–
Dictyosiphon	M	–	M
Gracilaria	M	H	–
Hypnea	M	–	–
Neoagarhiella	L	M	–
Porphyra	L	H	H
Zostera	M	L	–

* Data from Lubchenco, 1978.

Ampithoe are similar (though not identical), while those of *Idotea* are almost inverse. Why might this be? First, *Idotea* moves more freely than either of the other two. It can spend most of its time in algae that offer favorable habitat characteristics and still make trips to nutritious food sources; habitat and nutritional aspects of algae can be handled separately. *Ampithoe*, although capable of spurts of rapid swimming, stays in its tube and moves outside only when necessary; *Littorina* is a slow-moving snail. Such animals cannot deal separately with habitat and food characteristics, but must balance the two sets of selective pressures against each other in arriving at preferences. For these animals, attractiveness and edibility scales should correlate closely.

There are hints that, for *Ampithoe* and *Littorina*, habitat considerations are less important than dietary ones in molding preferences. These animals tend to inhabit calmer waters (Bousfield, 1973; Lubchenco, 1978) and may have less need for a habitat offering support and protection from wave energy. They may be less vulnerable to predators as well, for *Littorina* has a hard shell and *Ampithoe* rarely leaves its tube.

Because algae may serve as habitat as well as food for many herbivores (and especially for small sedentary or slow-moving ones), it will be difficult to make broad generalizations about preferences. Information about the life-style of an organism will be necessary, for food preferences may be influenced to a great degree by non-nutritional factors.

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