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Feeding Upon Complementary Resources**



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## SELECTIVITY AND GROWTH OF THE GENERALIST HERBIVORE *DOLABELLA AURICULARIA* FEEDING UPON COMPLEMENTARY RESOURCES<sup>1</sup>

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**Abstract.** An assumption of most optimal diet theory is that different resources are substitutable, that is, that they are identical in all relevant aspects and so can be ranked in value using a single currency, such as energy. However, this assumption is probably not valid in many cases. The sea hare *Dolabella auricularia* (Gastropoda: Opisthobranchia: Anaspidea) grew far better upon an ad libitum mixture of four species of algae than upon any of the algal species alone, suggesting that algae were complementary resources. When offered three pairs of algae in 4:1 and 1:9 ratios, *Dolabella* changed its foraging behavior so that the rarer alga was preferred. Consequently, the mixtures of algae consumed were more similar between treatments (ratios) than the mixtures of algae offered. Replicate *Dolabella* were maintained on six single algal diets for 6–7 d and then offered the maintenance alga and another alga at equal abundances. Preference for a species of algae was always higher when it was not the maintenance diet compared to when it was. These results suggest that *Dolabella* actively maintains a mixed diet because it is nutritionally superior to any single diet. An alternative hypothesis (the nonadditive toxin hypothesis) suggests that herbivores might consume a mixed diet because a mixture of plant secondary metabolites is less toxic than any one metabolite alone; consequently, herbivores can consume more total biomass of a mixed than of a single diet. However, sea hares fed single- and mixed-species diets did not consume more of mixed diets than of single-species diets, and animals fed a mixed diet grew better than those fed single diets even when the biomass of algae offered was held constant. If resources are complementary, as suggested here, several important implications follow: (1) consumers will not rank resources in any absolute way because the value of each will depend upon what else is consumed, (2) consumer specialization will be opposed by the benefits of a mixed diet, and (3) consumer foraging will tend to destabilize the resource community, because rarer resources will be disproportionately consumed.

**Key words:** algae; Anaspidea; complementary resources; *Dolabella auricularia*; foraging theory; herbivory; mixed diet; Opisthobranchia; preference; sea hare; selectivity.

### INTRODUCTION

Foraging theory has traditionally used energy as a common currency to compare the value of different food types (Schoener 1971, Pyke et al. 1977). This approach is valid only to the extent that food types are "substitutable" (sensu Tilman 1988), that is, that they vary little in their nutritional composition (Westoby 1978). For many herbivores and omnivores, this condition is probably not met (Pulliam 1974, Pyke et al. 1977, Morse 1980, Crawley 1983). Many herbivores may be more limited by protein than energy; however, attempts to explain food choices of herbivores as either a function of the energy or of the protein content of plants have had limited success (Paine and Vadas 1969, Vadas 1977, Milton 1979, Bryant and Kuropat 1980, Belovsky 1981, 1984, Owen-Smith and Novellie 1982, Horn 1989, Neighbors and Horn 1991, Dearing and Schall 1992). The common failure of energy or protein

maximization models to explain food choices of herbivores suggests that herbivores may be concerned with multiple aspects of food quality.

A small body of theory has developed around the idea that consumers might be attempting to maximize several nutrients in their diet simultaneously (Rapport 1971, 1980, Marten 1973, Westoby 1974, 1978, Pulliam 1975, Leon and Tumpson 1975, Covich 1976, Belovsky 1978, Abrams 1987, Tilman 1988). If different foods are better sources of different limiting nutrients (i.e., foods are complementary resources, sensu Tilman 1988), consumers might survive on only one or another, but would do best on some mixture (Westoby 1978). In the case of complementary resources, the value of different food types cannot be ranked in any absolute sense, because the value of one food depends upon what else is included in the diet. Rather, preference for a particular food should increase as its relative availability decreases in the environment. This feeding behavior, "negative switching" (sensu Abrams 1987), would maintain the consumer on a mixed diet

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that varies less in composition than do the available resources, because more foraging effort is put into obtaining rare resources (Westoby 1974). In contrast, some predators have been shown to increase their preference for more common food types ("switching," Murdoch 1969, Oaten and Murdoch 1975) when there is a cost (such as time spent in learning) to consuming more than one prey type (Bence 1986, West 1986, 1988).

The importance of a "balanced diet" is well appreciated for humans and livestock (e.g., Zorrilla-Rios et al. 1989, 1991, Chung and Baker 1991, Leeson and Caston 1991): entire journals are devoted to the science of nutrition. Yet, ecologists have been slow to consider the possible importance of mixed diets in explaining foraging choices. There is abundant anecdotal evidence that many organisms supplement an energy-rich diet with food items that are energy poor but rich in other nutrients (Smith 1968, Carroll and Janzen 1973, Morton 1973, Butterfield and Coulson 1975, Gill and Wolf 1975, Morse 1975, 1980, Wolf 1975, Klumpp and Nichols 1983, Thomas 1984, also see Turpin and Johnston 1991). In laboratory studies, a variety of insects has been shown to select a nutritious diet when offered an array of artificial foods each of which was deficient in some nutrient (Waldbauer and Bhattacharya 1973, Waldbauer et al. 1984, Cohen et al. 1987, Simpson et al. 1988, Chyb and Simpson 1990, Simpson and Simpson 1990, Simpson and White 1990, Simpson et al. 1990, 1991, Bernays and Bright 1991). However, only a handful of similar studies has been conducted using natural foods. These have found that a variety of consumers either perform (digest, grow, reproduce, or survive) better on a mixed diet (Curtis and Hurd 1979, MacFarlane and Thorsteinson 1980, Lobel and Ogden 1981, Krebs and Avery 1984, Watanabe 1984, Chinajariyawong and Walter 1990, Dall et al. 1990, Bjornald 1991, but see Larson et al. 1980, Steinberg and van Altena 1992), or exhibit frequency-dependant selection such that individual food types are disproportionately consumed when rare (Greenstone 1979, Kitting 1980, Birkeland and Neudecker 1981, Stamps et al. 1981, Chandra and Williams 1983, Cottam 1985, Guzman and Robertson 1989). Only rarely have both growth on single and mixed diets and selectivity for mixed diets been examined in a single system (e.g., Rapport 1980, Lobel and Ogden 1981).

In addition to the complementary diet hypothesis, there is an alternative, but not mutually exclusive, hypothesis that could also explain the choice of and better performance on mixed diets. Freeland and Janzen (1974) suggested that consumers that feed upon chemically defended prey might eat a mixed diet to avoid consuming too much of any one defensive compound. We will call this the "nonadditive toxin" hypothesis. It requires that the effects of different defensive compounds are less than additive, so that a mixture of compounds is less toxic than any one alone. This could occur if different defensive compounds attacked dif-

ferent targets in the consumer, were detoxified by different metabolic pathways, or reduced each other's toxicity. There is evidence, for example, that some terrestrial plant tannins can reduce the toxicity of alkaloids, saponins, and some other plant defensive compounds (Bernays et al. 1989). More generally, the effects of many plant defensive compounds are poorly understood and not yet predictable, especially in marine systems: compounds that are structurally very similar can have very different effects on consumers; different consumers can respond differently to individual compounds; and there may be little relationship between feeding deterrence and toxicity (Hay and Fenical 1988, Bernays et al. 1989, Bernays 1991, Hay 1991). Thus, we cannot yet predict, based solely on knowledge of the plant secondary metabolites involved, whether the nonadditive toxin hypothesis is likely to hold in any particular case.

Studies finding better growth on mixed diets have rarely tested between the complementary diet and nonadditive toxin hypotheses. The nonadditive toxin hypothesis suggests that a consumer fed a mixed diet will be able to consume considerably more biomass than it did of a single diet (Freeland and Janzen 1974). Theoretically, if the consumer can eat  $a$  grams of diet A and  $b$  grams of diet B over a certain time period ( $a$  and  $b$  being set by the toxicity of the defenses), it could eat  $a + b$  grams of a mixed diet (in practice, the actual amount consumed might be limited to  $<a + b$  grams by the consumer's gut volume). Improved growth on a mixed diet would then be the result of greater total nutrient intake. In contrast, a consumer foraging on complementary diets might not consume a greater mass of a mixed diet than of a single diet. Under the complementary diet hypothesis, greater growth on the mixed diet is not the result of greater total nutrient intake, but rather of a better mix of nutrients.

Here, we experimentally examine the importance of a mixed diet for a single marine herbivore, the sea hare *Dolabella auricularia*. We examine growth on four single-species diets and on a mixture of all four, and examine whether individual *Dolabella* change their foraging preferences so that rarer foods are disproportionately consumed. We then perform two tests between the complementary diet and nonadditive toxin hypotheses to explain the patterns we observed.

#### STUDY SYSTEM AND EXPERIMENTAL APPROACH

We worked with the sea hare *Dolabella auricularia* (henceforth, *Dolabella*), a large (to  $\approx 1$  kg wet mass), herbivorous, opisthobranch gastropod. Postmetamorphic *Dolabella* live to  $\approx 16$  mo, lay benthic egg masses from which larvae hatch in 9–10 d, and have a larval duration of at least 31 d at 24–26°C in the laboratory (Switzer-Dunlap and Hadfield 1977, 1979). On the island of Guam (13°25' N, 144°55' E), *Dolabella* occurs in shallow (<2 m) subtidal areas of mixed sand and boulders.

Common macroalgae at these sites include the red algae *Acanthophora spicifera* and *Galaxaura oblongata*, the brown algae *Dictyota cervicornis*, *D. bartayresii*, and *Padina tenuis*, and the green alga *Halimeda macroloba* (see Tsuda and Wray 1977 and Tsuda 1981 for taxonomic authors). *Padina* is the most common of these. The green alga *Enteromorpha clathrata* and the brown alga *Sargassum cristaefolium* are less common in these habitats, but do overlap in distribution with *Dolabella*. In the laboratory *Dolabella* consumes a variety of macroalgae from all three major divisions: Chlorophyta, Phaeophyta, and Rhodophyta (Pennings and Paul 1992); field diets probably also include an unknown proportion of microalgal "turfs." Examination of stomach contents and sequestered secondary metabolite profiles suggests that *Dolabella* consumes a wide mixture of algae in the field (S. C. Pennings and V. J. Paul, unpublished data). Because *Dolabella* is deterred from feeding by algal toughness and calcification (Pennings and Paul 1992), we chose to focus our experimental work on three common algae (*Dictyota cervicornis*, *Enteromorpha clathrata*, and *Padina tenuis*) that are readily eaten by *Dolabella* (Pennings and Paul 1992). *Dictyota* and *Padina* are thin blades and *Enteromorpha* is a thin tube; consequently, all three are very soft (as measured by a penetrometer). *Padina tenuis* is lightly calcified but is still readily eaten by *Dolabella* (Pennings and Paul 1992).

*Dolabella* can sequester secondary metabolites from algae (Faulkner 1984, 1988; V. J. Paul and S. C. Pennings, personal observations), and is usually not deterred from feeding by crude organic extracts of algae (Pennings and Paul 1992), making it unlikely that its foraging choices would be patterned so as to avoid consuming too much of individual secondary metabolites. Moreover, *Enteromorpha clathrata* contains no known secondary metabolites (V. J. Paul, unpublished data). For both these reasons, we felt it unlikely that the nonadditive toxin hypothesis would apply to our experimental system. However, *Dictyota cervicornis* and *Padina tenuis* do seem to contain secondary metabolites that deter feeding by reef fishes, although these metabolites have not been fully isolated and identified (Wylie and Paul 1988).

We performed three groups of experiments with *Dolabella*. We first compared growth on a mixed diet to that on single-algal diets. Second, we performed two sets of experiments with pairs of algae, testing the hypothesis that *Dolabella* preferences for algae would vary as a function of the relative abundances of the algae. Third, we performed two experiments to distinguish between the nonadditive toxin and the complementary diet hypotheses for the maintenance of a mixed diet.

#### METHODS

We conducted experiments at the University of Guam Marine Laboratory in a large outdoor aquarium with circulating seawater. We collected *Dolabella* from Apra

Harbor, Guam, and algae from several areas around the island. Before each experiment, we starved *Dolabella* overnight; on the following day we weighed them and placed them individually in 20-L translucent flow-through plastic cages submerged in the large aquarium. Individual *Dolabella* were never used more than once in any single experiment; some animals were used in two different experiments. We ran no-*Dolabella* control trials for each of the short-term experiments to determine mass changes of algae in the absence of herbivory (Peterson and Renaud 1989). Algae were spun in a salad spinner to remove water before they were weighed. Because *Dolabella* feed nocturnally (S. C. Pennings, personal observations), feeding experiments were run overnight.

To compare *Dolabella* growth on a mixed diet with that on single-species diets, we grew *Dolabella* on one mixed-species and four single-species diets. Replicate *Dolabella* ( $n = 3$  each) were fed *Dictyota cervicornis*, *Enteromorpha clathrata*, *Padina tenuis*, *Sargassum cristaefolium*, or a mixture of all four in similar amounts. Algae, given ad libitum, were replaced every 1 or 2 d. Animals were weighed at the beginning of the experiment and again after 9 wk growth. Data (percent change in mass of *Dolabella*) were analyzed with ANOVA; initial mass of animals (range: 77–195 g) did not differ between the five treatments (ANOVA:  $F_{4,10} = 1.61$ ,  $P = .25$ ).

To test the prediction that individual *Dolabella* would change their preference for one species of algae vs. another as the relative abundance of the species changed, we fed *Dolabella* pairs of algae at 4:1 and 1:9 ratios, with sufficient algae offered so that the rarer species was not completely consumed. These ratios were a compromise between our desire to use fairly extreme ratios (1:9) so as best to detect any effect, and our limited ability to collect large amounts of *Dictyota* (constraining us to a 4:1 ratio). Eight replicates were performed for each of these ratios of *Dictyota* vs. *Padina*, eight for each ratio of *Padina* vs. *Enteromorpha*, and seven for each ratio of *Dictyota* vs. *Enteromorpha*. The mass change of algae in paired no-*Dolabella* control trials was used to correct the mass change of algae in *Dolabella* trials to yield the amount of each alga actually consumed (see Peterson and Renaud 1989 for a discussion of no-herbivore controls in these types of experiments). Preferences of *Dolabella* for algae were calculated using Manly's index corrected for depletion:

$$\alpha_i = \frac{\ln[(n_{i0} - r_i)/n_{i0}]}{\sum_{j=1}^m \ln[(n_{j0} - r_j)/n_{j0}]}, \quad i = 1, \dots, m$$

where  $m$  is the number of food types,  $n_{i0}$  is the amount of type  $i$  initially present, and  $r_i$  is the amount of type  $i$  consumed (Chesson 1983). Manly's index has the property that it does not change as resource availability changes, unless consumer behavior also changes (Ches-

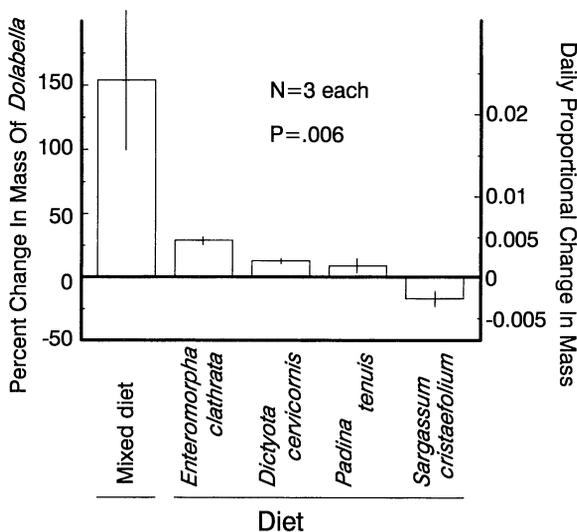


FIG. 1. Growth of *Dolabella* on five ad libitum diets over a 9-wk period. The mixed diet was composed of the other four single-alga diets in similar amounts. Data are means  $\pm$  1 SE,  $n = 3$  for all diets. Means that are not significantly different (ANOVA with Tukey comparisons,  $P < .05$ ) share a common horizontal line.

son 1983). In this case, with two food types ( $m = 2$ ), Manly's index yields the value 0.5 if the consumer eats each food in proportion to its abundance. Values  $>0.5$  indicate high (greater than random) preference; values  $<0.5$  indicate low preference, and, because the  $\alpha_i$  sum to 1, preference for one food type is simply 1 minus preference for the other. Because  $\alpha$  is approximately normally distributed, we tested for a change in preference for an alga between the two treatments (ratios of algae) for each of the three pairs of algae by using  $t$  tests (Chesson 1983).

The second experiment was similar to the first, but instead varied abundance of algae over time. We fed replicate *Dolabella* a single alga ad libitum for 6 or 7 d and then offered them a choice between equal amounts of that alga and another. We ran 7–9 replicates for each of the above three pairs of algae, giving a total of 6 treatments (3 pairs of algae  $\times$  2 feeding histories/pair). As above, we corrected mass loss of algae in the experimental trials by that in paired no-*Dolabella* control trials, and calculated preferences of *Dolabella* for each alga using Manly's index corrected for depletion. For each pair of algae, we tested for a change in preference between the two treatments (feeding histories) by using a  $t$  test. In some cases, we used  $t$  tests to compare groups with unequal variances (as determined by an  $F$  test). The degrees of freedom in these cases are computed using Satterthwaite's approximation and a generalized  $t$  distribution; therefore, they may obtain noninteger values (Snedecor and Cochran 1980).

To determine if the nonadditive toxin hypothesis could explain our results, we performed a consumption experiment by feeding *Dolabella* all single, paired, and

multiple diets of *Dictyota*, *Enteromorpha*, and *Padina*, overnight, for a total of seven treatments. If the non-additive toxin hypothesis applied, animals fed multi-species diets should consume a greater mass of food than animals fed single-species diets. As above, the mass loss of algae in experimental trials was corrected by that in paired no-*Dolabella* control trials. The adjusted amount eaten, expressed as a percentage of the *Dolabella*'s body mass, was compared for the different treatments using ANOVA.

Similarly, if the complementary diet hypothesis was correct, animals fed the same biomass of single- and mixed-species diets should grow better on the mixed-species diet because of a better mix of nutrients. In contrast, if the nonadditive toxin hypothesis was correct, animals fed the mixed diet would not do better if the total biomass eaten was constrained, because the total energy intake on the mixed diet would not be greater than that on the single-species diets. We fed *Dolabella* rationed amounts of *Dictyota*, *Padina*, or a 1:1 combination of the two, for 6 wk. Each *Dolabella* ( $n = 3$  per treatment) was initially fed 160% of its body mass. When all animals had completed or almost completed eating this, they were fed a second portion of 160% their body mass. When the experiment was terminated, the animals fed *Padina* had not completely consumed it; animals fed a mixed diet had eaten all the *Dictyota*, but not all the *Padina*; and animals fed *Dictyota* had eaten it all. Because distributions were markedly non-normal and variances heterogeneous, percent growth of animals on the three diets was compared using the Kruskal-Wallis nonparametric ANOVA. Initial masses of animals on the three diets (range: 81–177 g) did not differ significantly using either a parametric or nonparametric test (ANOVA:  $F_{2,6} = 0.70$ ,  $P = .53$ ; Kruskal-Wallis nonparametric ANOVA:  $H = 1.42$ ,  $P = .49$ ).

## RESULTS

Percent growth of *Dolabella* differed significantly among diets (Fig. 1, ANOVA:  $F_{4,14} = 7.15$ ,  $P = .006$ ; similar results obtained with a Kruskal-Wallis nonparametric ANOVA). After 9 wk animals fed a mixed diet had grown significantly more than animals fed any of the four uni-algal diets (Tukey means comparisons,  $P < .05$ ). We did not include *Sargassum cristaeifolium* in the following experiments because logistics constrained us to working with only three species of algae, and *Sargassum* appeared to be the least palatable and poorest for growth of the initial four (also see Pennings and Paul 1992).

Selectivity of *Dolabella* for algae was strongly affected by the relative abundance of the algae in the diet (Fig. 2). For each pair of algae offered, *Dolabella* significantly shifted its preferences in the direction of greater consumption of whichever alga was rarest. In the first case, *Dolabella* fed *Dictyota* and *Padina* in a 4:1 ratio showed no preference between them ( $\alpha = 0.5$ ),

but strongly preferred *Dictyota* ( $\alpha > 0.9$ ) when *Dictyota* and *Padina* were fed in a 1:9 ratio (selectivity for *Dictyota* differed between treatments:  $n = 8$  each,  $t_{14} = 4.93$ ,  $P = .0002$ ). In the second and third cases, *Padina* : *Enteromorpha* and *Dictyota* : *Enteromorpha*, again offered in 4:1 and 1:9 ratios, *Dolabella* always changed its feeding preferences so that selectivity was greatest ( $\alpha \geq 0.7$  in each case) for whichever alga was rarest (selectivity for *Padina* differed between treatments:  $n = 8$  each,  $t_{14} = 3.48$ ,  $P = .004$ , selectivity for *Dictyota* differed between treatments:  $n = 7$  each,  $t_{12} = 16.71$ ,  $P < .0001$ ). As a result, the mixtures of algae consumed in the two treatments were always more similar than the mixtures of algae offered (Fig. 3). For the *Padina* : *Enteromorpha* and *Dictyota* : *Enteromorpha* pairs, the mixtures of algae consumed were intermediate to those offered. For the *Dictyota* : *Padina* pair, the ratio consumed was  $\approx 4:1$  in each treatment.

Selectivity of *Dolabella* for algae was also strongly affected by their previous diet (Fig. 4). For each pair of algae offered in a 1:1 ratio, *Dolabella* significantly

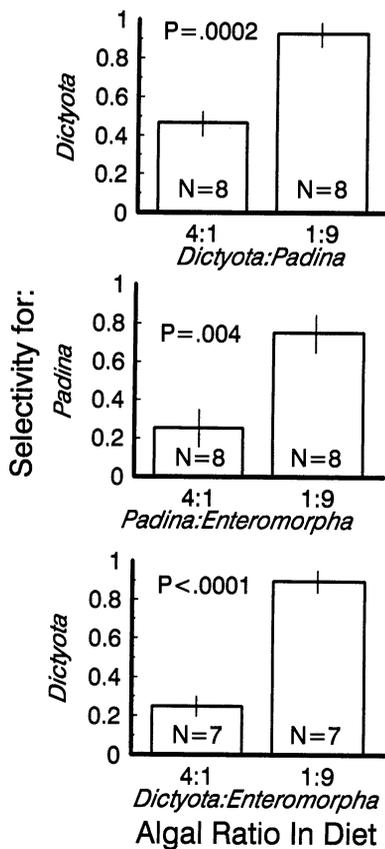


FIG. 2. Selectivity (Manly's index) of *Dolabella* for an alga as a function of its relative abundance. Trials were run with two ratios of each of three pairs of algae. Selectivity = 0.5 indicates no preference. Because selectivity values sum to 1, selectivity for the second alga of each pair = 1 - selectivity for the first alga. Data are means  $\pm$  1 SE and are compared with  $t$  tests.

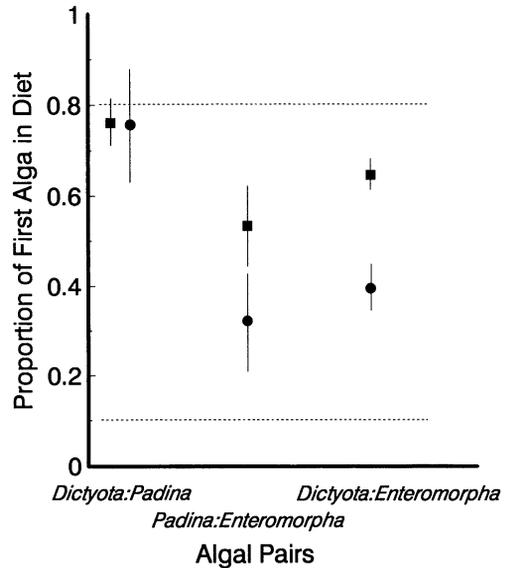


FIG. 3. Mixes of algae consumed compared to mixes offered in the ratio experiment. Data (means  $\pm$  1 SE) indicate, for each pair of algae, the proportion of the first in the diet. ■: 4:1 ratio offered; ●: 1:9 ratio offered. Dotted lines indicate the 4:1 and 1:9 mixes of food initially offered. Because *Dolabella* preferred a more balanced diet than was offered (except for the *Dictyota* : *Padina* 4:1 ratio), they disproportionately consumed the rarer algae. As a result, the mixture of algae available at the end of the experiment was similar to (*Dictyota* : *Padina* 4:1 ratio) or more extreme than (all other cases) the mixture initially offered.

shifted its preferences in the direction of less consumption of the alga that it had been maintained on for the previous week (sample sizes given in Fig. 4, *Dictyota* : *Padina*:  $t_{8,3} = 4.05$ ,  $P = .004$ ; *Padina* : *Enteromorpha*:  $t_{12,2} = 3.18$ ,  $P = .008$ ; *Dictyota* : *Enteromorpha*:  $t_{13} = 2.35$ ,  $P = .035$ ).

Consumption of seven diets by *Dolabella* differed significantly, primarily because of the relatively low consumption of *Padina* (Fig. 5, ANOVA:  $F_{6,55} = 5.00$ ,  $P = .0004$ ). In contrast to the predictions of Freeland and Janzen (1974), in no case was the consumption of a two-species mixed diet significantly greater than that of either of its components alone (ANOVA with Tukey means comparisons); rather, consumptions of all the paired mixes appeared intermediate to consumption of the individual components alone. Consumption of the three-species mixed diet was significantly greater than that of *Padina*, but not of *Enteromorpha* or *Dictyota*. *Dolabella* consumed very similar total amounts of all the single-species and mixed-species diets other than *Padina*, suggesting that, on these relatively high-preference (Pennings and Paul 1992) diets, individual *Dolabella* ate as much as they could (that is, until their digestive systems were full). Consumption of *Dictyota* and *Padina* was similar, but consumption of *Enteromorpha* was less than values obtained in a previous experiment (Pennings and Paul 1992). The very different consumption of *Enteromorpha* in the two ex-

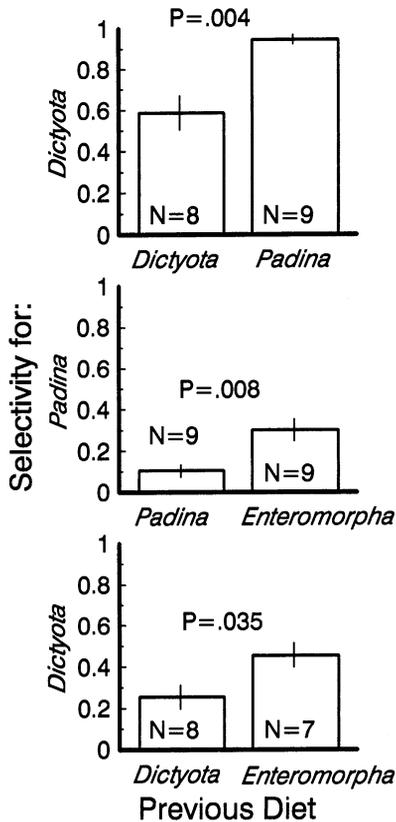


FIG. 4. Selectivity (Manly's index) of *Dolabella* for an alga as a function of the *Dolabella*'s previous diet. Trials were run with three pairs of algae. Selectivity = 0.5 indicates no preference. Because selectivity values sum to 1, selectivity for the second alga in each pair =  $1 -$  selectivity for the first alga. Data are means  $\pm 1$  SE, and were compared with *t* tests.

periments was probably a function of intraspecific differences in plant quality. *Enteromorpha* on Guam appears quite variable in quality depending upon environmental conditions (S. C. Pennings, *personal observation*), although a variety of other factors (season, type of cage, mass of animals) also varied among these experiments.

In the 6-wk experiment, growth of *Dolabella* on rationed diets differed significantly between treatments (Fig. 6; Kruskal-Wallis nonparametric ANOVA,  $H = 6.49$ ,  $P = .039$ ). Poor growth of animals fed *Padina* might be explained by the fact that they had not completely finished eating their ration. However, because animals fed the mixed diet ate slightly less than those fed *Dictyota* (not all the *Padina* was finished), the superior growth on the mixed diet can only be explained by superior utilization of this diet, supporting the conclusion that these algae are complementary resources. In retrospect, considering the results of the *Dictyota* : *Padina* ratio experiment (Fig. 3), the results of this growth experiment might have been even more dramatic had we fed animals their preferred 4:1 ratio of

these two algae, rather than the 1:1 ratio we actually used.

#### DISCUSSION

The results of this study demonstrate that *Dictyota*, *Enteromorpha*, and *Padina* are complementary resources for *Dolabella*, and that, as predicted, *Dolabella* foraging behavior tends to maintain a mixed diet. *Dolabella* grew better upon a mixed diet than upon the individual components of that diet, whether they were offered ad libitum or rationed. Individual *Dolabella* also changed their feeding preferences so that an alga that was rare, or that had not been encountered for some time, was foraged on more selectively compared to that same alga when it was common. As a result, *Dolabella* consumed a mixed diet that varied less than did the availability of the foods.

There is a myriad of reasons why a mixture of algae might be nutritionally superior to any one alone. Research for aquaculture has shown that marine fish and invertebrates are sensitive to a host of food qualities including the relative proportions of protein, carbohydrate, and lipid, the amino acid composition of the protein, the composition of the lipids, and the presence of vitamins and minerals (New 1976, Conklin et al. 1977, Lovell 1989, Dall et al. 1990). Any of these factors could vary between algae, causing a mixture of algae to provide the best diet. For example, Lowe and Lawrence (1976) found that an urchin best assimilated protein from one alga, lipids from another, and carbohydrates from a third, although they did not test whether a mixed diet yielded the best growth. Similarly, algae are known to vary in their amino acid pro-

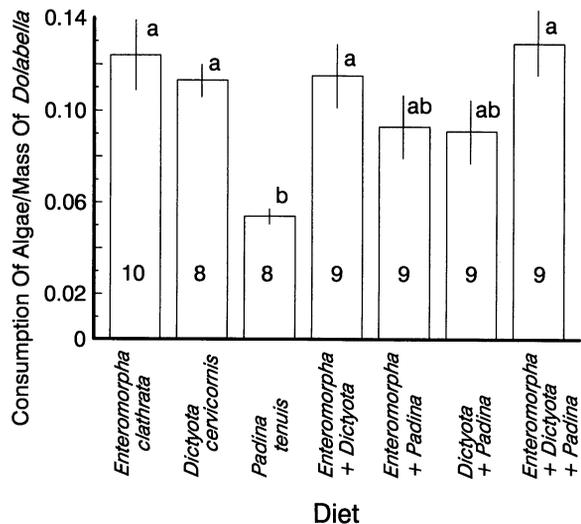


FIG. 5. Overnight consumption of mass on seven diets by *Dolabella*, expressed as a fraction of *Dolabella* body mass. Data are means  $\pm 1$  SE. Means that are not significantly different (ANOVA with Tukey comparisons,  $P < .05$ ) are indicated by common superscript letters. Sample sizes are indicated within the bars.

files (Carefoot 1967, 1982), suggesting that a mixture of algae might provide the best mixture of amino acids. We are aware of no direct tests of this from marine systems, but some work has suggested that sea hares are tolerant to deprivation of individual amino acids (Carefoot 1987). Greenstone (1979) found that a lycosid spider tended to feed upon a mixture of three insect species, thereby consuming a mixture of amino acids closer to that found in the spiders' own bodies than that provided by any single prey species. However, Greenstone did not test whether growth was in fact better upon a mixed diet. Although marine organisms require minerals, it is generally thought that these can be obtained directly from seawater (Biddle 1977, Halver 1989, Lovell 1989, Dall et al. 1990), making it unlikely that mineral deficiencies would create the need for mixed diets as may often be the case in terrestrial systems (Smith 1968, Belovsky 1978). Finally, if gut microbes play a role in the digestion of plant material, the ingestion of additional protein might stimulate microbe growth, leading to superior digestion of plant matter. This phenomenon is well known for some livestock (Zorrilla-Rios et al. 1989, 1991), and may play a role in superior assimilation of a plant-animal diet by turtles (Bjorndal 1991). It is also a possibility for sea hares because they contain microbes in their digestive systems that probably aid digestion of plant matter (Carefoot 1987, Vitalis et al. 1988), and algae are known to vary in their protein content (Carefoot 1967, 1987, Hambrook and Sheath 1987). In general, the nutritional needs of marine invertebrates are poorly known (Carefoot 1980, 1987, but see Carefoot 1984), with the partial exception of economically important species such as some crustaceans (e.g., New 1976, Biddle 1977, Dall et al. 1990), making it difficult to assess without further experimentation which nutritional quality of algae is most likely to be responsible for mixed diets in *Dolabella*.

Compared to other algae common on Guam, *Dictyota*, *Enteromorpha*, and *Padina* are all highly palatable to *Dolabella* (Pennings and Paul 1992). Given a wider range of algal species, factors such as toughness and calcification play important roles in feeding choices by *Dolabella*; however, algal secondary metabolites rarely deter feeding by *Dolabella* (Pennings and Paul 1992). Algae that are well defended against an herbivore are unlikely to be consumed regardless of potential nutritional benefits. Thus, herbivores whose feeding choices are highly constrained by algal secondary metabolites may be unable to select the mixtures of algal species that would be of the greatest nutritional benefit. Similarly, it is possible that there are algal species that would be extremely nutritious to *Dolabella*, but that are not consumed because they are too tough or are calcified.

An alternative hypothesis that might explain our results is the nonadditive toxin hypothesis. We suspected that this hypothesis would not apply to this system

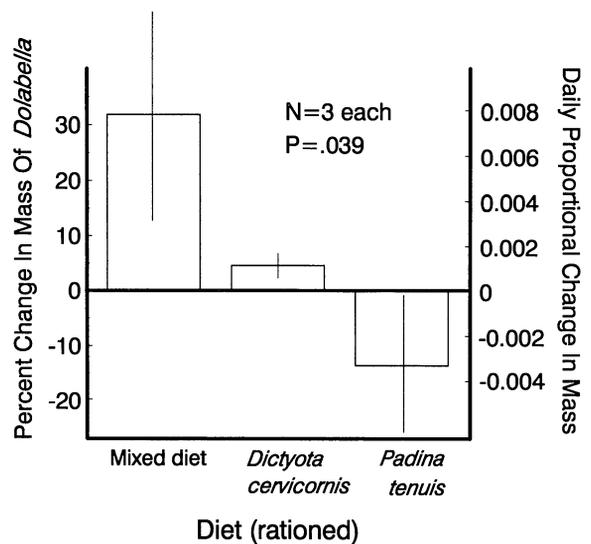


FIG. 6. Growth of *Dolabella* on three rationed diets over a 6-wk period. The mixed diet was composed of a 1:1 ratio of *Dictyota* and *Padina*. Data are means  $\pm$  1 SE,  $n = 3$  for all diets.

because *Dolabella* are resistant to algal secondary metabolites (Pennings and Paul 1992) and because *Enteromorpha* contains none (V. J. Paul, unpublished data). Our experimental results supported this expectation. The nonadditive toxin hypothesis predicts that consumption of a mixed diet would be greater than consumption of single-species diets; with the possible exception of low consumption of *Padina* compared to the triple diet, this prediction was not met. Rather, it seemed that *Dolabella* were feeding to the capacity of their digestive systems upon these fairly palatable foods. In every case, consumption of the mixed diets was very similar to consumption of at least one of the single diets alone. The nonadditive toxin hypothesis also predicts that growth on a mixed diet would not be superior to that on single-species diets if the biomass consumed was similar. This prediction might explain the observed poor growth on *Padina* in the rationed-food growth experiment, because not all the *Padina* was consumed, but it cannot explain the superior growth of animals fed the mixed diet compared to the *Dictyota* diet. Thus, we conclude that the nonadditive toxin hypothesis does, in fact, not apply to this system. However, the combination of an herbivore that is resistant to many secondary metabolites and a group of plants that do not all contain secondary metabolites may be unusual; moreover, there is evidence that some terrestrial plant secondary metabolites can interact in a nonadditive manner (Bernays et al. 1989); thus, the nonadditive toxin hypothesis may well apply to other systems.

A further possibility, somewhat of a hybrid between the complementary diet and nonadditive toxin hypotheses, is that different plants contain antagonistic

compounds that act as digestibility reducers. Under this hypothesis, growth would be better on a mixed diet because of improved digestion, and the patterns of consumption and growth would mimic those obtained under the complementary diet hypothesis. This hypothesis is difficult to evaluate for marine systems because almost nothing is known about the mode of action of marine secondary metabolites (Hay and Fenical 1988, Hay 1991). Moreover, even in terrestrial systems the generalization that certain classes of compounds (e.g., tannins) act as digestibility reducers has been strongly questioned (Bernays et al. 1989). We have no evidence to support this hypothesis, and the fact that *Enteromorpha* has no secondary metabolites argues against it; however, it remains a possibility for further research as our understanding of the physiological effects of marine secondary metabolites grows.

#### *How common are complementary resources?*

Although complementary diets have not received a great deal of attention from ecologists, there is considerable indirect evidence (cited in the *Introduction*), from both field and laboratory studies, that suggests that they may be of importance in a wide variety of systems, both terrestrial and marine. Previous studies with herbivorous marine invertebrates have obtained mixed results. The mud snail *Ilyanassa obsoleta* grew and survived better on a mixed diet of spinach and shrimp than on either alone (Curtis and Hurd 1979), and the snails *Tegula* spp. grew better or had a higher gonad index upon a mixed diet than upon any single diet (Watanabe 1984). Consumption of the mixed diet by *Tegula* spp. was similar to consumption of the most preferred single diet (Watanabe 1984), suggesting that the complementary diet hypothesis explains these results better than the nonadditive toxin hypothesis. In contrast, growth was not better on a mixed diet than on single-species diets for the sea hare *Aplysia californica* (McClelland 1984) or for the urchins *Strongylocentrotus drobachiensis* and *Tripneustes gratilla* (Larson et al. 1980, Steinberg and van Altena 1992). It is not obvious if these differences reflect differences in the physiologies of the respective herbivores or are a function of the particular algae chosen for the experiments. Clearly, more work remains to be done before we can truly assess the generality of our results. However, we offer two hypotheses regarding the generality of complementary diets in nature.

First, complementary diets will be more common in generalists, because they have a wider pool of food species to select nutritional "matches" from. Many moderately polyphagous species are composed of individuals that actually are monophagous (Fox and Morrow 1981). Individuals from such species can commonly be induced to prefer a particular host by feeding on it for a period of time, such that they subsequently avoid a change of diet, and may in fact perform poorly if switched to a new, but otherwise suitable, host spe-

cies (Phillips 1977, Cassidy 1978, Scriber 1979, 1981, 1982, Grabstein and Scriber 1982, Jensen 1989, Karowe 1989, Trowbridge 1991). In contrast, many grasshoppers, which are often polyphagous as individuals, seem to actively mix foods in their diets; preference for a food often declines with experience, and novel foods rise in preference (Lee and Bernays 1988, Bernays and Raubenheimer 1991, Howard and Bernays 1991, Bernays et al., *in press*). The sea hare *Aplysia punctata* could be habituated upon either of two preferred foods after feeding on one for 80 d, such that the other was then avoided, although this effect quickly faded over five subsequent 2-d preference trials (Carefoot 1967). Similarly, McClelland (1984) found that small *Aplysia californica* could be induced to prefer different algae by feeding over 6 wk; however, this effect declined over three successive 6-wk sampling intervals as the animals aged. A likely reason why Carefoot (1967) and McClelland (1984) found induction of preferences with *Aplysia* spp., whereas we found the opposite with the closely related *Dolabella*, is that *Dolabella* is more generalized than are most *Aplysia* spp. (Carefoot 1987, Pennings 1990a, b, Pennings and Paul 1992); significantly, *A. californica* become more generalized as they grow (Pennings 1990a), which may explain McClelland's (1984) observation that only young (small) *A. californica* could be induced to prefer particular algae. Of course, many other factors such as the length of the habituation period also differed between these studies on sea hares.

Second, resources will be increasingly substitutable at successively higher trophic levels. Plants utilize a variety of individual nutrients that are essential (*sensu* Tilman 1988): none can be substituted for another. When an herbivore eats a plant, it consumes a package of nutrients that, although they may not be in the perfect proportions for an animal, at least approximate a reasonable diet (i.e., every plant contains at least some protein, some carbohydrate, etc.). Thus, plants are likely to be complementary resources for herbivores, because although a mixed diet is best, a single diet could potentially sustain life, at least for a while. In contrast, because the nutrients necessary to sustain animal life are likely to be very similar to those contained in another animal, prey may often be substitutable resources for predators. Most theory regarding diet choice has developed around predators, and assumes that resources are substitutable. If, as we suggest, resources for herbivores are often complementary, it will be necessary to explicitly incorporate the concept of complementary resources into theory in order for theory to be successful in predicting the diet choices of herbivores.

#### *Implications*

To the extent that the results obtained here generalize to other herbivores, they suggest a number of important implications. First, it may not be possible

to rank plants in any absolute order of preference to an herbivore, because the value of a plant changes depending upon what else is consumed. The assumption that the rank preference of foods is invariant is central to traditional foraging models (Schoener 1971, Pyke et al. 1977), including some focused specifically upon herbivores (e.g., Courtney et al. 1989). Nevertheless, we were able to reverse the rank order of preference for two algae simply by varying the relative abundance in which they were offered, and we were able to change the degree of preference between two algae by varying herbivore feeding histories. This is not simply a methodological concern relating to the best experimental design to avoid such effects. Rather, understanding this sort of variation is vital to understanding the feeding ecology of such herbivores.

Second, the question "Why be a specialist?" is currently of considerable interest in the plant-herbivore field (e.g., Bernays and Graham 1988, Hay et al. 1989, 1990a, b, Trowbridge 1991). Our results, if general, suggest a constraint that may tend to resist specialization of herbivores: a mixed diet is better (Westoby 1974). Understanding when this constraint is important and when it is not may help explain patterns of specialization among different taxa and/or habitats.

Finally, herbivores that forage upon complementary resources will tend to destabilize plant communities, because plant species that become rare will be consumed at disproportionately higher rates, and species that become common will be consumed at disproportionately lower rates. The consequences for community dynamics are manifold, and have only begun to be investigated with mathematical models (Abrams and Shen 1987).

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