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Prey nutritional quality and the effectiveness of chemical defenses against tropical reef fishes

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Summary. Many coral-reef seaweeds and sessile invertebrates produce both secondary chemicals and mineral or fibrous skeletal materials that can reduce their susceptibility to consumers. Although skeletal materials often have been assumed to function as physical defenses, their deterrent effectiveness may derive from their reduction of prey nutritional quality as well as from noxiousness of the skeletal material itself. To test the relative importance of prey nutritional quality and chemical defenses in susceptibility to predation, we offered reef fishes on Guam a choice of artificial foods varying in nutritional quality (4% versus 22% protein) and in secondary chemistry (spanning approximately natural concentration ranges). Field feeding assays were performed with pachydictyol A from the pantropical brown seaweed genus *Dictyota*, manoalide from the Micronesian sponge *Luffariella variabilis*, and a brominated diphenyl ether from the Micronesian sponge *Dysidea* sp. The results indicated that chemical defenses were less effective in high- than in low-quality foods. In paired assays with metabolite-free controls, all three compounds at natural concentrations significantly reduced feeding by reef fishes only in assays using low-quality food, and not in assays with high-quality food. When fishes were offered an array of artificial foods varying in both food quality and metabolite concentration, food quality significantly affected fish feeding in all three cases, while secondary chemistry was significant in only one. Thus differences in nutritional quality, within the natural range among reef organisms, can be comparable to or greater in importance than secondary chemistry in affecting feeding preferences of their consumers. Reduced nutritional quality may be an important selective advantage of producing indigestible structural materials, in addition to their roles as physical support and defense, in coral reef organisms.

Key words: Chemical defenses – Coral reefs – Nutritional quality – Plant-herbivore interactions – Predator-prey interactions

Plants and sessile animals produce a diverse array of defenses that reduce their susceptibility to damage from predators, including tough structural materials (Steneck and Watling 1982; Harvell et al. 1988) and noxious chemical substances (Rosenthal and Janzen 1979; Hay and Fenical 1988; Paul 1992). In areas of especially high predation risk, many organisms combine several types of defenses. For example, on coral reefs, where predation and herbivory are intense, many of the most conspicuous and abundant sessile organisms produce both deterrent secondary metabolites and structural materials such as mineral skeletons or organic fibers that are commonly believed to serve a protective function (Hay 1984; Paul and Hay 1986; Sammarco et al. 1987; Harvell et al. 1988; Hay et al. 1988b).

The protective roles of chemical and physical defenses in mediating interactions between plants or sessile invertebrates and their predators have received primary emphasis in discussions of consumer-prey interactions in both terrestrial (Feeny 1970; Rosenthal and Janzen 1979; Coley 1983, Rhoades 1983) and marine ecosystems (Steneck and Watling 1982; Littler et al. 1983; Harvell 1984; Paul and Hay 1986; Hay and Fenical 1988; Duffy and Hay 1990). Here we present evidence from field experiments that variation in nutritional quality within the natural range found among reef species is of comparable importance to chemical defenses in affecting an organism's susceptibility to predators. We argue that reduction of prey nutritional quality, and thus attractiveness to consumers, may be an important selective advantage of the large quantities of indigestible mineral and/or fibrous materials characteristically produced by coral-reef invertebrates and seaweeds.

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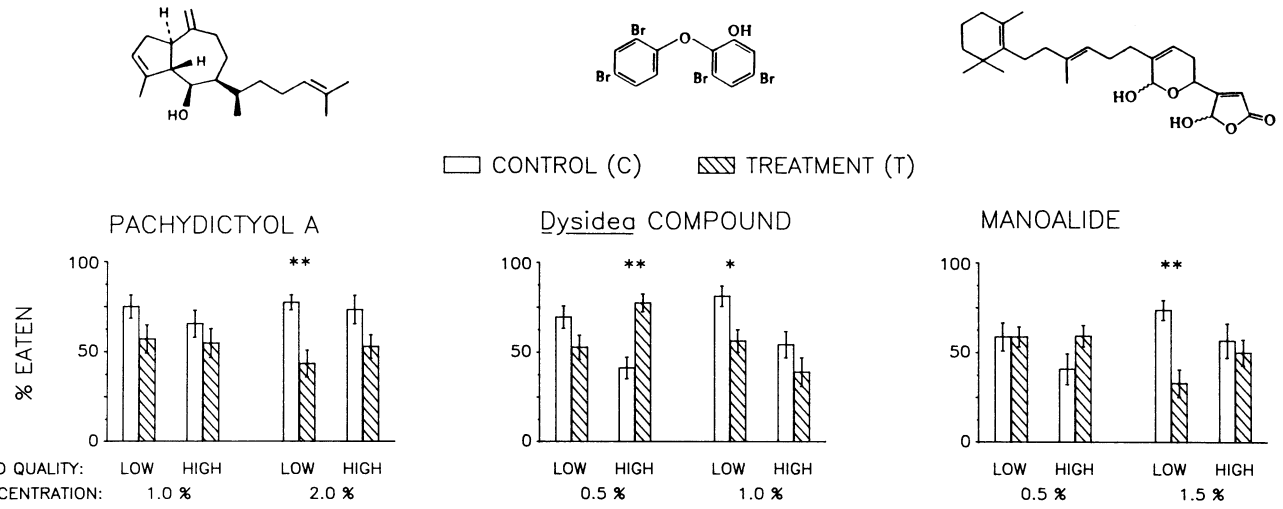

Fig. 1. Results of assays testing the effects of three secondary metabolites on feeding by natural assemblages of reef fishes in Apra Harbor, Guam. Metabolite-treated foods were paired with metabolite-free controls, and each compound was tested at the same concentrations (expressed as % dry mass) in both low-quality (LOW) and high-quality (HIGH) foods (see Table 1). Sample sizes ranged from 16–20 in these paired assays. Differences between treatment and control foods in the number of food cubes completely eaten were assessed with Wilcoxon's paired-sample test. * $0.05 > P > 0.01$, ** $P < 0.01$ (see Results for exact P values)

Methods

We compared the importance of secondary chemistry and nutritional quality for fish feeding preferences by manipulating these characteristics in artificial foods and offering them to natural assemblages of reef fishes in the field. Secondary metabolites were incorporated into carageenan-based foods and deployed, along with appropriate controls, on Fingers Reef in Apra Harbor, Guam (13°25′N, 144°55′E). Three secondary metabolites (Fig. 1) were assayed, one from a seaweed and two from sponges.

The diterpene alcohol pachydictyol A occurs in several species of the pantropical brown algal genus *Dictyota* and deters feeding by numerous fishes and sea urchins (Hay et al. 1987a, b, 1988a, c); its concentration is usually $< 1\%$ of dry mass but may exceed 1% in some populations (Hay et al. 1987b). We tested pachydictyol A at 0.5 and 2.0% of dry mass in our artifical foods.

The Indo-Pacific sponge *Dysidea* sp. (near *D. pallescens,* P. Bergquist, personal communication) produces a brominated diphenyl ether. In specimens of *Dysidea* sp. from Guam this compound constituted $\geq 34\%$ of the total organic extract when isolated by flash column chromatography; since the total organic extract averaged 5.2% of sponge dry mass ($n = 2$), we estimate that this compound comprised 1.5–2.0% of dry mass in sponges from Guam (V.J. Paul and J.E. Duffy unpublished). We tested it at 0.5 and 1.5% of dry mass.

Finally, the sesterterpene manoalide is produced by the Indo-Pacific sponge *Luffariella variabilis* and is the major one of two compounds occurring in extracts of this sponge from Guam (D.J. Faulkner, personal communication). Organic extract yields of *L. variabilis* from Guam averaged 4.8% of sponge dry mass ($n = 12$); assuming that manoalide constitutes at least 50% of this extract, we estimate that it occurs at $\geq 2\%$ of sponge dry mass. We tested manoalide at 0.5 and 1.5% of dry mass. Neither manoalide nor the *Dysidea* compound have been tested previously for feeding deterrent activity.

To assess the relative importance of nutritional quality versus secondary chemistry in prey susceptibility to predation, each compound was assayed in two food types that differed in gross nutrient composition. These foods were made by incorporating different proportions (Table 1) of corn starch, which is 100% carbohydrate, and freeze-dried *Tubifex* worms (hereafter tubifex; Pets Pacifica brand, $\geq 42\%$ protein, $\leq 6\%$ fat, $\leq 2\%$ fiber, 15% ash). The two food types were identical in wet mass, dry mass, and volume; they differed only in the relative proportions of starch and tubifex. The "low-quality" food in our experiments was intended to approximate uncalcified plant tissue (see Montgomery and Gerking 1980) by being low in protein (4% of dry mass, Table 1) and high in carbohydrate, while the "high-quality" food (22% protein) was intended to be closer to spicule-free tissue of marine animals (see Giese 1966). Since growth and feeding are positively related to protein concentration of food in a variety of ecologically diverse fishes (Millikan 1982; Horn 1989), we hypothesized that our high-quality food would be preferred by reef fishes over the low-quality food.

Table 1. Recipes for the artificial foods used in field feeding assays. Each batch of food made 80–90 of the cubes used in experiments

Ingredient	Composition	
	Low-quality food	High-quality food
Carageenan	2.5 g	2.5 g
Corn starch	6.0 g	2.0 g
Freeze-dried Tubifex	1.0 g	5.0 g
Water	100 ml	100 ml
Protein (% of dry mass)	4%	22%
Dry mass	8.5 g	8.5 g
Wet mass	108.5 g	108.5 g

Carageenan, starch, and water (Table 1) were mixed at room temperature and then heated in a microwave oven for 75 s. Pulverized tubifex was then gradually stirred into the hot mixture. After heating for another 10 s, the metabolite, dissolved in a minimal quantity of diethyl ether, was added to the mixture and stirred vigorously. The same quantity of ether without metabolite was added to control foods. The hot fluid was poured into a tray with multiple chambers, each containing a rubber O-ring, and allowed to cool. When separated from the tray, the cooled mixture yielded food cubes, approximately 1 cm on a side, each bearing an O-ring. Cubes of a given food type were attached via the O-rings to a polypropylene rope (4 cubes per rope in paired assays, 10 per rope in multiple-choice assays), which served as one replicate of that treatment.

An initial assay tested whether fishes fed differentially on the high- and low-quality foods. Four cubes of high-quality food,

containing no metabolite or solvent, were attached to a rope. Four cubes of low-quality food, also without metabolite or solvent, were attached to a second rope. Replicated pairs ($n = 18$) of these ropes were attached to the reef at a depth of 2–4 m; members of a pair were separated from one another by about 0.5 m, while replicate pairs were separated by 1 to several m. When fishes had removed roughly half of the cubes from a pair, both ropes were retrieved, and the number of cubes completely eaten from each rope was scored. Differences between treatments in the number of cubes eaten were tested using Wilcoxon's paired-sample test.

Feeding deterrence: paired assays

Two kinds of assay were performed for each compound. Paired assays, of the kind commonly used to measure feeding deterrence (Hay and Fenical 1988), employed a pair of ropes, one bearing four cubes of compound-treated food (treatment) and the other bearing four cubes of the same food type containing only solvent (control). The two ropes were attached to the reef, within about 0.5 m of one another, at a depth of 2–4 m. Replicate pairs ($n = 16$–20) were separated by 1 to several m. After fishes had removed about half of the cubes from a pair, ropes were retrieved and the data analyzed as in the assay described above. Each compound was tested in both low-quality and high-quality food types.

Feeding deterrence: multiple-choice assays

Multiple-choice assays were performed to assess more rigorously the relative importance of nutritional quality and defensive chemistry in food choice by reef fishes. In these assays, three batches of each food quality were prepared, representing two concentrations of a secondary metabolite, and a control with no metabolite. The six resultant food types (2 quality treatments × 3 metabolite treatments) were offered in a choice assay to fishes in the field. Ten cubes of a given food type were attached to a rope, and an array of ropes, containing one of each of the six treatments placed in close proximity to one another, was deployed on the reef. Twelve replicate arrays were deployed for each compound. When fishes had removed roughly half of the cubes from a replicate array, all ropes in that replicate array were retrieved simultaneously, and the mass of food cubes eaten was scored.

Multiple choice assays such as these cannot be analyzed by ANOVA because all treatments (food types, in this case) are present in a given replicate array and are thus presumably exposed to the same individual fishes; this arrangement violates the assumption of independence required by ANOVA (Peterson and Renaud 1989). To avoid this problem, we analyzed the data by deriving indices of the effect of food quality, and of secondary chemistry, and comparing the magnitude of the two indices as follows. The "Effect of Food Quality" is a measure of the change in food consumption caused by changing food quality; it was defined for each replicate by subtracting the amount of low-quality food eaten from the amount of high-quality food eaten at each of the three compound concentrations (i.e. two concentrations plus control), and averaging these three values. The "Effect of Secondary Chemistry" similarly reflects the change in amount of food consumed that was caused by changing the concentration of the secondary compound; it was defined for each replicate by 1) subtracting amount eaten of the low-quality control food from that of the low-quality food with the higher metabolite concentration, 2) computing the same difference for high-quality foods, and 3) taking the average of these two. Calculation of the Effect of Secondary Chemistry used only data for the higher metabolite concentration because using both low and high concentrations would require that they each be subtracted from the same control value, thus rendering the two numbers non-independent, and possibly biasing the calculated variable. Basing our calculation on only two values per replicate in this way would tend to increase its variance, possibly lessening the liklihood of detecting a significant Effect of Secondary Chemistry (relative to the Effect of Food Quality, which is based on the average of three values per replicate). We suspect, however, that this bias is more than offset by the greater values calculated for the Effect of Secondary Chemistry when data for the lower metabolite concentration are omitted, and that, overall, this method should increase the probability of detecting a significant Effect of Secondary Chemistry.

The significance of the "main effects", food quality and secondary chemistry, were each tested using a 1-sample t-test, and their combination of food quality and secondary chemistry; when the value of this variable is significantly > 0 (as for the *Dysidea* compound), it means that food quality had a significantly greater effect on food consumption than did secondary chemistry. $n = 12$ for each comparison. Data are from multiple-choice feeding assays (Fig. 2)

Table 2. Relative importance of food nutritional quality and secondary chemistry in affecting feeding by reef fishes on Guam. Each index (defined in Methods: Feeding deterrence: multiple-choice assays) is expressed as the mean (±1 SE) change in food consumption (as both mass and percentage eaten) caused by that factor. EFQ + ESC = the net change in food consumption caused by the

Experiment Index	Change in food consumption		P[1]
	Mass (g)	%	
Pachydictyol A			
Effect of food quality (EFQ)	2.51 ± 0.36	23.50 ± 3.29	< 0.0001*
Effect of secondary chemistry (ESC)	−0.93 ± 0.60	−7.31 ± 5.80	0.1532
EFQ + ESC	1.58 ± 0.87	16.20 ± 8.45	0.0964
Dysidea brominated diphenyl ether			
Effect of food quality	2.93 ± 0.42	28.43 ± 3.88	< 0.0001*
Effect of secondary chemistry	0.88 ± 0.80	3.66 ± 3.93	0.2987
EFQ + ESC	3.80 ± 0.91	32.08 ± 4.65	0.0015*
Manoalide			
Effect of food quality	1.95 ± 0.59	19.15 ± 5.45	0.0073*
Effect of secondary chemistry	−2.19 ± 0.56	−20.73 ± 5.21	0.0025*
EFQ + ESC	−0.24 ± 0.93	−1.58 ± 8.60	0.8006

[1] P values are from one-sample t-tests (for EFQ and ESC) or paired-sample t-tests (for the sum EFQ + ESC) performed on data for mass eaten. * denotes values significant at $P = 0.017$, the comparisonwise P value required to control for an experimentwise α of 0.05 for 3 planned comparisons, according to the Dunn-Sidak method (Sokal and Rohlf 1981): $\alpha' = 1 - (1 - 0.05)^{1/3}$

relative importance was tested via a paired-sample t-test. An experimentwise alpha level was calculated for the 3 planned comparisons in each assay using the Dunn-Sidak method (Sokal and Rohlf 1981): $\alpha' = 1-(1-\alpha)^{1/k}$, where k = the number of planned comparisons.

Results

When foods containing no compound or solvent were deployed in the field, the high-quality food was strongly preferred over the low-quality food ($P<0.001$, Wilcoxon's paired-sample test), confirming that fishes recognize these artificial foods as different in attractiveness; $67 \pm 6\%$ of the high-quality cubes were completely eaten, compared with $10 \pm 4\%$ of the low-quality cubes. Fishes observed feeding on the foods in this and the following assays included the damselfishes *Abudefduf sexfasciatus, A. saxatilis,* and *Amblyglyphidodon curacao,* the wrasses *Cheilinus fasciatus, Thalassoma hardwickii* and *T. lutescens,* the butterflyfish *Chaetodon ulietensis,* and the triggerfish *Balistipus undulatus*. The three damselfish species appeared to be the major consumers of food cubes in these experiments.

Feeding deterrence: paired assays

All 3 compounds deterred feeding by reef fishes in the field when presented in paired assays with compound-free controls; the effectiveness of the deterrence varied, however, with food quality and compound concentration (Fig. 1). Specifically, all three compounds were less effective deterrents in high-quality foods than in low-quality foods. Pachydictyol A, at 2% of food dry mass, significantly reduced fish feeding in the low-quality food ($P=0.009$, Wilcoxon paired-sample test) but not in the high-quality food ($P=0.127$). Similarly, the *Dysidea* compound, at 1% of dry mass, reduced fish feeding in the low-quality food ($P=0.029$) but not in the high-quality food ($P=0.296$). Manoalide also was a significant deterrent at high concentration (1.5%) in the low-quality food ($P=0.006$) but not in the high-quality food ($P=0.658$). At lower concentrations neither pachydictyol A nor manoalide significantly affected fish feeding in either food type, and the *Dysidea* compound actually enhanced feeding at 0.5% in the high-quality food ($P=0.005$).

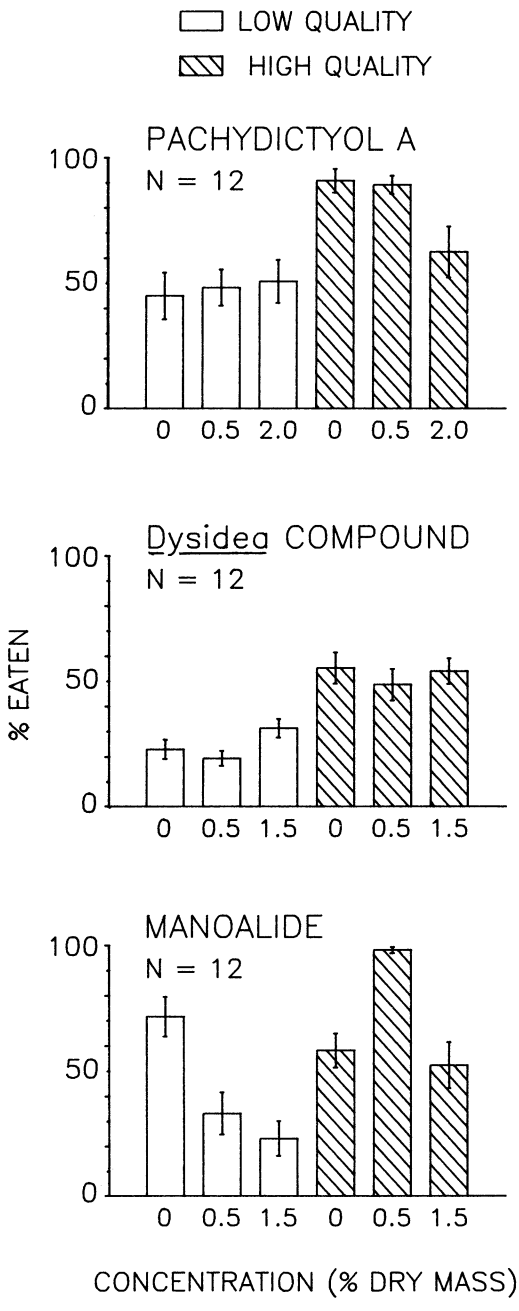

Fig. 2. Results of multiple-choice feeding assays testing the relative importance of food quality and secondary chemistry in feeding by reef fishes on Guam. Foods were offered to fishes in replicated arrays ($n=12$) of 6 ropes, with each rope bearing one of the six food types (2 food qualities × 3 metabolite concentrations). Statistical analyses of the results are presented in Table 2

Feeding deterrence: multiple-choice assays

The multiple-choice assays demonstrated that, for all three compounds, the effect of food quality was of similar or greater magnitude to that of secondary chemistry (Table 2, Fig. 2). Specifically, the Effect of Food Quality was significant for all three compounds, while the Effect of Secondary Chemistry was significant only for manoalide (Table 2), despite the fact that all three compounds significantly deterred fish feeding in the paired assays (Fig. 1). If only the high-quality food treatments are considered, however, pachydictyol A at 2% was also deterrent relative to the compound-free control ($P<0.020$, t-test). Most interestingly, the Effect of Food Quality was significantly greater than the Effect of Secondary Chemistry for the *Dysidea* compound (i.e. EFQ + ESC > 0, Table 2), while the effects of these two factors were not significantly different for pachydictyol A or manoalide.

Discussion

The most consistent result of these experiments was an important effect of food nutritional quality on fish feeding. Interestingly, the effectiveness of chemical defenses appeared to be inversely related to food quality; in the paired assays, all three compounds at high concentrations significantly deterred feeding in low-quality food but not in high-quality food (Fig. 1). In the multiple-choice assays, where fishes had simultaneous access to all combinations of food quality and secondary metabolite concentration, the effect of food quality was significant and of comparable or greater magnitude to that of secondary chemistry for all three metabolites tested (Fig. 2, Table 2). These experiments suggest that differences in nutritional quality within the natural range occurring among coral reef organisms may be as important as, or more important than, demonstrated chemical defenses in affecting susceptibility to predators.

Despite extensive data on the importance of prey nutritional quality (Horn 1989) and secondary chemistry (Hay and Fenical 1988, Paul 1992) in determining feeding rates of fishes, the interaction between these factors previously has not been studied experimentally. Likewise foraging theory, though reasonably successful in predicting consumer responses to prey caloric and nutrient composition (Belovsky 1984; Pyke 1984), has been less successful in integrating the role of prey chemical defenses (Neighbors and Horn 1991). We are aware of only one other experimental study comparing food quality and chemical defenses. Pennings and Paul (in press) tested the feeding deterrent activity of extracts of the green seaweed *Halimeda macroloba,* and of $CaCO_3$, against a sea hare. In contrast to the trends documented here (Fig. 1), the *Halimeda* extract was similarly deterrent in foods with and without $CaCO_3$ added at 50% of dry mass (which could be considered low- and high-quality foods respectively). However, these authors demonstrated that addition of reagent-grade $CaCO_3$ (i.e. in the form of powder, not spicules) alone greatly reduced feeding by this animal, supporting our findings of an important role for nutritional quality in food choice. Since multiple-choice assays comparable to those in Fig. 2 were not conducted, the relative importance of *Halimeda* chemistry and calcification cannot be as easily assessed.

The legitimacy of comparing food quality and secondary chemistry depends on whether the levels used for these two factors in our assays are similarly realistic, i.e. whether a fish is likely to encounter this range in food quality and secondary chemistry among the foods it normally samples. Natural concentrations of pachydictyol A have generally been estimated at $\leq 1\%$ of dry mass in *Dictyota* species (Hay et al. 1987b), so the higher concentration used here is likely above natural levels. This only increases our confidence in the importance of nutritional quality, however, since food quality was more important to fish preference than pachydictyol A despite the latter's unnaturally high concentration. On the other hand, the concentrations of manoalide and the *Dysidea* compound used in this study may be slightly lower than those occuring naturally in Micronesian sponges (see Methods). Thus while it is not clear how closely the concentrations we used approximate mean values for organisms in the field, they appear to be within the natural range for both sponge compounds. In any event, the trend for feeding deterrence to be less effective in higher-quality foods was consistent for all three compounds.

The two nutritional quality treatments also appear to be within the natural range for marine algae and sessile invertebrates. Published values for protein concentration in seaweeds range from 0.8% of dry mass in the calcareous red *Jania* sp. to 13.2% in the green *Ulva* sp. (Montgomery and Gerking 1980), a 16-fold difference. Among sessile marine animals, (soluble) protein concentrations have been reported from 4.9% of dry mass in the sponge *Sphaerotylus antarctica* (McClintock 1987) to 51% in the anemone *Anthopleura xanthogrammica* (Giese 1966), a 10-fold difference. Thus both marine herbivores and carnivores have access to prey species spanning a wide range in protein content. In fact, the natural range in protein content among marine organisms is greater than what we used, and the significant effect of food quality in assays of all three metabolites (Table 2) may thus be conservative.

Although the chemical basis by which fishes discriminated between low- and high-quality foods is unknown, whether they cue on protein or some other substance does not affect our results as long as the cue is positively correlated with food nutritional value. Since fishes preferred high-quality food over low-quality food in the absence of secondary metabolites (see Results), this appears to be the case.

The effects of secondary chemistry on fish feeding were less consistent than those of food quality. The lack of significant feeding deterrence by pachydictyol A and the *Dysidea* compound in the multiple-choice assays is curious, since both compounds deterred feeding in the paired assays (Fig. 1). Moreover, pachydictyol A deters feeding by numerous species of herbivorous fishes and urchins worldwide (Hay 1987a, b, 1988a, c). The lack of significant feeding deterrence by these compounds in the multiple-choice assays, and the inconsistencies between the two types of assays generally (e.g. the *Dysidea* compound at 0.5%, Figs. 1,2), may have resulted from the complex design of the multiple-choice assays, i.e. the large number of alternate foods available. For example, food "patch size" was considerably larger in multiple-choice than in paired assays, since each replicate array in the former bore a total of 60 food cubes, while each replicate pair in the latter bore only eight cubes. The larger patch size in the multiple-choice assays may have minimized the impact of random sampling of the foods by fishes, and thus produced a more accurate picture of their feeding preferences; alternatively, the greater number of choices in the multiple-choice assays may have overwhelmed the fishes' capacity for decision-making and thus obscured feeding preferences seen more clearly in the paired assays. In any case, the significant effect of food quality was considerably clearer than that of secondary chemistry in the multiple-choice assays (Table 2, Fig. 2). Interestingly, manoalide's trend toward feeding

stimulation at 0.5% in the high-quality food was consistent in both types of assays (Figs. 1, 2), suggesting that this non-linear pattern of feeding response with metabolite concentration may be a real phenomenon. We are unaware of other reports of such non-linear effects of compound concentration on feeding, but the analogy with plant extracts used in small quantities by humans as flavor-enhancers (spices) is interesting. One practical implication of these results is that tests of chemical feeding deterrence should use experimental foods that match the source organism's nutritional (and probably physical) composition as closely as possible.

A corollary of the trend toward an inverse relationship between food quality and effectiveness of chemical defenses is that more nutritious tissues, such as those of most sessile animals, should be better defended than less nutritious ones, such as those of seaweeds. Quantitative data on concentrations of secondary metabolites in marine organisms are too scarce to evaluate this possibility with any rigor. However, it is interesting that concentrations of non-polyphenolic metabolites in seaweeds are rarely reported to exceed 5% of plant dry mass, and are usually much lower (Hay and Fenical 1988); in contrast, there are several reports of similar secondary metabolites in octocorals reaching 12–18% of dry mass (Harvell et al. 1988; Wylie and Paul 1989) or 8% of wet mass (Schneider et al. 1977). Comparisons among individuals or tissues of a species also suggest stronger chemical defense of more nutritious tissues. Inverse relationships between concentrations of secondary metabolites and content of mineral spicules or ash have been demonstrated in green algae (Hay et al. 1988b), gorgonians (Harvell and Fenical 1989), and soft corals (Wylie and Paul 1989). These relationships generally are interpreted as showing that chemical and structural defenses can compensate for one another to some extent (Hay et al. 1988b, Harvell and Fenical 1989). However, indigestible structural materials may also decrease the prey's nutritional attractiveness. Since many reef predators, such as parrotfishes, pufferfishes and triggerfishes, can consume even heavily armored prey (Neudecker 1979; Palmer 1979; Wellington 1982; Steneck 1983), an additional function may be likely for the abundant mineral and fibrous materials in reef seaweeds and invertebrates. Our results suggest that reduced nutritional attractiveness could be an important component of the function of these materials in reef organisms.

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