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Specialist Herbivores Reduce Their Susceptibility to Predation by Feeding on the Chemically Defended Seaweed *Avrainvillea longicaulis*

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Source: *Limnology and Oceanography*, Vol. 35, No. 8 (Dec., 1990), pp. 1734-1743

Published by: American Society of Limnology and Oceanography

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## Specialist herbivores reduce their susceptibility to predation by feeding on the chemically defended seaweed *Avrainvillea longicaulis*

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### Abstract

The tropical green seaweed *Avrainvillea longicaulis* is a low preference food for coral-reef fishes, and it produces a brominated diphenylmethane derivative called avrainvilleol that significantly deters feeding by reef fishes in field bioassays. In contrast to the pattern for fishes, the ascoglossan gastropod *Costasiella ocellifera* and the crab *Thersandrus compressus* live on and eat only *Avrainvillea*. The gastropod sequesters avrainvilleol from its algal host and uses this compound as an effective defense against predatory fish. The crab does not sequester chemical defenses; however, it is camouflaged when on *Avrainvillea* and thus also experiences less predation when associated with this alga. Specialization on this chemically defended seaweed allows *Costasiella* to deter and *Thersandrus* to avoid predation. When coupled with other recent studies of specialist marine herbivores, these findings suggest that predator avoidance and deterrence are major advantages associated with the evolution of feeding specialization among herbivorous marine invertebrates.

There is considerable controversy regarding the factors selecting for feeding specialization among herbivorous invertebrates (e.g. Bernays and Graham 1988; Jermy 1988; Schultz 1988). Most investigations attempting to explain the evolution of feeding specialization (see Futuyma 1983; Futuyma and Moreno 1988) have focused on terres-

trial insects because such a high proportion (estimated at up to 90%, see Bernays 1989) are specialized feeders. Marine communities, however, may offer a more tractable and productive system for determining the factors selecting for host-plant specialization because they contain few specialist herbivores (Hay in press). Additionally, the rarity of specialist marine herbivores may mean that specialization occurs under a limited number of intense selection regimes. If so, then factors selecting for specialization may be more obvious in marine than in terrestrial communities.

Differences between marine and terrestrial communities in the proportion of specialist herbivores may occur, at least in part, from basic differences in the life histories of insects vs. marine invertebrates. Specialization of terrestrial insects may be favored by the common occurrence of short-lived adults equipped primarily for mating, dispersal, and careful placement of eggs on appropriate hosts. The less mobile juveniles are

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### Acknowledgments

Primary support was provided by National Geographic Society grant 3400-86 to M.E.H. Additional support was provided by NSF grants OCE 86-08663 and OCE 89-00131 to M.E.H. and OCE 86-00998 to V.J.P. and University of North Carolina Research Council grant 44132 to M.E.H. Work at Carrie Bow Cay, Belize, was facilitated by the Smithsonian Institution's Caribbean Coral Reef Ecosystem Program (this is publication 311 from that program). Work in the Bahamas was conducted from the RV *Columbus Iselin* (University of Miami) which was funded by the NSF through grant CHE 86-20217 to W.F.

Suzanne Fredericq and Max Hommersand provided algal identifications. Brian Kensley identified the crab.

equipped primarily for feeding and growth on the host where they are placed by the adult. In contrast to terrestrial insects, most marine herbivores disperse widely in the plankton as relatively short-lived juveniles that have limited options for selecting particular host plants on which to settle.

Alternately, the generalized feeding by marine herbivores might occur because seaweeds are less structurally or chemically diverse than terrestrial plants (i.e. have a greater degree of "sameness"). This explanation seems unlikely given the tremendous diversity of secondary metabolites produced by seaweeds (Faulkner 1988) and the structural and morphological complexities of seaweeds (Taylor 1960).

The relative scarcity of specialization among marine herbivores may therefore be due to their broadly dispersing larvae and the difficulties of highly selective settlement by juveniles (Hay and Fenical 1988; Hay in press), especially in habitats where the probability of larvae being consumed by predators increases dramatically as larvae approach the bottom (Gaines and Roughgarden 1987). Although these contrasts between terrestrial and marine herbivores may explain differences in the proportion of specialized feeders, we see no a priori reasons to suspect that the processes selecting for specialization would be fundamentally different in marine than terrestrial communities.

Several recent studies of seaweed chemical defenses have noted that seaweeds containing compounds that deter fish feeding are often selectively consumed by small, relatively sedentary herbivores such as amphipods, polychaetes, and ascoglossan gastropods (collectively termed mesograzers); the metabolites that deter fishes do not affect, or may stimulate, feeding by the mesograzers (see Hay in press; Hay et al. 1989, 1990). It has been hypothesized that the preference of some mesograzers for seaweeds that are chemically defended has been driven primarily by the advantages of decreased predation that mesograzers might experience while living on a host plant that is seldom eaten or visited by fishes (Hay et al. 1987a, 1988a,b; see also Bernays and Graham 1988). Resource partitioning or

other factors commonly hypothesized to select for feeding specialization are thought to be less important because mesograzer populations are often limited by predators but rarely limited by food (Van Dolah 1978; Nelson 1979a,b; Edgar 1983a,b). Although we developed this hypothesis working with generalist mesograzers that fed preferentially on chemically defended host plants, we reasoned that the effect of host-plant fidelity on susceptibility to predation might be more clearly investigated with specialist herbivores because we could limit the number of alternate hosts that would need to be considered.

In this study we focused on the chemically defended green seaweed *Avrainvillea longicaulis*, its specialist grazers (a crab and an ascoglossan sea slug), and the effects of host-plant specialization on the susceptibility of these mesograzers to predation by a common reef fish.

#### Methods

*Organisms and study sites*—Most of our studies were conducted in January 1988 from the Smithsonian Institution's field station on Carrie Bow Cay, Belize. A few collections and follow-up studies were conducted in summer 1988 and 1989 on-board ship during cruises that visited numerous reefs throughout the Bahamas. The site in Belize is described at length by Rutzler and Macintyre (1982).

The green, fan-shaped seaweed *A. longicaulis* was common in the 3–4-m-deep seagrass (*Thalassia*) bed immediately adjacent to Carrie Bow Cay. This seaweed produces a brominated diphenylmethane derivative (Fig. 1) that is ichthyocidal, antibacterial, and deters feeding by a damselfish in laboratory assays (Sun et al. 1983). In the Caribbean, *A. longicaulis* grows from the low-tide line to depths of 30 m (Taylor 1960) and occurs on reefs, sandy plains, and in seagrass beds. Because *A. longicaulis* cannot always be separated from *Avrainvillea nigricans* (both may be the same species—see Norris and Bucher 1982), it is possible that a few individuals of *A. nigricans* may have been included in our field identifications.

The ascoglossan gastropod *Costasiella ocellifera* (= *C. lilianae*) is a specialist feeder

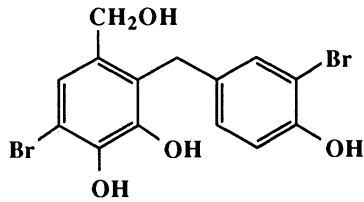


Fig. 1. The structure of avrainvilleol.

on species of *Avrainvillea* (Jensen 1980). Like other ascoglossans (Trench 1975), it sequesters functional chloroplasts from its algal host; these are stored intracellularly and continue photosynthesis with an appreciable portion of the fixed carbon being transferred to the ascoglossan (Clark et al. 1981). *Costasiella ocellifera* is a direct developer. It lays eggs on the plant from which it feeds and the young undergo their complete metamorphosis in the egg capsule. Thus, there is no larval dispersal stage. In Belize and in the Bahamas, we found *C. ocellifera* only on *Avrainvillea*.

Little is known about the crab *Thersandrus compressus*. It is compressed and has hairlike projections over its body and legs (illustrated in Fig. 2). These projections give it a feltlike appearance that, along with its green coloration, allows the crab to blend perfectly with the surface of *Avrainvillea*. When on *Avrainvillea*, the crab is extremely cryptic. In the field, we commonly detected gastropods (*Costasiella*) that were only 2–3 mm long but did not see crabs on the same plants even though the crabs were as large as 15 mm in carapace width. We often would not detect crabs until plants were returned to the laboratory and examined more closely. In both Belize and the Bahamas, we found these crabs only on *Avrainvillea*. Nothing is known of the life-history attributes of this crab. We presume that it has broadly dispersing zoeae like other crabs.

*Seaweeds used by Costasiella and Thersandrus*—We extensively searched numerous reef and grass-bed habitats around Carrie Bow Cay for both of these herbivores. Although they appeared to occur only on *Avrainvillea*, we also thoroughly searched other related genera of green seaweeds such as *Udotea*, *Caulerpa*, *Rhypocephalus*, *Penicillus*, and *Halimeda*. In addition to visual searches in the field, we collected numerous

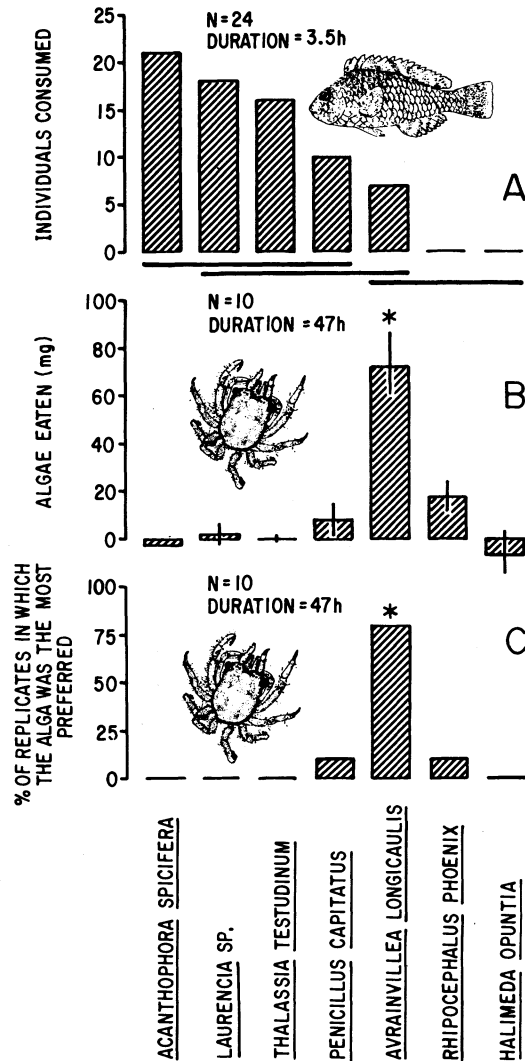


Fig. 2. Feeding on seven common seaweeds by reef fish (A) and by *Thersandrus compressus* (B and C). Lines below panel A connect species that do not differ significantly ( $P < 0.05$ ,  $G$ -test). The asterisk in panel B indicates species for which mass change is significantly different in the presence ( $N = 10$ ) vs. absence ( $N = 5$ ) of crabs ( $0.0025 > P > 0.001$ ,  $t$ -test). Vertical lines through the bars show  $\pm 1$  SE. The asterisk in panel C marks the only species responsible for producing the significant ( $0.025 > P > 0.01$ ,  $G$ -test) among-species difference in the frequency of being the most heavily consumed alga.

individuals ( $> 20$ ) of these genera from habitats where *Costasiella* and *Thersandrus* were abundant and carefully examined each plant in the laboratory. Additionally, when we located *Avrainvillea* plants containing *Cos-*

*tasiella* in the field, we carefully examined the nearest individual of *Udotea flabellum* and *Halimeda* spp. (related green seaweeds that were common at Carrie Bow Cay and known to be fed upon by other species of ascoglossans) for *Costasiella*. We did so rigorously near 48 *Avrainvillea* plants occupied by *Costasiella*.

To determine feeding preferences of *Thersandrus*, we placed 10 crabs in individual, 1-liter bowls. Each bowl held pieces of the seven most common seaweeds from the seagrass bed with the highest density of crabs. Because crabs may find their foods visually, we used algal pieces all having about the same projected surface area. Each algal portion was blotted and weighed to the nearest milligram at the beginning of the experiment and after 47 h of exposure to crab grazing. Because no more than 37% of the wet mass of any portion was eaten during the assay, crabs always had access to all seven seaweeds. Five additional bowls, holding seaweeds but without crabs, served as controls; algae in these bowls were used to estimate changes in algal mass that were unrelated to crab grazing.

Effects of crab grazing were evaluated with a *t*-test to compare mass changes in replicates with vs. without crabs for each seaweed. Among-seaweed comparisons were not made because all seaweeds were simultaneously available, making grazing on the different species non-independent and invalidating ANOVA-type analyses (see Hay et al. 1988a; Peterson and Renaud 1989). We also determined the seaweed that was consumed most in each replicate and used a *G*-test to evaluate among-species differences in the frequency of being most heavily consumed.

Crab preferences were compared to those of reef fish by placing equal-length portions (5–6 cm) of each of these same seaweeds in lengths of three-strand rope and transplanting these ropes ( $N = 24$ ) onto patch reefs near the grass bed. After 3.5 h, the ropes were collected and each algal portion was scored as still present or completely consumed (see Hay 1984). Among-species differences in the frequency of being completely consumed were analyzed with a *G*-test.

Because ascoglossans do not consume

pieces of algae but feed by piercing algal cells and sucking the sap, algal consumption by *C. ocellifera* could not be measured directly. Additionally, amount of material actually consumed can be very small and difficult to measure because specialist ascoglossans may meet virtually all of their respiration needs with energy derived from the photosynthesis of sequestered chloroplasts rather than from plant-derived energy sources (Trench 1975; Clark et al. 1981). To get some indication of *Costasiella*'s preference among seaweeds, we placed individual animals in separate, 1-liter containers ( $N = 20$ ) with approximately equal-sized portions of *A. longicaulis*, *U. flabellum*, and *Udotea cyathiformis* (*Udotea* and *Avrainvillea* are related, co-occur in seagrass beds and on reefs, and are similar in gross morphology, except that *Udotea* is calcified). We then monitored which alga each animal occupied after 1, 2, 4, 5, and 12 h. This same assay was also performed for *T. compressus* ( $N = 14$ ). The assay was repeated for *Costasiella* with *Avrainvillea*, *Dictyota* sp., *Halimeda opuntia*, and *Penicillus capitatus* as the algal choices. This assay was monitored after 15, 30, and 60 min.

*Chemical defense of Avrainvillea and its herbivores*—We determined if avrainvilleol occurred in *A. longicaulis*, *T. compressus*, or *C. ocellifera* by using thin-layer chromatography to compare the diethyl ether extracts of several freshly collected individuals of each species to a purified avrainvilleol standard. About 50 *Costasiella* were placed in ether and returned to the University of Guam for careful determination of extract mass and mass of avrainvilleol per mass of ascoglossan.

To determine if avrainvilleol affected feeding by reef fishes, we treated the palatable seagrass *Thalassia testudinum* with avrainvilleol so that the compound would constitute 1% of *Thalassia*'s dry mass. This concentration is the natural average in *A. longicaulis* (Sun et al. 1983). *Thalassia* blades were cut into 6-cm lengths and blotted dry. Avrainvilleol dissolved in diethyl ether was then applied to the surface of each blade. Because avrainvilleol is hydrophobic, it stays on the surface of the blade after the ether evaporates. In quantitative tests

with a compound of similar polarity, 94% of the compound could be recovered from the treated plants after 24 h in seawater (Hay and Fenical 1988). Control blades were coated only with diethyl ether.

Four control blades were placed in a section of three-strand rope, four avrainvilleol-treated blades were placed in a second rope, and these paired treatment and control ropes were anchored within 1 m of each other on the shallow back-reef at Carrie Bow Cay where they were accessible to herbivorous reef fish. Twenty-five pairs of ropes were placed on the reef. After 4.5 h, the ropes were collected, and grazing was measured as the projected surface area removed from the blades on each rope (see Hay et al. 1987b). If all the *Thalassia* on both ropes, or no *Thalassia* on either rope, was eaten, that rope pair was excluded from consideration because it provided no information on relative palatability. This exclusion reduced the actual sample size from 25 to 20.

To see if avrainvilleol cued feeding or habitat choice by *Costasiella* or *Thersandrus*, we performed two similar assays. In the first, disks of *Ulva* sp., each 1 cm in diameter, were treated either with pure ether (=control) or with avrainvilleol in ether so that the compound made up 1% of algal dry mass. One treatment and one control disk were paired in 100-ml containers, each of which contained one crab ( $N = 15$ ) or one ascoglossan ( $N = 25$ ). These containers were monitored at irregular intervals over the next 4–14 h and the position of each crab or ascoglossan recorded. The second assay was identical except that the disks were made of *U. flabellum* and sample size for the crabs was 20.

The susceptibility of *Costasiella* to fish predation was tested by dropping three ascoglossans into each of five separate 19-liter tanks containing three to five bluehead wrasses (*Thalassoma bifasciatum*). The fate of each slug was recorded as eaten, damaged, or untouched. To see if *Costasiella* was chemically defended from fish, we applied the ether crude extract of *Costasiella* to freeze-dried krill and offered four or five of them to each tank ( $N = 5$ ) of wrasses along with four or five controls. For assays in Belize, controls were coated with the crude

extract of the palatable gastropod *Littorina* sp.; this procedure controlled for the possible effects of oils or other primary metabolites that would be found in all gastropods. Extracts of both *Costasiella* and *Littorina* were applied as 10% of krill dry mass (later determined to be only about 36% of *Costasiella*'s natural concentration). In the Bahamas, controls were coated only with ether and the *Costasiella* extract was applied as 25% of krill dry mass (~91% of natural concentration). In Belize, we also used the krill assay to test the effect of pure avrainvilleol, at a concentration of 5%, on feeding by *T. bifasciatum*.

To test the hypothesis that *Thersandrus* was protected from predation by being cryptic when on *Avrainvillea*, we dropped one crab on a small piece of *Avrainvillea* (2–3 × the diameter of the crab) and one crab of a similar size with no *Avrainvillea* into each of five tanks of wrasses in Belize and five tanks of wrasses in the Bahamas. Crabs in each tank were monitored for up to 5 min to see if they were eaten or damaged by the fish.

## Results

*Herbivore distribution on potential host plants*—Although we searched numerous algae in reef and seagrass-bed habitats in both Belize and the Bahamas, we found *T. compressus* and *C. ocellifera* only on *A. longicaulis*. Because *A. longicaulis* cannot always be confidently separated from *A. nigricans* in the field, it is possible that the latter species was also occupied. At Carrie Bow Cay *Costasiella* were abundant in the 3–4-m-deep *Thalassia* bed behind the island. Here we found as many as 13 *Costasiella* on single *Avrainvillea* plants. Plants tended to be either unoccupied by *Costasiella* or occupied by several individuals. At this site, after locating *Costasiella* on an *Avrainvillea* plant, we thoroughly searched nearby individuals of *U. flabellum* and *Halimeda* spp. for ascoglossans. None were found on other plants ( $N = 48$ ). This procedure was not repeated for *T. compressus* because the crab was so cryptic on *Avrainvillea*. In both our field and laboratory searches of various algal species, however, we found the crab only on *Avrainvillea*.

*Feeding preferences of reef herbivores*—When *A. longicaulis* and six other seaweeds common in the seagrass bed at Carry Bow Cay were transplanted onto nearby patch reefs, *Avrainvillea* was among those seaweeds least affected by fish grazing (Fig. 2A). The aversion of reef fish to *Avrainvillea* was due, at least in part, to *Avrainvillea*'s production of the brominated diphenylmethane derivative avrainvilleol. When *Thalassia* was treated with this compound and exposed to reef fish, avrainvilleol significantly decreased grazing on treatments (mean % eaten  $\pm 1$  SE =  $55 \pm 6\%$ ) relative to controls ( $66 \pm 5\%$ ) ( $0.02 > P > 0.01$ , Wilcoxon's paired-sample test,  $N = 20$ ). To prevent fish from depleting the controls and beginning to graze the treatments for lack of choice, we intended to remove transplants from the reef before more than half of the control material had been consumed. We failed. Seventy percent of our control replicates had  $> 70\%$  of their projected surface area removed. The above results may therefore be conservative.

In contrast to the pattern for reef fish, *T. compressus* preferentially consumed *Avrainvillea*. Of the seven seaweeds tested, *Avrainvillea* was the only one that showed a significant change in wet mass when exposed to crabs vs. when protected from them (Fig. 2B,  $P < 0.005$ , Mann-Whitney *U*-test). It was the most heavily grazed seaweed in 8 of the 10 replicates (Fig. 2C); in the other two instances it was the second most grazed seaweed. A *G*-test assessing the frequency of being most preferred (Fig. 2C) was significant ( $0.025 > P > 0.01$ ) when all species were assessed but showed no among-species differences when the data for *Avrainvillea* were excluded ( $0.9 > P > 0.75$ ).

When confined to containers with three to four local seaweeds, both the ascoglossan and crab occupied *Avrainvillea* in preference to all other species tested (Figs. 3 and 4,  $P < 0.025$ , *G*-test). Occupancy among other species did not differ significantly for either herbivore. The compound avrainvilleol had no demonstrable effect in directly cuing occupancy patterns by either the crab or ascoglossan (Table 1). When disks of *Ulva* sp. or *U. flabellum* were treated with avrainvilleol, paired with control disks treated only

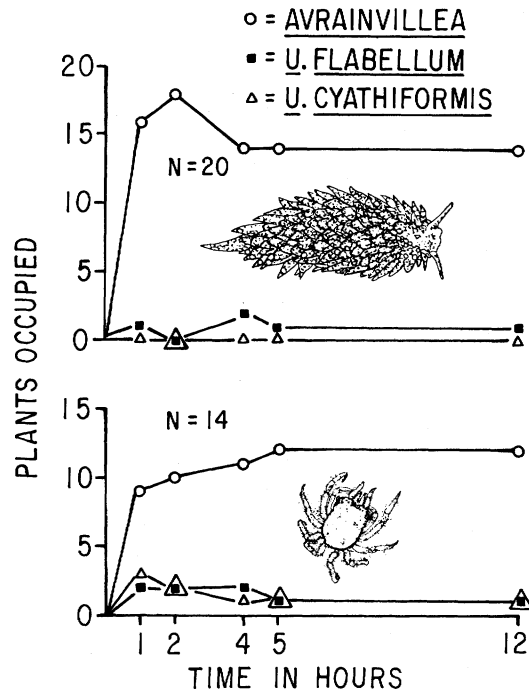


Fig. 3. Patterns of plant occupancy when *Costasiella ocellifera* (above) and *Thersandrus compressus* (below) were allowed to choose among three species of related green seaweeds. At all times, significantly more ascoglossans ( $P < 0.001$ ) and crabs ( $P < 0.025$ ) occupied *Avrainvillea* than any other seaweed (*G*-test). There were no significant differences between the other species of plants.

with ether, and presented to crabs ( $N = 15-20$ ) or ascoglossans ( $N = 20-25$ ), ascoglossans generally crawled around the containers ignoring both treated and control disks; crabs ignored most disks in the *Ulva* assay, but tended to occupy disks in the assay with *Udotea* (Table 1). When using *Udotea* disks, occupancy of treatment disks was significantly higher than control disks after 6 h ( $0.025 > P > 0.01$ , contingency table analysis), but did not differ significantly at 2, 5, or 14 h. Because we ran two assays and monitored them at several times, we consider this statistically significant but transitory effect a chance result of multiple testing.

*Herbivore chemistry and susceptibility to predation*—In both Belize and the Bahamas, thin-layer chromatography (TLC) of extracts from *Avrainvillea*, crabs, and ascoglossans, with purified avrainvilleol as a

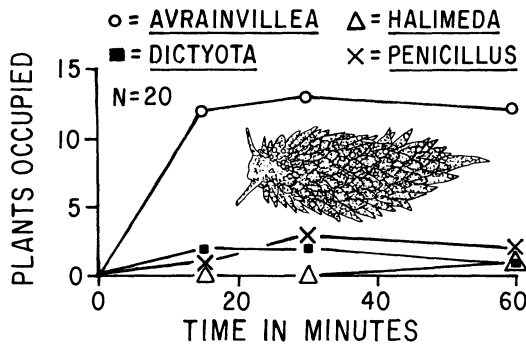


Fig. 4. Plant occupancy by *Costasiella ocellifera* when offered a choice of four seaweeds. At each sampling period, *Avrainvillea* was occupied significantly more frequently than any of the other species ( $P < 0.001$ ,  $G$ -test). There were no significant differences among the other species of plants.

standard, showed that avrainvilleol occurred in the plant and ascoglossan but not in the crab. TLC and proton NMR analyses of the ascoglossan also showed large amounts of plant pigments from *Avrainvillea*, indicating that the ascoglossan was sequestering chloroplasts as well as avrainvilleol.

That the crab does not sequester effective defenses was also suggested by its susceptibility to attack when exposed to *T. bifasciatum*. When individual crabs were dropped into 10 separate tanks containing these wrasses, all small crabs were completely eaten and all large crabs had all their legs eaten within  $\sim 1$  min. When similar-sized crabs were placed on pieces of *Avrainvillea* that were 2–3 times the width of their carapace and dropped into these tanks, only 1 of 10 was attacked during the  $\sim 5$  min that we monitored each tank ( $P < 0.001$ , Fisher's exact test).

When *Costasiella* were dropped into tanks with bluehead wrasses, the fish took the ascoglossans into their mouths but immediately spat them out unhurt. When the ether extract of *Costasiella* was applied to freeze-dried krill at a concentration of 10% (Belize) or 25% (Bahamas) of its dry mass, these krill were rejected significantly more often than controls coated with only ether or an equal mass of extract from the palatable gastropod *Littorina* (Fig. 5,  $P < 0.02$ ,  $N = 4$  or 5, paired  $t$ -test). The pure compound avrainvilleol strongly deterred feeding at 5% of krill dry mass (Fig. 5).

Table 1. Effects of avrainvilleol (at 1% of algal dry mass) on use of algae by *Costasiella ocellifera* and *Thesandrus compressus*.

Seaweed treated	Time (h)	No. on treatment	No. on control	No. on neither
<i>Costasiella</i>				
<i>Ulva</i> sp.	2–3	5	5	10
	8	0	0	20
<i>Udotea flabellum</i>	4	0	0	25
<i>Thesandrus</i>				
<i>Ulva</i> sp.	6	3	3	9
	2	8	8	4
<i>Udotea flabellum</i>	5	11	5	4
	6	13	5	2
	14	8	12	0

The single collection of about 50 *Costasiella* that we carefully extracted produced a lipid-soluble crude extract that equaled 27.5% of the total animal dry mass. From it, we purified avrainvilleol that equaled 2.7% of the ascoglossan's dry mass. Our crude-extract assays at 25 and 10% were thus near or considerably below natural concentrations. Our avrainvilleol assay at 5% appears to have been run at a high concentration. The chromatographic steps necessary to purify avrainvilleol from the small mass of ascoglossans available for extraction, however, involve some losses of compound (amount of loss was not determined). Thus 2.7% is a conservative estimate and 5% may not be much above natural concentrations. Similar ascoglossans are known to sequester algal-derived metabolites at concentrations of 7% of dry mass (Paul and Van Alstyne 1988).

#### Discussion

Both of the mesograzers investigated here experienced reduced predation due to their association with a host plant that was chemically defended from fish. The mechanisms reducing predation, however, differed between the two herbivores. Although *T. compressus* was found only on *Avrainvillea* and probably eats only *Avrainvillea* in the field (Figs. 2 and 3), it did not sequester chemical defenses from the alga. It simply avoided detection by being extremely cryptic when on its host plant. When removed from *Avrainvillea*, it was rapidly consumed. In



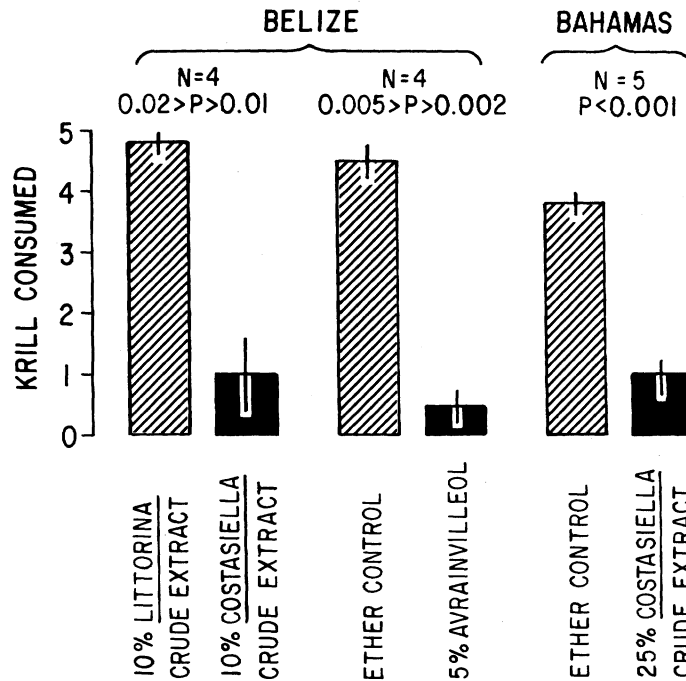


Fig. 5. The effects of crude lipid extracts from gastropods and of the pure compound avrainvilleol on feeding by the bluehead wrasse *Thalassoma bifasciatum*. Plotted are the mean number of krill consumed  $\pm 1$  SE ( $N = 4$  or  $5$ );  $P$  values are from paired  $t$ -tests.

contrast, *C. ocellifera* sequestered the alga's chemical defense. The ascoglossan was resistant to attack by wrasses, and both its lipid-soluble crude extract and the pure compound avrainvilleol significantly deterred feeding (Fig. 5).

Although it is often assumed that ascoglossans are defended by sequestered algal metabolites contained in the mucus and autotomized cerata that they release when disturbed (Lewin 1970; Faulkner and Ghiselin 1983; Jensen 1984), there are only two rigorous investigations of this phenomenon, and they do not confirm the generality of this assumption (Paul and Van Alstyne 1988; Hay et al. 1989). On Guam, the ascoglossan *Elysia halimeda* occurs exclusively on chemically rich green algae in the genus *Halimeda* and sequesters a compound that it modifies from those produced by *Halimeda* (Paul and Van Alstyne 1988). In field assays, this modified compound significantly deters feeding by both herbivorous and carnivorous fish. Recent investigations of two Australian ascoglossans specializing on the chemically defended

green alga *Chlorodesmis fastigiata* documented that alga-ascoglossan-predator interactions are not always so straightforward (Hay et al. 1989; Roussis et al. 1990). In the Australian studies, one of the ascoglossans was chemically defended, but its defense did not seem to be derived from its algal diet. The other ascoglossan did sequester algal defenses, but it could not be demonstrated that the alga-derived compound was the cause of this ascoglossan's distastefulness to fish.

In the study described here, *C. ocellifera* sequestered the untransformed algal metabolite, and this metabolite served as an effective defense against a common predatory fish (Fig. 5). Although this phenomenon has been assumed for more than 20 yr to be common among the ascoglossans, to our knowledge, ours is the first clear documentation that the actual algal metabolite provides an effective defense for the ascoglossan. The storage of a modified, but still effective, metabolite by *E. halimeda* (Paul and Van Alstyne 1988) and the uncertain nature, and source, of the defenses used by

the Australian ascoglossans clearly indicate that seaweed-ascoglossan-predator interactions are not as clearcut as they have been proposed to be and that they deserve additional study.

The Australian study was similar to our present investigation in that the green seaweed *Chlorodesmis* also supported a cryptic specialist crab that avoided predation by close association with the alga but did not sequester defensive metabolites from its host (Hay et al. 1989). The crab in Australia was directly cued to feed, however, by the cytotoxic compound produced by *Chlorodesmis*. The crab in our present study did not cue directly on *Ayravillea*'s defensive metabolite (Table 1).

Studies of specialist marine herbivores that combine biological and chemical data are rare, making generalizations difficult. Several specialist ascoglossans have been shown (Paul and Van Alstyne 1988; this study) or suggested (Lewin 1970; Faulkner and Ghiselin 1983; Jensen 1984) to sequester defenses from their algal hosts. In contrast, no herbivorous marine crustaceans are known to metabolically sequester defensive metabolites even though all known specialists in this group feed on chemically defended hosts (Hay et al. 1989, 1990; this study), and even some generalist amphipods selectively feed on seaweeds that are chemically defended from fish (Hay et al. 1987a, 1988a). This pattern contrasts dramatically with herbivorous terrestrial arthropods where specialists often sequester plant defenses (Duffy 1980), and where even generalist feeders sometimes sequester specific defensive metabolites from a wide variety of unrelated and chemically diverse plants (Blum et al. 1990).

When compared with terrestrial systems, marine communities support very few specialist herbivores and may therefore serve as simplified systems for investigating the factors selecting for feeding specialization. The relative importance of various factors in selecting for specialization has been debated among terrestrial ecologists for years with no clear consensus emerging (see e.g. Bernays and Graham 1988; Jermy 1988; Schultz 1988). The ultimate reasons for a greater proportion of feeding specialists

among terrestrial insect herbivores are not understood but may relate to the differing life-history patterns of terrestrial vs. marine invertebrates (i.e. the predominance of larval dispersal in marine species). A lesser degree of chemical diversity among marine plants does not appear to be an adequate alternative explanation for the paucity of specialist herbivores; marine plants, like terrestrial plants, produce a tremendous number of secondary metabolites, and they are distributed among a large number of structural classes (Faulkner 1988).

The limited information presently available indicates that most marine specialists are small herbivores of limited mobility that are subject to high potential rates of predation and that these herbivores tend to specialize on chemically defended plants that provide them with significant protection from their predators (Hay in press). In addition to the ascoglossan and crab studied here, this pattern holds for a specialist crab in Australia (Hay et al. 1989), a specialist ascoglossan in Guam (Paul and Van Alstyne 1988), and a specialist amphipod in the Caribbean (Hay et al. 1990). To date, all studies on seaweed-mesograzer-predator interactions support the hypothesis that one of the primary advantages of feeding specialization involves avoidance, or less commonly deterrence, of generalist predators. Similar advantages appear to occur for specialist herbivorous insects in terrestrial communities (Bernays 1989). This suggests that predation may select for feeding specialization in a wide variety of communities.

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Submitted: 21 February 1990

Accepted: 23 August 1990

Revised: 10 September 1990