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Source: *BioScience*, Vol. 40, No. 5 (May, 1990), pp. 368-375

Published by: American Institute of Biological Sciences

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Seaweed Adaptations to Herbivory

Chemical, structural, and morphological defenses are often adjusted to spatial or temporal patterns of attack

J. Emmett Duffy and Mark E. Hay

Herbivory on seaweeds can be intense, with nearly 100% of production being consumed in some habitats (Carpenter 1986). Seaweeds minimize damage from herbivores by any of three strategies (Lubchenco and Gaines 1981). They can escape in space or time so they do not co-occur with important herbivores or are not detected when they do co-occur. They can deter feeding by herbivores that encounter and recognize the plant. And they can minimize the decrease in fitness that results from herbivore attack.

Herbivory's profound effects on the organization of seaweed communities has been extensively reviewed (Carpenter 1986, Dayton 1975, Hay 1985, Lewis 1986, Lubchenco and Gaines 1981). In this article, we describe seaweed characteristics that diminish losses to herbivores.

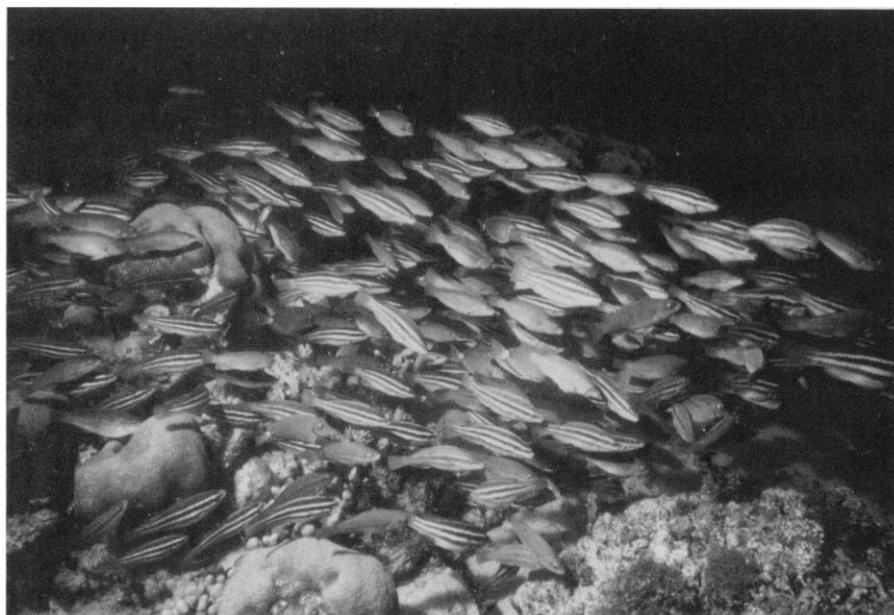
Seaweeds are consumed by a diverse assemblage of herbivores that includes fishes, urchins, gastropods, crabs, and numerous smaller herbivores such as amphipods, isopods, and polychaetes (collectively termed *mesograzers*). In tropical habitats, fish and urchins have the greatest effect on seaweed community struc-

Fish, urchins, and gastropods can each strongly affect seaweed communities

ture; in temperate communities, urchins and gastropods tend to be most important (Carpenter 1986, Gaines and Lubchenco 1982, Hawkins and Hartnoll 1983, Hay 1984a, in press a, Lubchenco and Gaines 1981). Although mesograzers such as amphipods can dramatically affect seaweed communities by destroying entire

kelp beds along several kilometers of coastline (Tegner and Dayton 1987), these events are rare. Mesograzer populations are usually maintained at low densities by predation, and they commonly have little obvious effect on most seaweeds (Duffy in press, Hay et al. 1988c). However, mesograzers can have subtle but important effects on some seaweeds, and the types of effects can differ dramatically among mesograzer species (Brawley and Adey 1981, Duffy in press).

Fish may have been especially important in selecting for antiherbivore traits in seaweeds (Hay in press a, Steneck 1983) because of their mobility, abundance, high metabolic rate, and, for some abundant tropical spe-



A dense school of parrotfish graze algae on a coral reef. Photo: M. Hay.

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cies, fused teeth (Figure 1), which allow them to feed on tough or calcified seaweeds. Urchins and gastropods can also be important in habitats where they reach high densities (Carpenter 1986, Hawkins and Hartnoll 1983).

Fish, urchins, and gastropods can each strongly affect present-day seaweed communities (Carpenter 1986, Hawkins and Hartnoll 1983, Hay 1985, Lewis 1986, Lubchenco and Gaines 1981), and the fossil record suggests they have played a major role throughout evolutionary time (Steneck 1983). In this article, we discuss how seaweeds escape, deter, or tolerate herbivory. The depth in which we cover each of these topics reflects the availability of rigorous experimental studies; we know little of the relative importance of these different traits.

Escaping from herbivores

Spatial refuges. Seaweeds can avoid herbivores by growing in habitats, in microhabitats, or at times of year in which herbivores are not active. For example, on tropical coral reefs where herbivores are abundant, many seaweeds that are physiologically capable of growing on topographically complex reef slopes occur only where herbivore densities are low—on topographically simple sand plains and reef flats (Hay 1981a, 1984b, 1985, Lewis 1986). Similarly, Caribbean patch reefs are often surrounded by halos of bare sand that are kept free of seagrasses by grazing fish and urchins (Ogden et al. 1973, Randall 1965). Because many reef-associated grazers are reluctant to venture more than approximately 10 m from the shelter of the reef, seagrasses thrive beyond this radius.

On a smaller spatial scale, seaweeds may live in cracks and holes inaccessible to herbivores. On intertidal rock surfaces along Pacific Panama, where herbivory is particularly intense, herbivore-resistant algal crusts dominate exposed surfaces, whereas less-resistant leafy algae occur primarily or exclusively in holes or cracks (Menge et al. 1985). Spatial escapes have been discussed in detail by Lubchenco and Gaines (1981) and Hay (1985).

In some cases, herbivores create

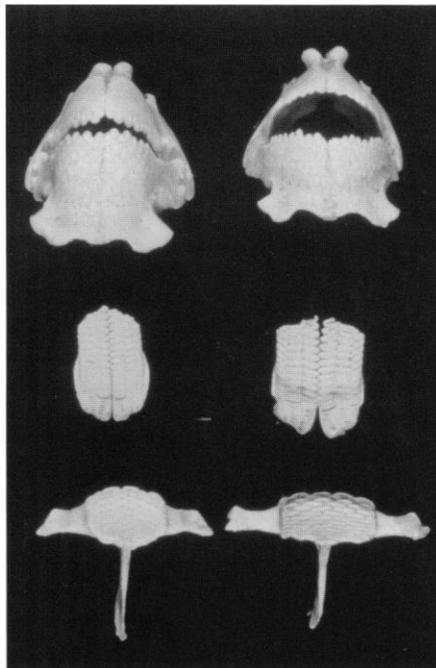


Figure 1. The beak-like teeth (top) and pharyngeal mill (middle and bottom) in the back of the throat from two species of Caribbean parrotfishes. The fused teeth enable the fish to bite into hard calcified surfaces to extract algal tissues. The pharyngeal mill functions like a mortar and pestle, grinding the seaweeds along with sediments and coral rock. Because these fish have no cellulases, they use their mouthparts to physically rupture the algal cells. Photo: S. M. Lewis.

spatial refuges for seaweeds. Reef damselfish are small, aggressive herbivores that establish gardens of palatable algae by removing unpalatable species and by vigorously defending their gardens against other herbivores. Though the damselfish feed in the gardens, these plots experience reduced herbivory relative to areas not defended by damselfish. A few seaweeds depend on these herbivore-created refuges, and algal diversity can be higher in damselfish territories than in either caged or uncaged areas outside territories (Hixon and Brostoff 1983).

Associational refuges. Herbivore-influenced communities are often dominated by unpalatable seaweeds that may create refuges for more palatable species (Hay 1986, Littler et al. 1986, Pfister and Hay 1988). For example, field experiments demonstrated that the palatable red alga

Hypnea musciformis was quickly eaten by fish when growing alone, but it grew more rapidly than it was consumed when placed in contact with its unpalatable competitor, the brown alga *Sargassum filipendula* (Hay 1986). During the yearly peak in herbivore abundance, *Hypnea* and other palatable seaweeds were found exclusively in association with unpalatable plants; at times of year when herbivores were less active, palatable plants were not strongly associated with unpalatable species.

In communities where associational refuges are important, species richness can increase rather than decrease as the community becomes dominated by a few unpalatable seaweeds (Hay 1986). In these cases, palatable algae that would have been eliminated by grazers can persist only in association with their unpalatable competitors. Similarly, on coral reefs, nearly twice as many taxa occur within 10 cm of the chemically defended brown alga *Styopodium zonale* as in similar-sized areas away from *Styopodium* (Littler et al. 1986). As a final example, brown algae in the genus *Desmarestia* concentrate sulfuric acid up to 18% of plant dry mass (Anderson and Velimirov 1982). In Chilean kelp beds heavily grazed by sea urchins, the palatable kelp *Macrocystis* cannot successfully colonize unless it invades an area encircled by *Desmarestia* plants, which appear to act as "acid brooms" that sweep the substrate and prohibit urchins from entering the area (Dayton 1985).

Associational refuges can thus be effective in a variety of marine habitats and against different kinds of herbivores. Interestingly, although the patterns and processes of associational resistance in marine and terrestrial systems are similar, the mechanisms producing them can be strikingly different. In the best-studied marine example (Pfister and Hay 1988), the palatable seaweed *Gracilaria* was grazed more by sea urchins when it occurred as a monoculture than when it occurred in a polyculture with the unpalatable alga *Sargassum*. The greatest grazing in monocultures occurred because individual urchins ate faster there.

This observation contrasts with terrestrial systems, where associational

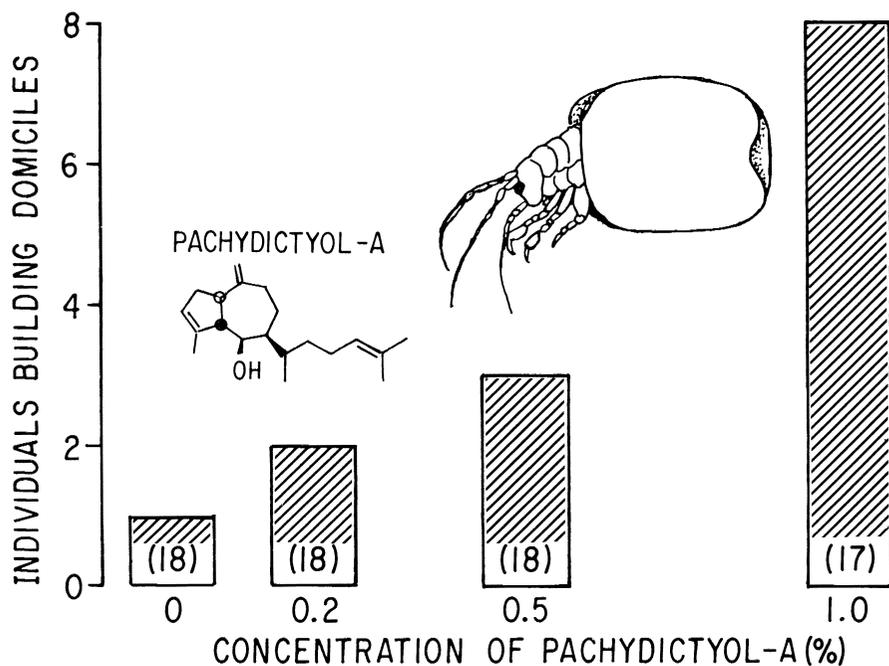


Figure 2. The number of amphipods (*Pseudamphithoides incurvaria*) building domiciles in 48 hours from discs of the green seaweed *Ulva* that were treated with differing concentrations of the diterpene alcohol pachydiectyol-A ($r^2 = 0.98$, $P = 0.011$). This compound deters feeding by fish and is the major secondary metabolite produced by the amphipod's host alga *Dictyota bartayresii*. When in domiciles built of *Dictyota*, the amphipods are immune to fish predation. (From Hay et al. in press.)

refuges have been reported to occur because herbivorous insects become more numerous in monocultures. These increased densities are due to insects finding the monocultures more easily, rarely leaving them, and reproducing while there (Bach 1980). In the marine study, urchins did not find monocultures more easily, and they emigrated from them more rapidly than from polycultures.

Temporal refuges. Often, herbivore activity is predictable in time as well as in space. For example, in temperate marine systems, herbivores are often active primarily during the summer. Several genera of algae have life histories that appear to capitalize on these seasonal changes in grazing pressure (Lubchenco and Cubitt 1980).

Complex life histories, including alternation of morphologically distinct generations that differ in growth potential and resistance to herbivores, are common among intertidal algae (e.g., *Ulothrix*, *Urospora*, *Petalonia*, *Scytosiphon*, *Bangia*, and *Porphyra*). Upright forms of these species are good competitors against other algae

but are susceptible to herbivores. Therefore, they occur primarily during times of the year when herbivore activity is low. The less competitive, but more herbivore-resistant, crustose forms dominate when herbivores are active. Though upright forms normally occur in the field only during winter, these forms persist during the summer if grazers are experimentally excluded (Lubchenco and Cubitt 1980).

Seaweeds may also minimize herbivore damage by producing their new, most palatable, growth during periods of relatively low herbivory. An extreme example is the tropical alga *Halimeda*; it synchronously produces its youngest and most nutritious portions at night while herbivorous reef fishes are not feeding (Hay et al. 1988b, Paul and Van Alstyne 1988a).

Size-related refuges. Seaweeds can also avoid being eaten if they become too large for herbivores to handle effectively. Such size-related immunity presumably results from a larger plant being tougher, or more easily recognized, if it is unpalatable. Because all algae must pass through a

small sporeling stage that is vulnerable to grazers, size-related susceptibility differences may be common. Even species that herbivores avoid as adults may have sporelings that are eaten by unselective grazers because they are too small to be distinguished from other plants, they are nutritionally superior to older plants of the same species, or they are easier for herbivores to manipulate.

The challenge then is for the plant to survive until it reaches a size at which it is less vulnerable to herbivores. Any of the refuge mechanisms mentioned above may be employed. For example, kelp sporelings are more vulnerable to herbivores than are larger kelps, and the kelp sporelings escape herbivores more often when hidden among filamentous brown algae than when growing on bare rock (Harris et al. 1984). Similarly, small (less than 3 cm) *Fucus vesiculosus* plants are more susceptible to grazing snails than are larger plants, and survival of small plants is enhanced by settlement in small cracks or among barnacles where herbivores cannot graze effectively (Lubchenco 1983).

Decreasing attractiveness to herbivores

For long-lived seaweeds, and those growing in areas such as tropical reefs where herbivores are abundant and active year-round, it may be difficult for seaweeds to escape their enemies through spatial or temporal refuges. In these situations, selection should favor seaweeds that are unattractive to herbivores.

Chemical defenses. Seaweeds produce a large number of secondary metabolites, including terpenes, aromatic compounds, acetogenins, amino acid-derived substances, and phlorotannin polyphenolics (Faulkner 1984, 1986). Although many of these compounds are known to function as defenses against herbivores (reviewed by Hay and Fenical 1988), they might also serve to deter pathogens and fouling organisms (Wahl 1989).

VARIANCE IN SUSCEPTIBILITY AMONG HERBIVORES. Recent field tests have demonstrated the effectiveness of a variety of terpenoid compounds in decreasing the overall

herbivore damage that seaweeds experience in their natural environment (Hay et al. 1987b, Hay and Fenical 1988, Paul and Van Alstyne 1988a). Laboratory experiments have clarified some of the interactions occurring in the field and have shown that a given compound is more effective against some types of herbivores than against others. Often compounds that deter grazing fish either stimulate or do not affect feeding by small invertebrate herbivores (mesograzers) that live on seaweeds; these mesograzers may gain protection from their predators by associating with chemically defended algae (Hay in press b, Hay et al. 1987a, 1988a,c, 1989, in press).

As examples, the amphipod *Amphiphoe longimana* and the polychaete *Platynereis dumerilii* both build and live in mucilaginous tubes attached to the algae on which they feed. Feeding and living on seaweeds that are preferred by fish might expose these mesograzers to indirect predation as the fish eat the algae. In North Carolina, both these mesograzers selectively feed on the brown alga *Dictyota dichotoma*, which produces diterpene alcohols that strongly deter fish and urchin feeding. These compounds either significantly stimulate or do not affect feeding by the mesograzers (Hay et al. 1987a, 1988c). A similar pattern has been documented for other fish, mesograzers, and chemically defended seaweeds on a tropical reef (Hay et al. 1988a).

In each of these cases, mesograzers selectively feed on chemically defended seaweeds that are repellent to fish. However, the mesograzers are not restrictively specialized to these chemically rich seaweeds; they are found on and feed from a wide range of unrelated algae. It appears that these mesograzers selectively graze toxic host plants because these plants provide microsites of reduced predation by herbivorous, omnivorous, or predatory fish (Hay et al. 1987a, 1988b,c).

Although feeding specialization is typical among terrestrial insects, it is rare among marine herbivores (Hay in press b). The few marine herbivores that do specialize are small, relatively sedentary, and live on plants that provide them protection against predators (Hay in press b,

Hay et al. 1989, in press, Paul and Van Alstyne 1988b).

For example, the amphipod *Pseudamphithoides incurvaria* lives in a mobile bivalved domicile it builds from the chemically defended seaweed *Dictyota bartayresii* (Hay et al. in press). When in domiciles, the amphipods are rejected by predatory fish; when removed from domiciles, they are rapidly eaten. The alga they use for domiciles produces the diterpene alcohol pachydictyol-A. This compound deters feeding by fishes but stimulates domicile building by the amphipods. Amphipods will not normally build domiciles from the green seaweed *Ulva*; however, they will do so when *Ulva* is treated with pachydictyol-A (Figure 2).

The Great Barrier Reef crab *Caphyra rotundifrons* is found only in patches of the chemically defended green alga *Chlorodesmis fastigiata*, which appears to be its only food (Hay et al. 1989). *Chlorodesmis* produces a cytotoxic terpene that deters fish feeding but significantly stimulates feeding by the crab (Figure 3), which experiences reduced predation by associating with the chemically defended seaweed (Hay et al. 1989). Crabs tethered in patches of *Chlorodesmis* were rarely consumed by predators; those tethered in the open

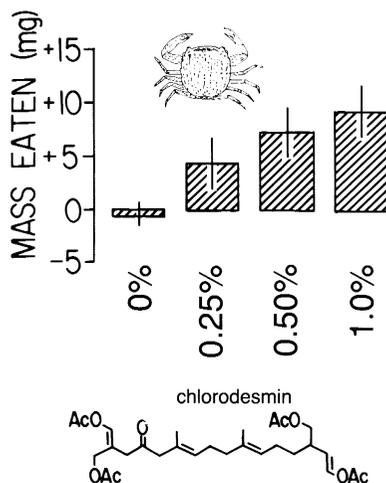


Figure 3. Amount of nonhost seaweed consumed by the specialist crab *Caphyra rotundifrons* when the seaweed was coated with increasing concentrations of the cytotoxic compound chlorodesmin, which is produced by the crab's normal host plant *Chlorodesmis fastigiata*. Vertical lines are standard errors. (Figure modified from Hay et al. 1989.)

or in patches of a palatable green alga were eaten rapidly.

Last, many shell-less gastropods in the order Ascoglossa (Figure 4) are specialized feeders on chemically rich green algae (Jensen 1980). These herbivores sequester both chemical defenses (Paul and Van Alstyne 1988b) and functional chloroplasts from their algal hosts. Sequestered chloroplasts continue to photosynthesize within the animal's cells for as long as three months, helping to meet the energetic needs of the herbivore (Trench 1975). Sequestered seaweed metabolites make the ascoglossan distasteful to predators (Paul and Van Alstyne 1988b). Ascoglossans are the only group of marine herbivores that show a high proportion of specialized feeders.

DISTRIBUTION OF CHEMICAL DEFENSES WITHIN AND AMONG PLANTS. Studies of variation in defensive chemistry among conspecific plants, and among parts of individual plants, are just beginning. Two examples suggest that plants allocate chemical defenses preferentially to parts that are especially valuable or vulnerable to attack. First, Steinberg (1984) found higher concentrations of phenolics in reproductive fronds of the kelp *Alaria marginata* than in vegetative blades, and both laboratory and field experiments demonstrated reduced grazing on the reproductive fronds. Second, in the green alga *Halimeda*, young plants and the nitrogen-rich (and thus highly nutritious) new growth of older plants contain concentrations of defensive metabolites an order of magnitude higher than older, less valuable, plants or plant parts (Hay et al. 1988b, Paul and Van Alstyne 1988a). These patterns suggest that allocation of defenses represents a trade-off between costs and benefits.

In several tropical green algae, populations on herbivore-rich reefs have higher metabolite concentrations, produce a larger number of metabolites, and are more resistant to herbivores than conspecific populations from nearly grass beds where herbivory is much lower (Paul and Fenical 1986, Paul and Van Alstyne 1988a). This pattern is consistent with the hypothesis that multiple defenses become more necessary as herbivore diversity increases (Hay 1984b,

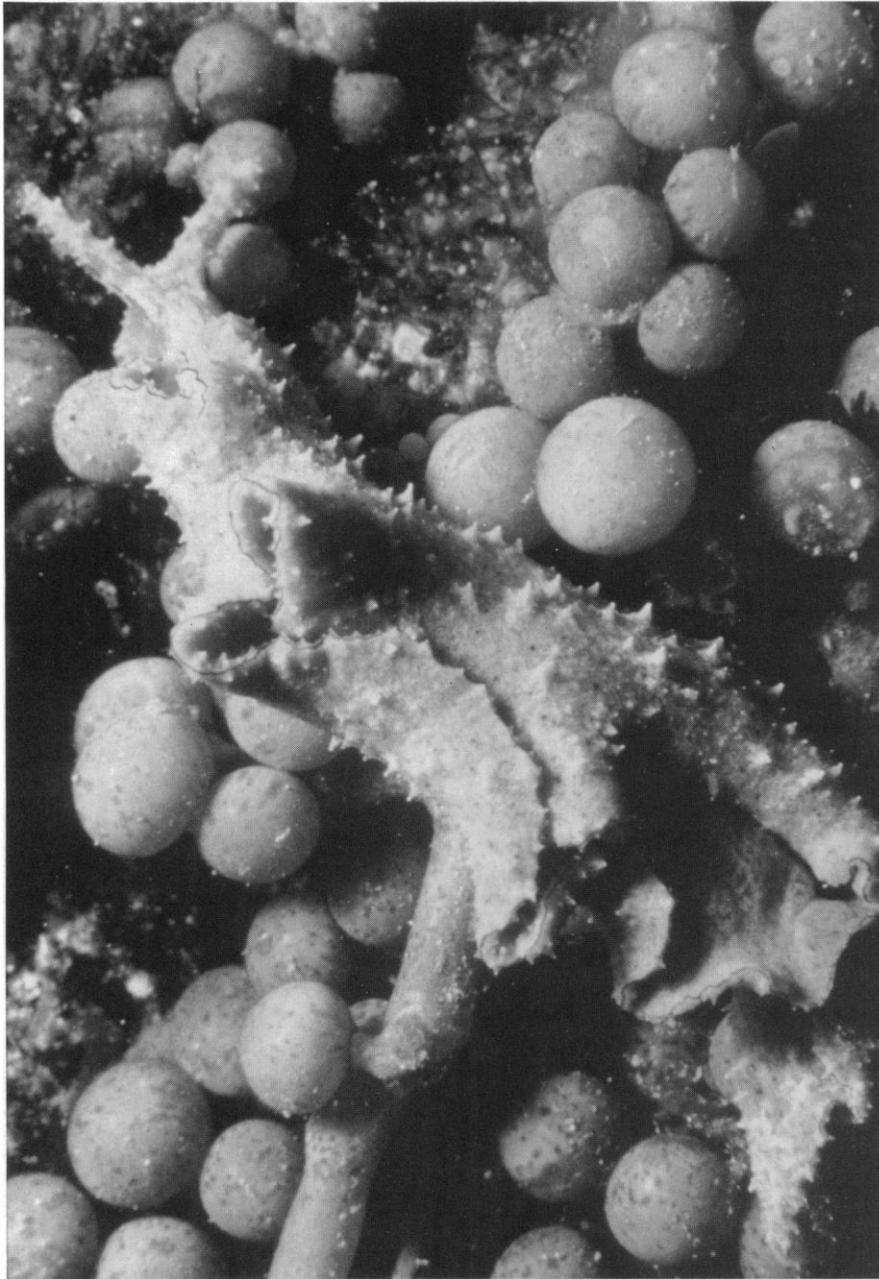


Figure 4. An ascoglossan gastropod (commonly called a sea slug) grazing on the chemically rich green alga, *Caulerpa racemosa*. Most ascoglossan gastropods (like this *Elysia* sp.) sequester both chemical defenses and functional chloroplasts from their algal hosts. The chemicals defend ascoglossans against their own predators; the chloroplasts continue photosynthesis for as long as three months and meet most of the energetic needs of the ascoglossans. Photo: M. Hay.

Lubchenco and Gaines 1981).

There are intriguing geographic patterns in chemical defense. Most seaweed secondary metabolites have been isolated from tropical species (Faulkner 1984, 1986). This chemical diversity presumably reflects the more intense herbivory in the tropics (Gaines and Lubchenco 1982). How-

ever, this trend is not universal. The concentrations of phenolics in temperate brown algae are substantially higher than in related species from tropical regions (Steinberg in press).

Curiously, many brown seaweeds in Australia and New Zealand have two to three times the phenolic content of similar species from the North

Pacific (Steinberg 1989, in press). Estes and Steinberg (1988) suggest that this pattern results from different histories of herbivore pressure in the two regions. These authors argue that, in the North Pacific, predation by sea otters kept herbivorous urchin populations low, resulting in relatively weak selection for phenolic defenses in brown seaweeds from this region. Conversely, the absence of sea otters in the South Pacific allowed herbivores to maintain high densities there, and large brown seaweeds evolved high phenolic contents in response to their grazing. Interestingly, South Pacific herbivores appear to have adapted to these chemically defended plants, and they are much more tolerant of phenolics than are their North American counterparts (Steinberg in press).

Morphological/structural defenses. Marine algae come in a great variety of sizes, shapes, and textures, from delicate threadlike filaments to giant kelps to rock-hard crusts. In several cases, seaweed morphology correlates with susceptibility to grazers (Lewis et al. 1987, Littler and Littler 1980, Steneck and Watling 1982). Although the possible confounding effects of chemical defenses need to be more rigorously investigated (Hay 1984b, Lewis 1985, Paul and Hay 1986), it is clear that some structural and morphological features of algae reduce their vulnerability to some grazers.

In an extensive literature review, Steneck and Watling (1982) showed that the morphology of plants eaten by gastropods correlates reasonably well with the structure of their mouthparts. Morphological categories have been less useful for explaining food preferences by other groups (Duffy in press, Hay 1984b, Lewis 1985), although soft filaments are grazed by most herbivores, whereas crusts and heavily calcified upright forms are exploited by only a few.

The clearest examples of morphologically defended algae occur in the red algal family Corallinaceae. These algae grow as thin, flat, heavily calcified crusts. Eighty to ninety percent of the dry mass of these crusts may be ash (primarily calcium carbonate), and they are often the most abundant plants in intensely grazed habitats such as reefs and urchin barrens (Ste-

neck 1983, 1986).¹ Because of their excellent preservation in the fossil record, Steneck (1983) was able to trace their morphological changes through geologic time; he described an adaptive radiation of corallines in response to the evolution of herbivores with increasingly powerful mouthparts and abilities to excavate calcareous substrates. Grazing scars on fossil corallines suggested that the fused teeth of parrotfish (Figure 1) represented a dramatic advance in the ability of herbivores to damage seaweeds and may have favored corallines over other seaweeds (Steneck 1983).

Examples of morphological defenses exist among the noncalcareous fleshy algae as well. Like other sessile organisms, many seaweeds can adjust their morphology to prevailing physical and biological conditions, including grazing pressure. For instance, clonal seaweeds often form short, tightly packed and highly branched turfs in grazed areas; this turf growth form can significantly reduce losses to grazing (Hay 1981b). Additionally, some reef seaweeds have two morphologically distinct forms that differ in growth rate and susceptibility to herbivory; transition between the forms is mediated by changes in grazing pressure (Lewis et al. 1987). As an example, in high-herbivory habitats, the brown alga *Padina* occurs as a prostrate turf that is relatively resistant to grazing. Within 96 hours of excluding herbivorous fishes, the turf changes into a rapidly growing blade-like form, which is susceptible to herbivores but is a superior competitor against other benthic algae and sessile invertebrates (e.g., corals); it may even overgrow and kill corals (Lewis 1986, Lewis et al. 1987).

Low nutritional quality. A potential defense that has been mentioned (Lubchenco and Gaines 1981), but not addressed experimentally, is low nutritional quality. Plants that are critically low in required nutrients, such as nitrogen, might be little used by herbivores. Because herbivores would probably be minimally affected by nutritional deficiency if many alternate foods of adequate quality

were available as supplements, this strategy may be effective only for species that form large monocultures (e.g., some seagrass or brown algal beds).

Defense costs. Seaweeds employ a remarkable array of structural and chemical armament against herbivores. The benefits of these features prompt the question, Why don't all seaweeds possess such defenses? Defenses against herbivores may be costly and selected against in habitats with predictably low rates of herbivory (Hay and Fenical 1988).

This explanation is supported by the differential allocation of chemical defenses to more susceptible or valuable plant parts (Hay et al. 1988b, Paul and Fenical 1986, Paul and Van Alstyne 1988a, Steinberg 1984); the induction of chemical (Van Alstyne 1988) or morphological (Lewis et al. 1987) defenses after attack; the concentration of chemically and morphologically defended seaweeds in habitats most affected by herbivores and their low abundance in habitats with minimal herbivory (Hay 1984b, Steneck 1986); and the competitive interactions between defended and undefended plants in the absence of herbivores (Estes and Steinberg 1988, Hay 1985, Lewis 1986). However, there are no direct experimental assessments of these costs, and it is unclear how such costs could be measured or what currency (e.g., energy or nitrogen) is appropriate (Hay and Fenical 1988).

Spatial escapes can also entail costs. Algae often escape herbivores by growing in physically stressful habitats, thereby entailing large costs in growth rate and fecundity relative to plants protected from grazers in more physically benign but herbivore-rich habitats (Hay 1981a). Physiological adaptations to the rigors of these habitats may entail additional costs. In a similar way, palatable plants that escape herbivores by associating with unpalatable competitors may experience an 80% reduction in growth rate due to competition (Hay 1986). Although the costs of using these refuges can be high, the alternative is often local extinction.

Patterns in the allocation of chemical defenses within a plant also provide evidence for the costliness of

defenses. The high concentration of defensive compounds in the most valuable or vulnerable plant parts (Hay et al. 1988b, Steinberg 1984), and correspondingly low concentrations in less vulnerable parts, suggests that allocation of defenses represents a trade-off between costs and benefits. Another way to allocate defenses is to increase metabolite production when herbivores are more active, as in the brown alga *Fucus vesiculosus*, which increases phenolic concentration by 20% after simulated herbivore damage (Van Alstyne 1988). When transplanted into the field, these clipped plants lost only half as much tissue as undamaged controls.

Integrated approaches to defense

In the field, structural, chemical, and nutritional characteristics may act in concert to decrease a seaweed's attractiveness to herbivores, and these characteristics may be coordinated with patterns of temporal and microhabitat escape (Hay 1984b, Hay et al. 1988b, Lewis et al. 1987, Paul and Hay 1986, Paul and Van Alstyne 1988a). Such integrated defense should be particularly important in environments such as coral reefs, where the diversity of potential enemies is high. For example, Littler and Littler (1980) suggested that late successional seaweeds tend to be less nutritious, tougher, and more toxic because of a suite of physical and biological selective pressures.

Most studies have focused on how one particular trait affects herbivory; few have assessed the potential importance of covariation of deterrent traits. The tropical green alga *Halimeda*, for example, minimizes losses to herbivores by using a combination of heavy calcification and chemical defenses, both of which vary in time as tissue value and susceptibility to herbivory change. This alga also produces its valuable new growth at night, when herbivorous fish are not feeding (Hay et al. 1988b). Such complex defensive strategies could be common.

Tolerating herbivory

It is surprising that the dominant plants in areas of most intense herbivory represent the extremes of sus-

¹M. M. Littler, 1990, personal communication. Smithsonian Institution, Washington, DC.

ceptibility to herbivores: small, highly susceptible filamentous forms (Carpenter 1986), heavily calcified, very resistant, crustose corallines (Steneck 1983, 1986), and upright, calcified seaweeds like *Halimeda* that are also defended chemically (Hay et al. 1988b, Paul and Van Alstyne 1988a). These seaweeds may depend on grazing to prevent overgrowth by superior competitors (Carpenter 1986, Hay 1981a, Lewis 1986, Steneck 1986). Sometimes this service entails loss of the plant's own tissue.

One alternative to costly structural and chemical defenses is to channel all energy into rapid growth and reproduction in an effort to outpace herbivores. By producing tissue rapidly, and by having basal portions that escape herbivory due to the topographic complexity of the substrate, small filamentous algae can often persist despite losing much of their tissue to grazers (Carpenter 1986, Lewis 1986). This strategy allows inconspicuous filamentous algae to make up most of the plant biomass on moderately grazed areas of some tropical reefs. These plants in fact produce more mass when grazed, because continuous cropping prevents self-shading, and herbivore excretion may increase available nutrients (Carpenter 1986).

Some intertidal seaweeds that are resistant to herbivores as adults ensure survival through the vulnerable juvenile stage by a massive recruitment that swamps the ability of molluscan herbivores to eat the young plants. Under these conditions, the plants may quickly reach a size at which they no longer suffer mortality at normal herbivore densities (Dayton 1975). In extreme cases, algal growth may be heavy enough to alter the habitat in such a way that it becomes unsuitable for some herbivores (Underwood and Jernakoff 1981).

Losses to herbivores are sometimes minimized by ingested propagules or vegetative portions remaining viable and being dispersed by the herbivore, a situation reminiscent of seed dispersal by birds and mammals. For several opportunistic algae exposed to grazing by gastropods, gut passage significantly increases the production of motile spores and also the growth rate of sporelings relative to the uningested controls (Santelices and

Ugarte 1987).

In contrast, spores and vegetative portions of late successional plants are rarely resistant to digestion. However, grazing may still provide some benefits. Amphipods graze on cystocarps (reproductive structures) of the red alga *Iridaea laminarioides*, releasing spores into the water column when the cystocarps are opened (Buschmann and Santelices 1987). Spores released by amphipods are as viable as naturally released spores, and, surprisingly, ungrazed fronds often have cystocarps that remain closed and do not naturally release their spores. The percentage of such unopened cystocarps is significantly greater at sites without amphipods than at sites with high amphipod densities. Though a lower proportion of spores ingested by amphipods germinated compared with uningested spores, those that did germinate had higher growth rates, presumably due to nutrients absorbed by plant cells during passage through the herbivore gut (Buschmann and Santelices 1987).

Some freshwater phytoplankton show even stronger positive reactions to grazing. When the green alga *Sphaerocystis Schroeteri* is consumed by the zooplankton *Daphnia magna*, more than 90% of the cells are undamaged, and the nutrient enrichment that occurs during gut passage may increase growth rates by as much as 63%; this enrichment more than compensates for the slight damage the grazers do to the algal population (Porter 1976). In situ grazing experiments have indicated that this alga increased in number as the number of grazers increased. It appeared to rely on grazers as a rich localized source of nutrients.

Conclusions

Seaweeds employ a wealth of chemical, structural, and morphological defenses against herbivory and often manipulate these defenses according to spatial or temporal patterns of herbivore attack. Defenses may differ greatly in effectiveness against different herbivores, and multiple defenses are common in areas where herbivores are diverse and abundant. Several lines of evidence suggest that defenses are costly and are selected

against where herbivory is predictably low. Some seaweeds benefit from moderate grazing because herbivores remove competitors, supply limiting nutrients, or disperse the seaweed's propagules.

Acknowledgments

Preparation of this paper and our recent studies of seaweed-herbivore interactions were supported by the National Science Foundation (OCE 86-08663 and 89-00131), the National Geographic Society (3400-86), the Lizard Island Research Foundation of the Australian Museum, and the Charles A. Lindbergh Fund, Inc. We thank J. A. Miller, V. J. Paul, and two anonymous reviewers for helpful comments on the manuscript.

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