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ABSTRACT

Coexistence of potential competitors within diverse tropical communities has often been explained as a result of fine scale resource partitioning. This is assumed to have resulted from an evolutionary history of competitive encounters and is usually inferred from shifts in abundance that occur between habitats with different physical characteristics. Seaweeds on coral reefs show predictable patterns of distribution that can be interpreted as habitat partitioning. However, manipulative experiments show that most seaweeds are habitat generalists and that both between- and within-habitat patterns of distribution are often controlled by herbivores. Spatial changes in herbivore effectiveness create a mosaic of habitats that differ in the degree to which they favor poorly defended but competitively superior seaweeds versus well defended but competitively inferior ones. If herbivory is decreased, the mosaic nature of the habitat is reduced and many well defended species are excluded by competition. This pattern occurs across a large range of spatial scales and can explain between habitat differences in seaweed communities that occur hundreds of meters apart, within-habitat differences that occur only a few meters apart, and microhabitat differences that occur on a scale of centimeters or millimeters. A portion of the microhabitat pattern is created by the seaweeds themselves. For example, consumption of palatable seaweeds is significantly reduced when they grow on unpalatable seaweeds. These associational defenses increase species richness by allowing palatable forms to invade grazed areas after unpalatable forms establish and create microsites of reduced herbivory.

Foraging by reef herbivores is constrained by a number of habitat characteristics that do not directly affect the physiological performance of reef macrophytes. For the seaweeds, this differential use of space by herbivores often produces a spatial mosaic of selective regimes in an area that would otherwise be treated as one uniform habitat; this interaction results in elevated species richness for the reef system as a whole.

RESUME

La coexistence de compétiteurs potentiels à l'intérieur de diverses communautés récifales a souvent été expliquée par le fait d'un partage très subtil des ressources. Cette coexistence résulterait d'une évolution de la compétition, évolution qui serait dûe aux variations d'abondance observées entre habitats à différentes caractéristiques physiques. Les algues des récifs coralliens montrent des modalités de répartition prévisibles, qui peuvent être interprétées comme un simple partage de l'habitat. Cependant, des expériences ont montré que la plupart des algues sont ubiquistes, et que les modalités de répartition intra et inter-habitats sont souvent contrôlées par les herbivores. Les variations de l'efficacité des herbivores créent une mosaïque d'habitats dans la mesure où leur présence favorise les alguiers pauvrement défendus mais plus compétitifs, à l'encontre de ceux qui sont bien défendus mais peu compétitifs. Si la densité des herbivores décroit, la structure en mosaïque de l'habitat se réduit, et un grand nombre d'espèces bien défendues sont exclues par compétition. Ces modalités se retrouvent à différentes échelles spatiales, et peuvent expliquer les différences qui existent entre les communautés d'alguiers distantes de quelques centaines de mètres, les différences qui apparaissent à l'intérieur d'un habitat, à quelques mètres de distance, et les micro-différences qui apparaissent à l'échelle du centimètre et du millimètre. Les modalités de répartition à l'échelle du micro-habitat sont, en partie, mises en place par les algues elles-mêmes. Par exemple, la consommation d'algues agréables au goût est réduite de façon significative lorsqu'elles se fixent sur des algues non agréables. Ce type de défense par association augmente la richesse spécifique, par réduction de l'impact des herbivores. Le pâturage des herbivores du récif est limité par un grand nombre de caractéristiques d'habitats qui n'affectent pas directement la performance physiologique des macrophytes. Pour les alguiers, ces différentes utilisations de l'espace entraînent la formation d'une mosaïque spatiale de régimes sélectifs dans une aire qui serait sinon considérée comme un habitat uniforme. Cette interaction permet d'augmenter la richesse spécifique du récif dans son entier.

INTRODUCTION

Most investigations of diversity in marine communities have focused on the maintenance of within-habitat diversity due to selective predation on potential competitive dominants (Paine 1966) or on the importance of small-scale disturbance and patch formation (Paine & Levin 1981) in maintaining several successional states within a habitat. In this paper I argue that species richness of seaweeds on, and near, coral reefs is maintained in large part by mosaics of herbivore impact that are relatively permanent and predictable. Although many seaweeds are almost always restricted to some characteristic habitat (i.e., shallow reef-flat, deep sandy plain, shallow fore reef, etc.), experimental evidence shows that most of these restrictions are herbivore induced and not a result of habitat partitioning based on differing physiological requirements (Hay 1981a, Hay et al. 1983, Lewis 1984a). When spatial variations in herbivory are reduced, habitats that differ greatly in algal species composition often become homogeneous (Lewis 1984). This results in a lowering of total species richness due to a loss of between-habitat diversity. In most instances, the seaweeds that invade and become dominant following herbivore removal are relatively palatable macrophytes (often Padina, Sargassum, or Turbinaria) that exclude, or significantly decrease the abundance of, both herbivore resistant macrophytes and herbivore tolerant filamentous forms. This is consistent with a growing body of plant literature suggesting that the evolution of effective herbivore deterrents can be achieved only by diverting energy and nutrients from other plant needs. Thus, defenses appear to be costly and, in the absence of herbivory, less defended individuals or species will have higher fitness than more heavily defended individuals or species (Rhodes 1979, Hay 1984a). Several previous studies on seaweed-herbivore interactions have documented patterns consistent with this hypothesis (Lubchenco 1978, Littler & Littler 1980, Hay 1981a, b, 1984a, Hay et al. 1983, Littler et al. 1983a, b) and Lubchenco & Gaines (1981) present a clear graphical depiction of the model (their Fig. 2). Rhoades (1979) reviews similar patterns for terrestrial plants.

In this paper, I review the available information on how herbivory affects algal distribution on several spatial scales. Patterns in seaweed distribution that occur over a scale of several meters to many kilometers and involve habitats with clearly different physical characteristics are called between-habitat patterns. Patterns occurring on a scale of only a few meters and within areas that appear relatively homogeneous are called within-habitat patterns. Patterns occurring on a scale of centimeters are called microhabitat patterns. Patterns occurring over large geographic ranges are mentioned, but not examined in detail. Each of these is discussed below.

Between-habitat patterns

Large differences in seaweed biomass and species composition often occur on different reefs or among different habitats on the same reef. Near-shore reefs often support a high biomass of fleshy macrophytes compared to mid-shelf and outer-shelf reefs where encrusting corallines and small filamentous algae are common (Stephenson & Searles 1960, Russ 1984a). Although significant differences in physical parameters undoubtedly occur among these habitats, available evidence suggests that the differences in seaweed communities may be maintained primarily by differences in herbivory. The decrease in macroalgae with increasing distance from the mainland is correlated with a significant increase in the mass,

species richness, and density of herbivorous scarids and acanthurids (Williams & Hatcher 1983, Russ 1984a, b). Similar correlations often occur on different portions of the same reef (Adey et al. 1977, Miller 1982, Lewis 1984b).

Early studies on the effects of herbivores on seaweed communities showed that reef-associated herbivores contributed to the generation of the halo of relatively bare sand that separated reefs from seagrass beds (Randall 1965, Ogden et al. 1973), and that a similar pattern appeared to occur where reefs merged with algal covered sand plains (Earle 1972, Dahl 1973). Shallow reef flats also appeared to suffer less herbivory since macrophytes that were common on reef flats were consumed when moved to reef slopes (Littler & Doty 1975). A combination of caging and transplant studies conducted on Caribbean reefs showed that macrophytes typical of deep sand plains or very shallow reef flats were not only capable of growing on reef slopes but often experienced dramatically increased fitness there so long as they were protected from reef associated herbivores (Hay 1981a, Hay et al. 1983). This pattern of herbivore activity and density being highest on shallow fore reefs, and significantly less on deeper fore reefs, shallow reef flats, sandy lagoons, and deep sandy plains has now been documented for several Caribbean, Pacific, and Indian Ocean reefs (Bouchon-Navaro & Harmelin-Vivien 1981, Hay 1981c, 1984a, b, Hay et al. 1983, Hatcher & Larkum 1983, Williams & Hatcher 1983, Lewis 1984a, b, Russ 1984b).

After comparing the photosynthetic rates, growth rates, and morphological characteristics of seaweeds from reef-slope habitats with seaweeds from sand-plain and reef-flat habitats, Hay (1981a, b, Hay et al. 1983) predicted that reduced herbivory on the reef slope would lead to invasion by reef-flat and sand-plain species that would competitively exclude species typical of the reef slope. Numerous correlative patterns (Hay 1981a, b, 1984a) and several unreplicated herbivore exclusions (John & Pople 1973, Tsuda & Kami 1973, Sammarco et al. 1974) supported the hypothesis but it was not adequately tested.

Recent studies by Lewis (1984a, b) on the Belizean Barrier Reef are the first, adequately replicated, studies that critically test this hypothesis. She excluded adult herbivorous fishes from shallow (-1.5 m) back-reef habitats using fences with a mesh size of 2.5 cm. Before the exclusion, and in control areas during the exclusion, macroalgae were very rare, crustose corallines and small filamentous algae were common, and about 20% of the substrate was unoccupied. After ten weeks of reduced herbivory, a comparison of exclusion versus control areas showed the following differences: cover of unoccupied space, Porites, Valonia, crustose corallines, and small filamentous algae had declined significantly; cover of the following macrophytes increased significantly: Padina jamaicensis, Turbinaria turbinata, Dictyota bartayresii, and D. cervicornis. In addition, several macrophyte species colonized the exclusion areas but not areas subject to fish grazing, and several macrophytes that were present in both treatments, reached reproductive maturity only in the exclusion. The macrophytes that dominated the exclusion areas were typical of nearby habitats that served as spatial escapes from herbivorous fish. Thus, two habitats with very different seaweed communities became relatively homogeneous following the exclusion of herbivores from one habitat. If this decreased between-habitat diversity occurred on a large scale, fewer species would be maintained in the reef system

similar results in that macrophytes (often species that were absent before herbivore exclusion) usually become dominant if exclusions are maintained for a sufficient length of time (Randall 1961, Tsuda & Kami 1973, Sammarco et al. 1974, Carpenter 1981, 1984 a).

Within-habitat patterns

The importance of territorial herbivorous fish in generating spatial mosaics of herbivore impact has been studied extensively and needs little elaboration here. Through aggressive defense of their algal mats, territorial pomacentrids create patches of intermediate grazing intensity where algal species richness, evenness, and diversity are increased relative to both areas that are available to all grazers or caged areas where all macroherbivores are excluded (Hixon & Brostoff 1983, Sammarco 1983). When all fish and urchins were excluded from an area, it became dominated by a few species of filaments or macrophytes by the end of the first year. When all grazers had access to an area, it became dominated by a few species of crustose corallines and rapidly colonizing filaments. Several species are found only inside of, or only outside of, defended algal mats (Brawley & Adey 1977, Hixon & Brostoff 1982). The territorial fish thus create distinct biotic patches on an otherwise more homogeneous background. This raises species richness of the community as a whole.

Other cases of herbivores creating mosaics of seaweed distribution on a physical background that the seaweeds would use in a homogeneous manner are less well studied. I will present several examples of the potential importance of this process on reefs; all of these examples are in need of further study.

Numerous investigations have shown that both the density of herbivorous fish (Bouchon-Navaro & Harmelin-Vivien 1981, Williams & Hatcher 1983, Russ 1984b, Lewis & Wainwright in press) and the rate of plant removal by herbivorous fish (Vine 1974, Hay 1981c, 1984b, Hay et al. 1983, Hay & Goertemiller 1983) decreases with depth on most reef slopes. If grazing over depth gradients decreases more rapidly than the decrease in algal production caused by reduced light, then deep areas may serve as spatial refuges from herbivores since production, even by species with few defenses against herbivores, could exceed consumption. If this pattern occurs predictably, then selection for herbivore deterrents should be reduced on the deeper portions of fore reefs. Partial tests of this hypothesis have yielded mixed results (Hay 1981c, Hay & Goertemiller 1983).

It is unclear whether herbivorous fish avoid deep sections of reefs because of lower production of their prey, a higher probability of being successfully attacked by predators due to the decreased light levels (Hobson 1972, Cerri 1983), or some combination of these, or other, factors. Avoidance of predators may be a factor since herbivores on heavily fished reefs, where most large predators have presumably been removed, make increased use of deeper habitats (Hay 1984b). However, this study was only correlative and, as such, must be viewed with caution.

Predators could have a large impact on the spatial pattern of habitat use by marine herbivores and thus indirectly affect the mosaic nature of grazing on reefs. In freshwater streams, alga eating minnows avoid both shallow areas where they fall prey to avian and terrestrial predators (Power 1984) and areas near larger predatory fishes (Power & Matthews 1983); in both cases algal biomass in these areas is significantly increased. This phenomena is unstudied on coral reefs but several investigations suggest its importance. For example, herbivorous fish

provide few hiding places and leave these herbivores more exposed to predators (Hay 1984a). Seaweeds from deep sand plains (Earle 1972, Dahl 1973, Hay 1981a, 1984a) and shallow sandy lagoons (Randall 1965, Ogden et al. 1973, Hay 1981c, 1984b) appear to suffer less herbivory for similar reasons. On a smaller spatial scale, Hoffman & Robertson (1983) show that some toadfish in Panama feed primarily on the seaurchin Diadema. Urchin density is significantly lowered near holes occupied by these predators (Hoffman & Robertson 1983) and areas near these holes often appear to support unusually dense stands of some seaweeds (Hay personal observation).

In areas where urchin predators are common, Diadema densities tend to be low and a large proportion of the individuals home to safe sites during the day (Carpenter 1984b). Under these conditions, predators may create fairly stable spatial patterns in Diadema grazing; areas near homing sites would be grazed heavily while those remote from home sites would be grazed only rarely. This could produce a spatial mosaic of selective factors favoring different species near versus far from Diadema and thus increase overall diversity. In areas with few urchin predators, Diadema densities are higher and few individuals home to safe sites (Carpenter 1984b). Under these conditions Diadema grazing will become more homogeneous and algal species richness may decline.

Herbivorous fish may also reduce their feeding in areas where their susceptibility to predation is increased. A possible example of this is shown in in Fig. 1. At Serrana Bank, Nicaragua (Caribbean) I placed 30 4 cm long pieces of the palatable seaweed (Hay 1984a) Laurencia papillosa in each of 4 habitats and after 19 h counted how many were completely eaten and how many remained (see Hay 1981c for methods). Habitats 1, 2, and 4 were all fairly open areas where approaching predators would be easily seen. Habitat 3 was in front of an overhang that I assumed might provide a good ambush site for predators. Although snapper, barracuda, and grouper often occurred beneath the overhang, both parrotfish and surgeonfish also appeared (I did not make quantitative counts) to be much more common here than in any of the other 3 habitats. Laurencia consumption in front of the overhang was significantly lower (p < .02 Contingency Table Analysis) than in any of the other habitats. In addition, mature plants of both Sargassum and
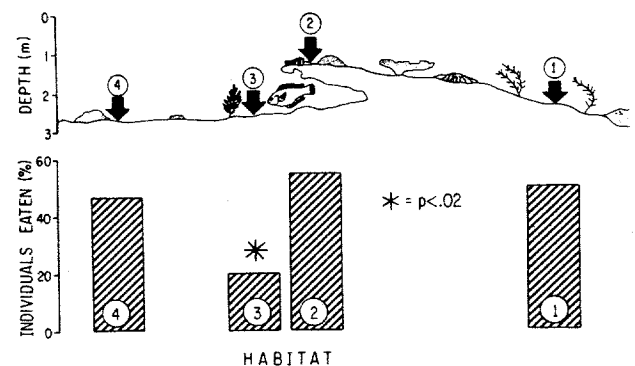
Figure 1. Loss of individuals of Laurencia papillosa as a function of location across shallow fore reef (habitat #1), reef crest (#2), and back reef (#3 & #4) at Serrana Bank, Nicaragua. N=30 for each habitat and the p-value is by Contingency Table Analysis.

Turbinaria were fairly common in front of the overhang; in the other 3 habitats these plants were either absent or present only as basal portions in crevices. When Sargassum and Turbinaria were moved from near the overhang to other areas of the reef, 10 to 30% of the individuals were eaten by fish within 36 h (Hay 1984a). These patterns are consistent with the hypothesis that predators may create mosaics of small safe sites where palatable prey can colonize even though they are rapidly eaten in immediately adjacent areas. This possibility and its effects on reef community structure deserves further study. It is also interesting that herbivorous fish appeared to be much more numerous near the overhang but consumed less algae there. This suggests that these fish do not necessarily avoid areas where predators are common but that they feed less there, possibly a consequence of decreased feeding time resulting from more time spent detecting and monitoring the activity of potential predators. A similar hypothesis has been presented, and partially tested, for freshwater (Cerri & Fraser 1983) and temperate marine communities (Schmitt & Holbrook 1985).

If different species of grazers use different portions of the reef, this may also produce a mosaic of selective regimes and enhance diversity. In recent studies on St. Croix, Carpenter (1984a) has shown that either fish or urchins alone can remove nearly 100% of yearly algal production. However, areas grazed by either fish or urchins differ markedly in composition of the algal community. Feeding preferences of parrotfish and surgeonfish also differ dramatically (Lewis 1984b) and since these fish make differential use of some portions of the reef (Bouchon-Navaro & Harmelin-Vivien 1981, Russ 1984a, Lewis & Wainwright in press) this may increase the variance in algal composition in an otherwise homogeneous habitat and thus increase species richness.

Microhabitat patterns

Brock (1979) studied the effects of herbivory and microhabitat complexity on species richness over a 43 day period in experimental microcosms in Hawaii. Herbivory was varied by altering the density of juvenile parrotfish and microhabitat complexity was altered by covering the bottom of the microcosms with mesh of differing sizes. On unstructured substrate, both species number and biomass of benthic organisms decreased with increasing fish density. When microhabitats were added, species number and biomass changed very little with increasing fish density. Thus availability of microhabitats was critically important in maintaining species richness when grazing rate was high.

Menge et al. (1983) conducted a longer term study on microhabitats in a tropical rocky intertidal community using naturally occurring holes and crevices and artificial holes made of Plexiglas. The biotic composition of these microhabitats was extremely variable because occupation of the holes by different benthic grazers was also very variable. When grazer occupation of holes was made more uniform, biological composition of holes became more uniform. Open surfaces between holes showed much less variability in species composition than holes because large mobile fish attacked them more uniformly. In this habitat, overall diversity was increased because holes provided biologically variable patches in a background of more homogeneous, fish-grazed rock.

Previous experiments have suggested that areas dominated by unpalatable seaweeds may provide microhabitats of reduced grazing intensity (Hay 1981b, Hay et al. 1983). If this is true, then

seaweeds that are preferred by reef herbivores might gain significant protection by growing on, among, or being overgrown by low preference species. I performed initial tests of this hypothesis on two reefs in the Florida Keys, USA. The palatable species Laurencia papillosa and L. gemmifera, either by themselves or intertwined with the less palatable species Dictyota sp. or Halimeda goreauii, were presented to herbivorous fish in the field. Four cm long branches of each species, and combinations of species, were woven between the strands of a 3-strand rope and placed on the reef slope at depths of 6-10 m (see Hay 1984a for an elaboration of the method). All algal species and combinations were present in each rope. Each species, or combination of species, was separated from the next by about 3 cm. Ropes were attached to coral branch tips so that the ropes were suspended .3 to .5 m above the bottom and thus available only to swimming herbivores. At the end of each trial (1.5 h on French Reef; 6 h on Sombrero Reef) all 30-31 ropes were collected and each individual was recorded as either still present or completely eaten. Consumption of Laurencia decreased by 70-80% when it was intertwined with Dictyota or Halimeda on either reef (Fig. 2). On French Reef, Dictyota was consumed more often when it was intertwined with Laurencia; on Sombrero Reef, consumption of neither Dictyota nor Halimeda was affected by association with the more palatable Laurencia.

Unquantified observations on these reefs indicated that palatable species such as Laurencia papillosa, L. gemmifera, and Hypnea spp. grew by themselves on reef flats where herbivory is usually reduced (Hay 1984a). On subtidal portions of the reef where herbivory was higher, these species were rare and occurred only beneath Dictyota or imbedded within clumps of Halimeda.
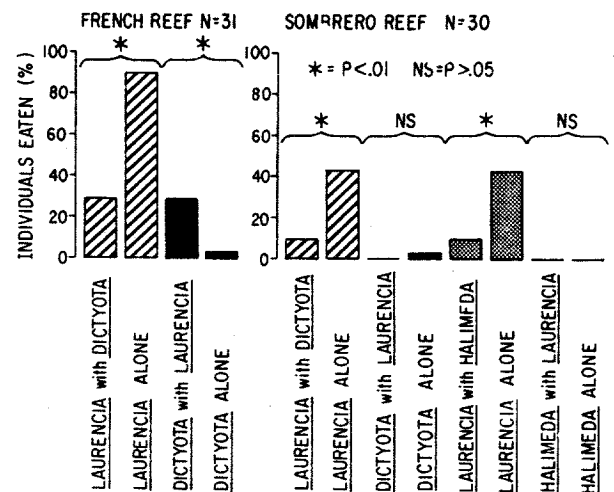

Figure 2. Herbivory on palatable (Laurencia papillosa at French Reef and L. gemmifera at Sombrero Reef) and unpalatable (Dictyota sp. on both reefs and Halimeda goreauii on Sombrero Reef) seaweeds when these are presented to reef herbivores alone or intertwined with each other. P-values are by Contingency Table Analysis.

Associational defenses, like those shown by Laurencia, may have important effects on the organization of reef communities and on the maintenance of species richness. High abundance of

one common organism is generally associated with a decrease in species numbers resulting from competitive exclusion. However, if the abundant organism is unpalatable and provides a safe microhabitat for more herbivore susceptible species, then its dominance of primary substrate may result in increased, instead of decreased, species richness. This phenomena remains unstudied on tropical reefs. However, in coastal North Carolina, USA, a large number of palatable seaweeds rapidly colonize new substrates that are protected from herbivorous fish. When fish have access to these substrates, colonization of palatable species is delayed for several months until unpalatable species become abundant and provide microhabitats of reduced herbivory. In this temperate community, colonization by palatable species like Hypnea and Enteromorpha is dependent upon less-palatable competitors like Sargassum which provide microhabitats that facilitate their invasion (Hay, work in progress).

Geographic patterns

Geographical differences in seaweed distribution are usually assumed to be due to changes in physical parameters such as temperature. However, numerous studies present correlative evidence suggesting that some portion of the geographic constraints on both specific species and morphological types may be explained by geographic differences in herbivory (Birkeland 1971, Vermeij 1978, Hay 1981a, Menge & Lubchenco 1981, Gaines & Lubchenco 1982, Hay & Gaines 1984). All of these studies suffer serious limitations due to the problems involved with testing hypotheses about such large areas; their geographical speculation must therefore be viewed with caution. However, the temperate-tropical gradients that have been proposed for shallow marine communities should provide many opportunities to investigate the possibility of herbivore-influenced distributional barriers.

SUMMARY

On all of the spatial scales discussed, seaweeds on coral reefs show predictable patterns of distribution that can be interpreted as habitat partitioning. However, most of the species that have been experimentally investigated are not specialists but are generalists that grow well in a wide variety of habitats if they are protected from herbivores. Thus, for coral reef seaweeds, herbivore effectiveness constitutes an axis for niche differentiation among seaweeds, just as seaweeds could provide separable resources allowing niche differentiation among herbivores. Spatially variable herbivore effectiveness creates a mosaic of habitats on an otherwise more homogeneous background; this appears to be a major factor promoting the high between-habitat diversity and species richness that is characteristic of coral reefs.

ACKNOWLEDGEMENTS

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