SYMPOSIUM nº 6

HERBIVORE-PLANT INTERACTIONS ON CORAL REEFS

RELATIONS ENTRE LES HERBIVORES ET LES VEGETAUX DANS LES RECIFS CORALLIENS

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INTRODUCTION

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It is commonplace that algal standing stocks are controlled primarily by grazing in most tropical reef habitats accessible to large populations of herbivores. Both Pacific and Caribbean tropical reef algae are subjected to intense grazing pressures by abundant and diverse assemblages of highly mobile fishes included within the families Acanthuridae, Scaridae, Kyphosidae, Pomacentridae and Blenniidae. Sea urchin grazing, especially by Diadema, also has a significant impact on the localized distributions and abundances of marine macroalgae throughout tropical waters. Numerous studies have shown up to a 15-fold decrease in frondose algal standing stocks under high grazing. Only in extreme shallows, high energy environments or the deeper waters of reef slopes does grazing activity diminish, and physical factors such as light energy appear to structure the abundant algal communities found to 100m and below.

There are at least 8 evolutionary strategies available to seaweeds for reducing losses due to the severe grazing pressures encountered on most tropical reefs. More than one of these herbivore-resistance mechanisms is often expressed by a given species: (1) occupation of refuge habitats that are physically unfavorable or unavailable to herbivores (e.g., sand flats, high wave energy zones, areas of high surface rugosity), (2) cryptic appearances or mimicry, (3) unpredictable spatial and temporal distributions, (4) rapid growth involving the replacement of vegetative and reproductive tissues while simultaneously satiating the appetites of grazers, (5) close association with unpalatable organisms, (6) carnivorous predators or (7) highly territorial animals and (8) allocation of materials and energy toward herbivore defenses. The last strategy has at least five non-mutually exclusive components that encompass: (a) toxins, digestion-inhibitors or unpalatable secondary metabolites, (b) reduced calorific contents, (c) morphological shapes and sizes that minimize accessibility, (d) textures that inhibit the physical processes of herbivore manipulation and feeding and (e) structural materials (e.g. $CaCO_3$) that decrease palatability or nutritional value.

Recently, the importance of the last five components (a-e) to tropical algae has been shown by bioassay experiments. Many of the forms that rely primarily on chemical defenses are able to maintain high photosynthetic rates, but remain susceptible to physical forces such as wave shear and sand scour. The synthesis of toxic secondary compounds by algae increases dramatically in herbivore-rich subtropical and tropical reef systems compared to temperate coastal environments. This correlation has fostered a rather speculative literature on algal chemical defenses. The stage has now been set for more precisely-controlled experiments involving hypothetical chemical-defense compounds used on natural reef populations at normal levels, with artifactual problems eliminated, to establish the adaptive significance of algal secondary metabolites.

In contrast to purely chemical defense mechanisms, the coarser and tougher species (thick forms, calcareous and encrusting forms) resist grazing (by herbivores with weak feeding structures) as well as other physical forces by means of relatively high proportions of structural materials. Calcareous encrusting algae are considerably less vulnerable to herbivore grazing than the softer non-calcareous algae and some may actually require herbivory to prevent inhibitory overgrowth. The low edibility of calcareous forms could be a result of reduced calorific contents and increased mechanical resistances to removal by scraping and biting mechanisms. However, it is now clear that this structural resistance to herbivory comes at the cost of dramatically lower photosynthetic and growth rates.

The role of fish grazing is relatively complex. Grazing intensity varies functionally by herbivore taxon and social interaction, as well as spatially from one reef habitat to another and temporally within any given habitat.

Considerable progress in regard to tropical plant-herbivore interactions is being made utilizing a functional/morphological approach from a costs/benefits perspective. Algal functional groups have been used as an effective means for interpreting complex plant community herbivory patterns, without having to deal with each of the component species. However, short-term studies on highly variable reef systems, where only several of the more closely related algal functional groups were compared, have not revealed clear correlative patterns in regard to either chemical or structural defenses. The functional-group technique has been used successfully in some cases to interpret evolutionary changes with respect to fluctuations in herbivory through geological time as well as biogeographical responses of algae to herbivore types.

From the perspective of the herbivore components of reef ecosystems, many questions remain unanswered. For example: What is the role of herbivory in controlling marine plant biogeographical patterns? Why have not more herbivorous fishes evolved in cold temperate systems to exploit the rich plant life? Why are tightly co-evolved plant-herbivore systems mainly present in the Mollusca and virtually none documented for reef fishes or echinoderms? What are the roles of micrograzers on reefs?

The disciplines of marine chemical ecology and functional morphology are still in their infancy, but offer exciting prospects for the future. A general trend in emphasis from descriptive-correlative viewpoints toward mechanistic-causative experimental approaches is underway in the burgeoning field of plant-animal interactions, and this is leading to improved predictive capabilities.

Recognition of the great importance of tropical algal-grazer interactions as structuring mechanisms for reef communities and in reef biogenesis will stimulate much research during the next decade.