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A test of the Menge-Sutherland model of community organization in a tropical rocky intertidal food web

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Summary. Menge and Sutherland (1976) predicted that in physically benign habitats: (1) community structure will be most strongly affected be predation, (2) the effect of predation will increase with a decrease in trophic position in the food web, (3) trophically intermediate species will be influenced by both predation and competition, and (4) competition will occur among prey species which successfully escape consumers. These predictions were tested in a tropical rocky intertidal community on the Pacific coast of Panama. The most abundant mobile species included fishes and crabs, which occupied the top trophic level, and predaceous gastropods and herbivorous molluscs, which occupied intermediate trophic levels. The most abundant sessile organisms were encrusting algae, foliose algae, barnacles, and bivalves. Diets were broad and overlapping, and 30.3% of the consumers were omnivorous. Each consumer group had strong effects on prey occurring at lower trophic levels: (1) Fishes and crabs reduced the abundance of predaceous snails, herbivorous molluscs, foliose algae, and sessile invertebrates. (2) Predaceous gastropods reduced the abundance of herbivorous molluscs and sessile invertebrates. (3) Herbivorous molluscs reduced the abundance of foliose algae and young stages of sessile invertebrates, and altered relative abundances of the encrusting algae. The encrusting algae, although normally the dominant space occupiers, proved to be inferior competitors for space with other sessile organisms when consumers were experimentally excluded. However, the crusts escaped consumers by virtue of superior anti-herbivore defenses and competed for space despite intense grazing. Observations do not support the hypothesis that the trophically intermediate species compete. Hence, with the exception of this last observation, the predictions of the Menge and Sutherland model were supported. Although further work is needed to evaluate other predictions of the model in this community, evidence from this study joins an increasing body of knowledge supporting the model. Contradictory evidence also exists, however, indicating that aspects of the model require revision.

Key words: Community regulation – Experiments – Food web – Rocky intertidal – Tropics

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In their model explaining the regulation of terrestrial food webs, Hairston et al. (1960), proposed that the importance of predation and competition alternated with trophic level: (1) carnivores (=top predators) are limited by the availability of prey (=herbivores), and are thereby regulated by competition for food; hence, (2) the abundance of herbivores is kept low by predation; and consequently, (3) plants, in the absence of control by herbivores, become abundant and compete for space. As used by Hairston et al. (1960), the term "regulate" referred primarily to control of abundances. Our use of this term includes this meaning, but is defined somewhat more broadly to include control of distribution, abundance, species composition, and diversity.

Inspired by these arguments, Menge and Sutherland (1976) proposed an expanded and somewhat different model. Like Hairston et al. (1960), Menge and Sutherland (1976) suggested that the top trophic level should be regulated by competition, but unlike Hairston et al. (1960), Menge and Sutherland (1976) suggested that under certain conditions, herbivores or organisms at the bottom trophic level (=basal species; Pimm 1980) may in fact be the "top" trophic level. These conditions are when the number of trophic levels (and/or consumers) effective in controlling prey are reduced by environmental harshness. Thus, whereas Hairston et al. (1960) was restricted to food webs with three trophic levels, Menge and Sutherland (1976) suggested that the number of trophic levels and consumer effectiveness varied with environmental conditions.

In contrast to the alternation between predation and competition as controlling agents proposed by Hairston et al. (1960), Menge and Sutherland (1976) suggested that the importance of predation as a regulating factor increased, and competition decreased at successively lower trophic levels. This prediction arose from the observation that in many food webs, consumers at higher levels feed on several lower trophic levels rather than on just the next lower trophic level. Finally, like Hairston et al. (1960), Menge and Sutherland (1976) suggested that basal species should compete for space or light, but only under conditions favoring an escape from predation. Thus, Menge and Sutherland (1976) proposed that the structure of the basal species assemblage is regulated by predation on juvenile stages, and that competition occurring among adults which successfully pass through this predation bottleneck has a lesser effect on basal species structure. Connell (1975) independently offered similar arguments, and suggested that es-