

FUNCTIONAL ANALYSIS OF A THERMAL SPRING ECOSYSTEM, WITH AN EVALUATION OF THE ROLE OF CONSUMERS¹

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Abstract. Low temperature ($< 40^{\circ}\text{C}$) alkaline thermal spring effluents in Yellowstone National Park support a benthic algal-bacterial mat fed upon by a single herbivorous brine fly (Diptera: Ephydriidae), which in turn is consumed by a number of arthropod predators (water mites, spiders, and a predaceous fly). A census of an entire spring ecosystem provided a framework upon which to integrate present knowledge of this system.

Growth of the algal-bacterial mat appears to be nutrient limited; measures of free CO_2 concentrations are good predictors of the differences in productivity within and among springs. *Paracoenia turbida*, the herbivore, saturates all suitable oviposition sites, and its larvae destroy all algae available below them. The larvae apparently suffer substantial density-dependent mortality late in their development, when they consume algal dams protecting them from hot water flows. Thus, they compete for limited space of suitable temperature. Algal-bacterial biomass persists because, at any one time, most of the mat is too hot for larvae, or is covered by flowing water and consequently unsuitable for oviposition. The brine fly eggs which constitute the prey for most predators are also largely unavailable because the flies insert them into the algal-bacterial mat, where they are difficult to remove and feed upon. The demand-availability ratio for fly eggs is high; therefore reproduction of the major predatory water mite, *Paratnuniella thermalis* (Hydrachnellae) is probably limited by the supply of available eggs.

Despite the abundance of their prey species, then, both primary and secondary consumers seem to be resource limited because most of their prey are unavailable. The important role of refuges in defining the biomass structure of this ecosystem prompted us to define four conditions which tend to limit consumer influence on prey density: (1) evolutionary specialization by consumers, which narrows the spectrum of potential food; (2) poor food quality which does not allow population growth; (3) evolved defenses of the prey; (4) the degree of uncertainty in resource distribution in space or time. Restrictions of type (4) are difficult to document and may often go unappreciated, but an example from the thermal spring system shows the uncertainty in resource distribution may be evolutionarily insoluble, and it may be a powerful constraint on consumer impact. There is little reason to believe that these conditions are any less powerful in complex than in simple systems. By analogy then, the ability of consumers to influence prey density in complex terrestrial and aquatic systems may also be severely limited. The importance of refuges in complex systems might be inferred from measurements of community responses to low-level enrichment or harvesting.

Even though their direct influence on prey densities is limited, consumers in the thermal spring ecosystem increase the net primary production of the system and increase the efficiency of energy transfer between the first and second trophic levels. Thus, they affect processes, not prey densities, in this system.

Key words: *Acarina*; blue-green algae; community structure; consumers; Diptera; Ephydriidae; population regulation; productivity; refuge; Wyoming.

INTRODUCTION

Hot springs are distinctly bounded natural systems that operate largely independent of their surroundings. Their hot water effluents maintain year-round temperatures above the summer maxima for adjacent systems, and lay down mineral substrates quite unlike adjacent rocks and soil. The biota of these

springs consists of a few thermophilic species of algae, bacteria, and arthropods which are also distinct from those of surrounding communities. Effluents between 30°C and 45°C support metazoan herbivores, predators, and parasites, as well as microorganisms, and may be regarded as easily studied analogues of larger and more complex systems.

Descriptions of the biology of the components of such low temperature alkaline thermal effluents in Yellowstone National Park have been published

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