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Spatial scale and the processes structuring a guild of larval trematode parasites

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3.1 INTRODUCTION

An individual host is a patch of habitat for a particular stage in the life cycle of a parasite (Price, 1980; Holmes and Price, 1986). It contains resources necessary for growth and development of this infecting stage, and for production of the next, usually dispersing, stage. Each individual host is an inherently bounded, discrete habitat, that is isolated from other similar habitat patches by an external environment that is inhospitable to the parasitic stage that infects the host.

As patches of parasite habitat, hosts are both self-reproducing and ephemeral. Excluding instances of vertical transmission and assuming life-long infection (as is the case for many parasitic infections of invertebrate hosts), empty patches are born via the recruitment of susceptible offspring to a host population, patches increase in size and change in a variety of other characteristics (e.g. morphology, biochemistry, etc.) during host ontogeny, and they disappear (along with their resident parasites) when the host dies. The rates at which these processes occur vary among host populations and in time.

In many ecological systems, the distribution and accessibility of resources vary with spatial and temporal scale, as do the processes that structure populations and communities (e.g. Andrewartha and Birch, 1954; Wiens, 1976; Price, 1980; Allen and Starr, 1982; Connell and Sousa, 1983; Dayton and Tegner, 1984; Sousa, 1984; Addicott *et al.*, 1987). Studies of processes

G. W. Esch et al. (eds.), *Parasite Communities: Patterns and Processes*

operating at different scales within systems of divided habitat patches have provided substantial insight in this regard. When strong asymmetrical interactions on the small scale, i.e. within a patch, preclude the coexistence of competitors, or of predators and their prey, the existence of multiple patches coupled by dispersal often promotes their coexistence on the larger scale (Hutchinson, 1951; Skellam, 1951; Huffaker, 1958; Cohen, 1970; Levins and Culver, 1971; Horn and MacArthur, 1972; Levin, 1974, 1976; Slatkin, 1974; Armstrong, 1976; Hastings, 1977, 1980; Caswell, 1978; Shorrocks *et al.*, 1979; Sousa, 1979; Lloyd and White, 1980; Atkinson and Shorrocks, 1981; Hanski, 1981, 1983; Ives and May, 1985; Murdoch *et al.*, 1985). Differential rates of dispersal among species, independent aggregation of species among patches, and an increased number of patches in the system enhance the likelihood that diversity will be maintained on the large scale, i.e. across all patches in the system.

The spatial scales of resources provided by hosts are hierarchical (Esch *et al.*, 1975; Margolis *et al.*, 1982; Holmes and Price, 1986; see also Chapter 1), and patterns and outcomes of interaction among parasites may vary among these scales. Nested levels in this hierarchy include: (a) tissues within a host, (b) an individual of a particular host species, (c) populations of a particular host species, and (d) communities of host species. The population of a particular parasite species that infects an individual host is called an infrapopulation; the collection of populations of different parasite species within a single host is an infracommunity. The assemblage of parasite species that infect a population of a particular host species is called a component community.

Populations of invertebrates that serve as intermediate hosts are commonly infected by several species of parasitic helminths (Denny, 1969; Wright, 1971; Brown, 1978; Rohde, 1982; Lauckner, 1980, 1983). To understand the processes that structure such assemblages of larval parasites better, I investigated patterns of species diversity of the helminths that infect the salt marsh snail, *Cerithidea californica*, at two different spatial scales. This parasite assemblage is composed solely of larval digenetic trematodes. Because the members are taxonomically similar and exploit a common resource, the assemblage is more appropriately referred to as a guild (*sensu* Root, 1967) than a community. The smaller of the two scales examined in this study is that of the individual snail, which potentially supports an infraguild of larval trematodes. The larger scale is that of the local host population and its component guild of parasites.

This chapter primarily examines patterns and processes at the second, larger scale, but summarizes what is known concerning structure and dynamics at the individual host scale. The latter is the subject of Chapter 3. Here, I examine several characteristics of local host and parasite popu-