

UNIVERSITY OF CALIFORNIA  
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The importance of spatial heterogeneity  
in organisms with complex life cycles: analysis of digenetic trematodes in  
a salt marsh community

A Dissertation submitted in partial satisfaction  
of the requirements for the degree of

Doctor of Philosophy

in

Division of Ecology, Evolution and Marine Biology

by

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March 1996

## **ABSTRACT**

**The importance of spatial heterogeneity in organisms with complex life cycles : analysis of digenetic trematodes in a salt marsh community**

**by**

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Populations of organisms often exhibit a surprisingly heterogeneous spatial distribution. Spatial heterogeneity may result from recruitment variation, habitat variability or post-recruitment processes such as competition, predation or disease. Parasites, particularly those with complex life cycles, can be used to study the generation of spatial heterogeneity and recruitment because the sampling units (their hosts) are biologically meaningful replicates and spatially heterogeneous in their distribution. Furthermore, the parasites must recruit from one host to another to complete the life cycle, and recruitment processes may intensify or diminish spatial variability. Spatial heterogeneity and recruitment of parasites can be studied at several levels; within individual hosts, host populations or host communities. Host behaviors or activities may also affect the distribution of parasites within individuals or populations. Specifically, the movement of a host in its' habitat (host vagility) may effectively diminish spatial heterogeneity of parasites as a host moves between areas of variable exposure risk.

Digenetic trematodes have complex life cycles, which require at least two hosts. In this study, the first intermediate host is the snail,

Cerithidea californica. Second intermediate hosts include the crab, Hemigrapsus oregonensis, two fishes, Gillichthys mirabilis and Fundulus parvipinnus, and the clam, Tagelus californianus. The snail population at Carpinteria Salt Marsh harbors 13 different trematode species. Of these 13 species, two parasitize the crab, two parasitize the fish, G. mirabilis, and one parasitizes the clam. Other larval trematode species infect F. parvipinnus, or don't require a second intermediate host (Austrobilharzia sp.).

The purpose of this study was to investigate processes that affect the spatial distribution abundance of larval trematodes at two host levels. This was accomplished by determining if spatial heterogeneity of larval trematodes in the snail population at Carpinteria Salt Marsh was reflected in second intermediate host populations, and determining the influence of second intermediate host vagility on infection patterns (Chapter 1). I experimentally examined this second issue by determining whether vagile versus restrained crabs had intermediate levels of infection, compared to control groups. A field survey was conducted to investigate spatial and temporal variability in emergence of infective larvae (recruits) from the snail source population (Chapter 2). I also estimated the proportion of infections expected in snails in the absence of intra-molluscan interspecific interactions (Chapter 3). This was done by using the proportion of infected snails in a model developed by Lafferty et al. (1994) which permitted an analysis of the importance of these interactions on the

abundance of larval trematodes. In addition, this analysis evaluated the effect of heterogeneous recruitment of larval trematodes to snails.

These studies confirmed that there was significant spatial heterogeneity of trematode infections in the snail, crab and clam populations, but not in fish. There was also a significant correlation between the density of infected snails and the abundance of trematodes for one of the species in crabs, Himasthla rhigedana; while Probolocoryphe uca showed a positive but non-significant association in crabs. There was no association between density of infected snails and the abundance of Euhaplorchis californiensis in fish, and a slightly negative association for Renicola buchanani. Abundance of Acanthoparyphium spinulosum in clams was not significantly associated with prevalence in snails.

Experimental investigations on vagile versus sedentary (control) sentinel crabs showed that all experimental crabs attained nearly 100% prevalence in a short (22 day) period. Vagile crabs obtained infection prevalences that were similar to control crabs, but infection intensities were generally lower than free-ranging resident individuals.

Emergence of infective larvae from the source snail population was intermittent on a daily basis and seasonally variable. Spatial and temporal heterogeneity was also observed in the diversity and abundance of infective larvae in the water. Temperature most strongly influenced emergence of infective larvae from snails; and there was a highly significant, positive correlation between temperature and daily abundance

in the field. Salinity had no effect on spatial or temporal emergence patterns. There were 9 cercarial species identified in the water samples, all which emerged from C. californica. For half of these species, there was a significant positive association between abundance of infective larvae in the water and abundance in the snail source population.

Interspecific interactions of larval trematodes in C. californica reduced the abundance of most species in the snail population; however, this study reports a greater number of double infections than other comparable studies of C. californica. Furthermore, heterogeneity in recruitment of larval trematodes to snails intensified these interactions rather than isolate species.

Finally, I am indebted to my major advisor, Armand Kuris, whose guidance and encouragement sparked my interest in larval trematodes. Thank you Armand, for giving me a shot at the PhD. Stephen Rothstein and Al Ebeling are responsible for my scholarship and attention to detail. I am grateful to all committee members for providing valuable comments and helpful recommendations on this project and manuscript.

California Sea Grant Graduate Student Research Fellowship, Sigma Xi, and the UC Natural Reserve System Mildred Mathias Graduate Student Fellowship generously sponsored this work.