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Multi-author Reviews

Population biology of freshwater invertebrates

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Introduction: Freshwater invertebrates as model systems in population ecology and genetics

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Population biology draws on several subdisciplines of biology, such as population ecology, population genetics, and life history theory. It is a rapidly growing, diversifying field at the nexus of general and community ecology, of genetics, biogeography, and especially of evolution. Not surprisingly, the conceptual issues addressed and the methodologies employed are daunting in their diversity. But the analysis of evolutionary processes and patterns, at the individual through species levels, is a unifying thread in population biological studies.

Why study the present aspects of the population biology of freshwater invertebrates in a series of articles? Various points may be enumerated here:

First, the general ecology of freshwater systems, termed 'limnology' for more than a century, has a long tradition as an ecological discipline, stressing earlier than other disciplines the ecosystem approach. It is in this field that ecologists have pioneered studies of energy flows, nutrient cycling, and related studies of the autecology of species to the framework of community and ecosystem ecology.

Second, experimental work on various freshwater organisms is frequently easier, especially on planktonic species, than work on terrestrial organisms. The latter typically live on a complex substrate environment with stronger fluctuation of environmental variables, such as small-scale temperature changes.

Third, freshwater ecosystems are often transient in nature, favoring the existence of species adapted to unpredictable environmental variables. Some concepts of population biology, such as energetics of rapid growth, effective dispersal, and ecological and evolutionary consequences of reproductive modes, can thus be studied in a more straightforward fashion with species from these systems.

Fourth, theory of ecology in general, and population biology especially, is frequently based on terrestrial rather than freshwater taxa, neglecting the wealth of information available in this field of ecology and genetics. One of the goals of this series of articles is to facilitate communication between ecologists of freshwater, marine, and terrestrial environments.

At one end of the spectrum of population biology are the community aspects of energy flow, nutrient cycling, biodiversity, and food-web structure, of which the contribution of B. Streit tries to give a general historical overview, present selected results, and summarize some current approaches and techniques.

Abiotic and biotic requirements for organisms to persist in ecological time define their ecological niche. Energy partitioning, patterns of resource use and competition for resources among species, are likely to influence species coexistence, and thus touch on mechanistic aspects of niches and biological diversity. These topics, together with a discussion of life history aspects, are treated in the contribution by N. Walz, presenting rotifers as a model group.

However, all these biological properties are not fixed species characteristics, but are themselves subject to evolutionary change within populations and species. Here, population biology proper comes to the fore. To understand microevolutionary processes, quantitative genetic techniques are powerful tools, and freshwater zooplankton life histories are increasingly used for examination of paradigms of evolutionary theory. It is this area in which K. Spitze reviews the empirical evidence for trade-offs which are predicted in optimality-based life history approaches. Evolutionary and ecological consequences of interspecific hybridization are thoroughly described by K. Schwenk and P. Spaak. Studying in detail the *Daphnia longispina* species com-

plex, they describe patchy distributions of hybrids and parentals, and emphasize that hybrids between two species can – temporarily – combine advantageous traits of either parent.

The first contribution (on energy flow and community structure) is rather general in nature, the other three contributions take their examples from limnic zooplankton, basically rotifers and cladocerans; the subsequent contributions focus on benthic organisms.

The importance of modes of reproduction is a common thread in population biology, touched upon in more than one of the articles: Many freshwater invertebrates reproduce by means other than gonochoric sexuality. In hermaphrodites, such as pulmonate snails, reviewed here by P. Jarne and T. Städler, self-fertilization provides opportunities for uniparental reproduction, with far-reaching consequences for population structure, maintenance of variability, and life history evolution. Similarly, several prosobranch snails reproduce by apomictic parthenogenesis, with closely related sexual forms still present, creating rare opportunities (at least for the animal kingdom) to investigate the causal factors which may maintain sex in the face of viable asexual alternatives. S. Johnson, C. Lively and S. Schrag review their extensive studies on freshwater snails from a largely ecological perspective, emphasizing the role of parasites for the maintenance of sexual reproduction in two prosobranchs, and the maintenance of outcrossing capability in a tropical pulmonate.

From a similar, primarily ecological perspective, B. Okamura and T. Hatton-Ellis discuss sexuality and local extinction/dispersal in the colonial – or modular – freshwater bryozoans. Modularity is prevalent in both marine and freshwater environments, yet most of our ecological and evolutionary models are cast in terms of unitary organisms.

An important aspect of contemporary community ecology, and also population biology, is the increasing dominance of invading species from other countries and continents, especially in those river and lake systems which are frequented by large vessels, such as the Rhine River in Europe and the Great Lakes in North America. Invading species have, in some river ecosystems, begun to outcompete indigenous species, in terms of biomass and energy flow. A contribution on this phenomenon, which influences multiple aspects of ecology, including energy flow and food-web structure, competition, predator-prey relationships and genetic processes, is provided by R. Kinzelbach. In addition to invertebrates, he draws some of the examples in his article from fish species.

In nearly every article, the contributors focus on historical aspects, as well as current and future approaches and methodologies. One of the contributions, the article by B. Schierwater, is entirely devoted to the advocacy of a new tool to study the population ecology of complex animal life cycles (e.g., metagenesis), using developmental genes.

As coordinators of this review, we are grateful to Cort Anderson, Luc De Meester, Matthew Dick, John Gilbert, Ramesh Gulati, Richard Harrison, Roger Hughes, Philippe Jarne, John Ryland, Stephen Stearns, Diethard Tautz, and Derek Taylor, who served as outside reviewers for individual papers, thus helping to improve the overall quality of this compilation. We thank them for their time and expertise. No effort could be made to achieve comprehensiveness – an impossible task with such a broad field. However, we hope that some of the excitement about recent developments in the population biology of freshwater invertebrates is conveyed by these contributions.