

## Planktonic biodiversity: Scaling up and down

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In 2001, Simon Levin remarked at a National Science Foundation meeting on biocomplexity that scientific disciplines are belief systems that progressively nurture memes by establishment of societies and journals (a meme being a unit of intellectual or cultural information—a key idea—that passes from mind to mind, spreading through colleagues and over generations [Dawkins 1976]). Levin also noted that an inevitable consequence of knowledge expansion is the development of specialized jargon, which, unfortunately, creates language barriers that impede the free exchange of ideas. Occasionally, we therefore need to pause, cut through the jargon, and attempt to integrate ideas across disciplinary boundaries. According to Levin and Pacala (2003), “. . . it is essential to develop ways to relate processes at the level of individual organisms to the populations of which they are members, and to the communities and ecosystems in which they reside. We must learn to scale from the small to the large, from the individual to the collective to the community, from the . . . plant to the biosphere.”

Integrating across disciplinary boundaries lies at the heart of understanding biocomplexity and Levin's admonishment that we must disarticulate ourselves from jargon is valuable advice. Still, jargon provides the shorthand of our daily lives; it will not go away. Therefore, in introducing this Special Issue, we first need to define a bit of the jargon. Two terms appear throughout this Special Issue that will be new to many *Limnology and Oceanography* readers: metapopulation and metacommunity; the former is a population of populations; the latter is a community of communities. Dispersal of individuals links the dynamics of populations within the metapopulation, while the dispersal of species plays an analogous role in the metacommunity. Another term needing definition is biocomplexity, a somewhat loaded term that summarizes a very big concept indeed: the structure of variation in nature. To study biocomplexity is to attempt to understand that structure. Organisms vary genetically and phenotypically, and that variation is expressed in the diversity of pathways by which ecosystems function. Organisms, and the ecosystem functions they influence, vary spatially and tem-

porally either because of external factors that impose structure or because of internal interactive processes that give rise to structure. Furthermore, in applying the concept of biocomplexity to understanding of ecological systems, it is clear that the human dimension cannot be held apart from the natural world; consideration of the full suite of human impacts and decision-making processes must therefore be included.

The practitioners of biological limnology and oceanography—the study of aquatic organisms and the ecosystems they create and inhabit—have for many decades been building an understanding of aquatic biocomplexity from the inside out. As new molecular, biogeochemical, experimental, and mathematical methods have become available (many developed by limnologists and oceanographers), the opportunities for piecing together the isolated nuggets of variation on which each of us has focused have grown dramatically so that we now can see the outlines of the broader structure of biological variation in lakes and oceans (Fig. 1).

In this spirit, we held a conference on “Planktonic biodiversity: Scaling up and down” at the University of Michigan (29 September–2 October 2002). Sessions dealt with interactions of mixing and spatial heterogeneity within the aquatic medium; the nature of local adaptation versus influences of dispersal; integration of genetic, species, and community diversity responses over the landscape; and scale-dependent biogeochemical coupling from ponds to entire watersheds. One central question pervaded the conference: Were there alternative explanations for conventional beliefs, revealed by invoking processes that operate at more complex spatial and temporal scales? Fifty talks spanned pond to coastal marine environments. The main themes and the presenters were as follows.

*Nature of diversity and the landscape*—Stanley Dodson, Lawrence Weider, Luc De Meester, James Rusak, Ralph Tollrian, Norman Yan, Shelley Arnott, John O'Brien, John Havel, Howard Riessen, Henry Vanderploeg, Charles Ramcharan, Scott McNaught, Gene Stoermer, Alan Tessier, Steven Threlkeld, Robert Placnik.

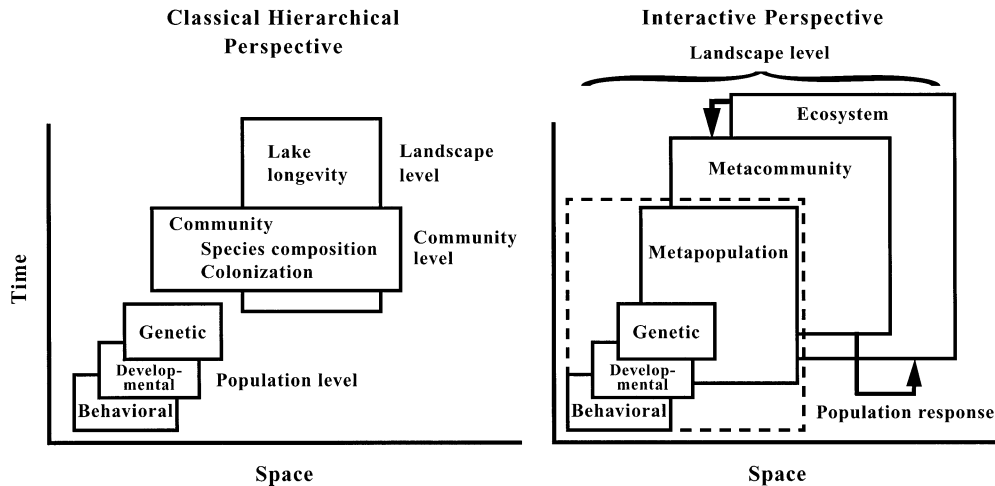


Fig. 1. Comparison between classical hierarchical and more interactive perspectives of population, community, and ecosystem responses. The interactive approach emphasizes metapopulation and metacommunity characteristics and metacommunity–ecosystem feedbacks across the landscape.

*Resurrection ecology and the storage effect: Benthic coupling through diapausing life stages*—Nancy Marcus, Charles Kerfoot, Lawrence Weider, Carla Cáceres, Luc De Meester, Piet Spaak, Dietmar Straile, Orlando Sarnelle, Dagmar Frisch.

*Modeling across time and space: Metapopulations and metacommunities*—Mathew Leibold, Mercedes Pascual, Florence Hulot, Hinnerk Boriss, Jon Norberg, James Gillooly, Andrea Belgrano.

*Patchiness, spatial/temporal scales of physical processes, complexity, and stability*—George Kling, Scott Hagerthey, Carol Folt, Gary Sprules, Percy Donaghay, Sally MacIntyre, James Churchill, Changsheng Chen, Nasseer Idrisi, Jon Anderson.

*Stoichiometry, competition, and biodiversity*—Christopher Klausmeier, Tanguy Daufresne, Irakli Loladze, Elena Litchman, William DeMott.

We thank the conference participants who submitted manuscripts for this *Limnology and Oceanography* Special Issue, which offers a sampling of the varied conference presentations.

The first group of papers in this Special Issue deal with dispersal, metapopulations, and metacommunities (i.e., local and regional controls on biodiversity). They remind us that lakes are islands imbedded in the terrestrial landscape. The insular nature of lakes has allowed aquatic ecologists and limnologists to draw convenient boundaries around the processes that regulate biodiversity at the local scale. However, this conceptual framework is rapidly changing. Just as terrestrial ecologists have come to recognize that local community diversity is determined by the interplay of local and regional processes (i.e., the size of the regional species pool, rates of species dispersal), we now recognize that planktonic diversity may be profoundly influenced by the interactions

between species, their local (within-lake) environment, and the exchange of species among lakes in a landscape.

The extent to which lakes and coastal marine systems function as metacommunities depends critically on the rates of exchange of species or even genotypes. Species (or genotypes) may disperse in both space and time. Havel and Shurin examine patterns of zooplankton dispersal in space, whereas the study of McNaught et al. provides an excellent illustration of how the plankton community may change following the invasion of a single, new species. Interestingly, in this case, the invader is no transoceanic exotic, it is *Leptodora kindtii*, a species found in many nearby lakes. This study underscores how little we know about the factors that control species exchange across a landscape or even the extent of spatial variation in planktonic biodiversity within a lake region. O'Brien et al. describe such landscape diversity patterns using an extensive data set from arctic lakes. In marine coastal environments, Idrisi et al. trace the relationship between life cycle and current-driven dispersal patterns, reminding us of the intricate interplay between physical and biological properties. On the theoretical side, Leibold and Norberg and then Norberg explore the metacommunity nature of lakes, focusing on the potential for lakes to function as complex adaptive systems. Finally, Rusak et al. demonstrate how diversity–productivity relationships in lakes may change over millennial time scales.

The second group of papers in this Special Issue focuses on benthic–pelagic coupling, resurrection ecology, and egg banks. Whereas spatial dimensions are stretched by metacommunity concepts, the temporal dimension is likewise expanded by consideration of dormant propagule pools and the biological information that they contain. Kerfoot and Weider use *Daphnia* hatched from eggs laid over a period of 80 yr to show that the *Daphnia* population evolved morphological defenses in response to a changing assemblage of predators, whereas Jarnigan et al. use lake sediment records of both dormant eggs and microfossils to follow the dispersal and persistence of the invading exotic cladoceran *Bythotrephes*.

These papers remind us that emergence from dormancy can affect ecological interactions at both the population and community levels. Cáceres and Tessier consider variation among lakes in the timing and extent of *Daphnia* diapause relative to overwintering populations. Rotifers hatching from diapausing eggs differ phenotypically (though not genetically) from females produced asexually in the water column in that they have large lipid stores and are less likely to be induced to switch to sexual reproduction. Gilbert and Schröder propose that this interesting trait is an adaptation for rapid population growth following a period of dormancy. Decaestecker et al. show that lake sediments contain the dormant stages of epibionts and parasites of *Daphnia* that remain infective for decades—a finding with substantial implications for the progress of disease dynamics and host-parasite coevolution.

Three papers, however, reveal potential constraints on the extent to which propagule pools may affect ecological and evolutionary processes. Through detailed sampling of diapause egg settling and resuspended sediments, Kerfoot et al. explore the spatial and temporal formation of a *Daphnia* egg bank and show that the time horizon in which emerging eggs might impact ecological dynamics is relatively short. Sarnelle and Knapp suggest that the potential for temporal migration (through the hatching of diapausing eggs laid in the past) to reestablish locally extinct populations may be limited when only a few eggs hatch, especially in the case of obligatory sexual species (e.g., copepods) where rare mates must find each other. Keller and Spaak show that, even if hatching numbers are high, the genetic structure of the egg bank may not be representative of the water-column population that produced it. This finding holds fascinating potential for its effect on long-term evolutionary processes and disconcerting implications for the usefulness of egg banks as reservoirs of microevolutionary history.

No research on biocomplexity in the plankton realm can claim to be uninfluenced by Hutchinson's classic 1961 work that identified the plankton paradox, i.e., how such diversity in form, function, and identity can persist in the seemingly homogeneous pelagic zone. This paradox has puzzled generations of scientists, and the ghost of Santa Rosalia also haunts this Special Issue. Can the synthesis being forged under the banner of biocomplexity finally solve it? Some steps toward moving around, over, and/or through it are suggested in the third group of papers in this Special Issue, which deal with ecological stoichiometry, food web interactions, and diversity.

One mechanism that might enhance diversity in the absence of obvious niches is that coexistence is enforced by mortality imposed by specialized parasites (Yan 1996), especially if resistance to parasitism trades off with superior competitive ability. Such possibilities are explored by Wolinska et al., who address not species' coexistence but the coexistence of hybrids of *Daphnia galeata* and *Daphnia hyalina*. They show that, while hybrid *D. galeata* × *hyalina* appear to be superior to the parental forms under many environmental conditions, the hybrids are significantly more susceptible to infection by a protozoan gut parasite and this likely maintains distinct parental populations, along with hybrids, in the same community. It is easy to see how future

biocomplexity research will increasingly need to come to grips with the often underappreciated effects of disease and parasitism. Beyond parasite-mediated indigestion, zooplankton must also cope with intense gradients of predation risk, temperature, and food resources that differ in both quantity and various aspects of quality, all of which potentially interact in complex ways. DeMott et al. consider the roles of energy versus biochemical versus stoichiometric aspects of food resources for *Daphnia* across vertical gradients in several Michigan lakes. Using a series of experimental manipulations, they show that intense grazing by *Daphnia* can result in residual food resources that are very poor quality, not due to insufficient P or essential fatty acid content, but due to low inherent digestibility. Thus, in these lakes, *Daphnia* are energy-limited while swimming in a seeming surfeit (or at least a sufficiency) of food. A particularly fascinating observation they made was that *Daphnia* grew best when they were able to feed on seston from the benthic boundary layer (material dominated by photosynthetic sulfur bacteria), a limnological example of forbidden fruit, as the animals cannot feed on this material in place because of the low O<sub>2</sub> concentrations at the sediment surface.

Weider et al. examine the genetic structure and elemental composition of *Daphnia* relative to the growth rate hypothesis, arguing that critical genetic and metabolic properties of organisms are interrelated. In Hulot and Huisman, allelopathic phytoplankton interactions are contrasted between a well-mixed and poorly mixed environment and in the presence of bacteria that degrade toxins. They discover that species diversity and biogeochemical cycling outcomes are very sensitive to the spatial scale of mixing. Ptacnik et al. consider the schizophrenic feeding behavior of microzooplankton and mixotrophic flagellates, which introduce omnivorous complexity into simple trophic schemes.

Work in this Special Issue also takes some steps toward coming to grips with the paradoxical diversity that we see in the phytoplankton, addressing both extrinsic components and inherent mechanisms. Lehman et al. present a comprehensive multivariate analysis of one of limnology's treasures, the long-term data set for Lake Washington compiled by the late Tommy Edmondson and coworkers. Considering taxon-specific net growth rates over relatively short intervals (7–14 d), the authors identify groups of phytoplankton taxa that respond in similar ways to key environmental variables such as temperature, stratification, light intensity, nutrients, and/or zooplankton. The analysis is truly massive, involving 500–1,200 data records for different phytoplankton taxa, and the results provide a unique glimpse into the full suite of complex drivers that are imposed on the plankton. It is some relief to see that a relatively straightforward set of interpretations emerges from this analysis, producing a narrowed focus on key groups of players and factors. It does not seem that we need a separate ecological story for every character in the play. One reason that this is so might be that all phytoplankton taxa must play by a similar set of fundamental rules that arises because of the shared resources (light, key nutrients) on which they all rely and the shared metabolism that they all use to convert those resources to maximize fitness in particular environments. Two theoretical papers (Litchman et al., Klausmeier et al.) shed some light on this.

Litchman and colleagues introduce the environmental reality of temporal variation in resource supply and the physiological reality of interplay between nutrient use and energy requirements to show that variation in resource supply regimes can reverse competitive outcomes and/or enhance species coexistence. Klausmeier et al. (this issue and 2004) also focus on nutrient use by phytoplankton, relating growth, storage, and uptake of different limiting nutrients (N, P) under conditions of rapid versus slow growth and how these properties might relate to taxon-specific strategies. These analyses bring a bit more mechanistic muscle to bear on issues that lie at the heart of a variety of key questions in ecosystem ecology, from the impacts of food quality in trophic interactions to the coupling of nutrients and carbon in global biogeochemical cycles.

Perhaps the opacity of Hutchinson's paradox will soon become as transparent as the pelagic zone. One lesson to carry from the papers in this Special Issue is that the key for increasing clarity as we lean over the side of the boat and look at the plankton world is to embrace and formalize multiple perspectives. We cannot make progress by considering predation in isolation from competition in isolation from parasitism; we cannot make progress by considering mineral and biochemical nutrients independent of food energy; we cannot make progress by focusing only on limited subsets of data from limited time windows. We need not just more information but better information and, perhaps most

importantly, information organized within explicit quantitative and conceptual frameworks that can accommodate it. Those frameworks need not be as complex as we fear, given the common set of resources and metabolic toolboxes that living things share. Thus, in place of biocomplexity, perhaps we should be working instead toward a theory of biosimplicity (Elser and Hessen, in press).

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