BIOLOGY

Perspectives in Ecological Theory

Edited by Jonathan Roughgarden, Robert M. May, and Simon A. Levin

This volume presents an overview of current accomplishments and future directions in ecological theory. The twenty-three chapters cover a broad range of important topics, from the physiology and behavior of individuals or groups of organisms, through population dynamics and community structure, to the ecology of ecosystems and the geochemical cycles of the entire biosphere.

The authors focus on ways in which theory, whether expressed mathematically or verbally, can contribute to defining and solving fundamental problems in ecology. A second aim is to highlight areas where dialogue between theorists and empiricists is likely to be especially rewarding. The authors are R. M. Anderson, C. W. Clark, M. L. Cody, J. E. Cohen, P. R. Ehrlich, M. W. Feldman, M. E. Gilpin, L. J. Gross, M. P. Hassell, H. S. Horn, P. Kareiva, M.A.R. Koehl, S. A. Levin, R. M. May, L. D. Mueller, R. V. O'Neill, S. W. Pacala, S. L. Pimm, T. M. Powell, H. R. Pulliam, J. Roughgarden, W. H. Schlesinger, H. H. Shugart, S. M. Stanley, J. H. Steele, D. Tilman, J. Travis, and D. L. Urban.

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PRINCETON PAPERBACKS

ISBN 0-691-08508-0

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Edited by **JONATHAN ROUGHGARDEN**
ROBERT M. MAY and
SIMON A. LEVIN

IV SCALE AND COUPLING IN ECOLOGICAL SYSTEMS

Chapter 10

Perspectives in Hierarchy and Scale

R. V. O'NEILL

The past two decades have seen a rapid change in the scale of ecological problems. In 1969, the National Environmental Policy Act required ecological assessment of impacts on surrounding ecosystems. From this local perspective we have moved to landscapes ecology, to the continental effects of acid precipitation, and to problems of nuclear winter, global carbon cycling, and climate change. The problems demand that we accelerate our ability to translate small-scale ecological principles to higher levels.

It is fortunate that the demand for answers at higher levels has been accompanied by the development of new tools for the investigation of scale. The combination of geographic information systems and remote-sensing capabilities permits us to work with large spatial data bases (e.g., Krummel et al. 1987). Aquatic ecologists have developed tools for rapid sampling of fine spatial scales (Auclair et al. 1982; Boyd 1973; Haury 1976) and remote sensing of ocean gyres. Statistical tools such as time-series analysis provide for analysis of pattern and scale (Fasham 1978; Mackas and Boyd 1979; Platt and Denman 1975). The statistical tools are augmented by models that attempt to explain pattern (Dubois 1975; Levin and Segel 1976; Scavia 1980). Finally, from the early explorations of Overton (1972) and Reichle, O'Neill, and Harris (1975), the theoretical basis for the hierarchy concept has been well established with texts by Allen and Starr (1982), Salthe (1985), Eldredge (1985), and O'Neill et al. (1986).

It is perhaps the juxtaposition of new problems and new techniques that has led to the remarkable convergence of the ecological community on the need to study problems of scale and hierarchy. Realization of this need is reflected in research on soil processes (Sollins, Spycher, and Topik 1983), vegetation analysis (Delcourt, Delcourt, and Webb 1983), and aquatic ecosystems (Bainbridge 1957; Steele 1978; Levasseur, Therriault, and Legendre 1984). In terrestrial systems, McIntosh (1985) points out that current trends reemphasize an interest in pattern and scale that dates back at least to Watt (1925, 1947) and the work of early biogeographers (O'Neill et al. 1986). In aquatic systems, the interest in scale (Powell et al. 1975; Cox, Haury, and Simpson 1982) is driven by a recognition of the physical constraints that shape aquatic hierarchies (Gower, Denman, and Holyer 1980; Legendre and Demers 1984) and by a desire to explain control mechanisms operating across temporal scales (Carpenter, in press). Such unparalleled convergence may represent a maturing of our science and unquestionably calls for the continued development and testing of hierarchy concepts.

PARALLEL LINES OF DEVELOPMENT

The current vitality of hierarchy considerations is indicated by four separate lines of development that are occurring simultaneously. By choosing only four, I do not mean to minimize other efforts but rather to tease out some trends in a rapidly developing field.

The first line of development, which I will characterize as the Empirical Approach, is actually a continuation of a longstanding interest among ecologists in detecting scales and pattern in ecological data (McIntosh 1985). Terrestrial studies that have focused on scale and pattern are exemplified by Bormann and Likens (1979). These authors show that, although a woodlot may never reach equilibrium, a landscape of sufficient scale can converge to an equilibrium mosaic with relative constancy in the fraction of the area occupied by various successional states. Increasingly, terrestrial studies are focusing on problems of scale (e.g., Addicott et al., in press; Maurer 1985; Wiens 1986; Wiens, Crawford, and Gosz 1985). The interest in scale is particularly evident in new fields of emphasis such as landscape ecology (Risser, Karr, and Forman 1984; Forman and Godron 1986). Pielou (1977), Ripley (1981), and Cliff et al. (1975) provide good points of entry into the theory and methodology that have developed for pattern and scale analysis.

A similar interest in scale is evident in geosciences and geomorphology. Schumm (1965, and in press) has pointed out that physical forces shaping the course of a river are disruptive at a fine time scale, continuously moving the system away from its current state. At larger scales, the forces act to equilibrate the overall course of the river, which remains constant for long periods of time. Stommel (1963) has made similar observations for oceanographic processes and demonstrates how the phenomena of interest change as the scale of observation changes.

The interest in understanding scale is widespread in aquatic ecology and often focuses on physical forces, such as hydrodynamics, that impose constraints on the ecosystem (Evans and Taylor 1980; Therriault and Platt 1981). The implications of pattern for aquatic ecosystem dynamics have been developed by a number of authors (Levasseur, Therriault, and Legendre 1984; Carpenter and Kitchell 1987) with particular emphasis on the need to look at larger-scale processes. Steele (1985), for example, has contrasted the scales of variability in terrestrial and marine ecosystems and drawn out the implications for long-term changes in community structure.

This Empirical Approach is so pervasive that it may appear to be all there is to the hierarchy concept. However, I will develop the premise that this is but one of a number of concurrent lines of development. Thus, for example, there is a second and completely independent line of research occurring in evolutionary biology.

In companion volumes, Salthe (1985) and Eldredge (1985) develop a hierarchical basis for a new and broader view of biological evolution. Their work, which I will characterize as the Evolutionary Approach, focuses on concrete biological entities, that is, organisms. They use this focus as a basis for explaining biological change at all levels of organization. They are particularly interested in biological change at higher levels, beyond the local population and beyond the explanatory power of population genetics. They point to large-scale phenomena such as stasis and mass extinction as part of the evolutionary history of the biosphere. One of their major points is that hierarchical principles provide an intellectual framework for dealing with change on all scales. This theme is also developed by Conrad (1983), who presents a mathematical theory for trade-offs in adaptability on different hierarchical levels. These authors see the hierarchical framework as essential for broadening the base of explanatory tools available to deal with evolutionary phenomena. The emphasis is on developing a philosophical base for evolution rather than on making specific testable predictions.

The mathematical development of Network Theory by Patten and his colleagues (1976; Hannon 1979; Patten 1982; Ulanowicz 1986) stands in marked contrast to the philosophical tone of Salthe (1985) and Eldredge (1985). This third branch of hierarchical thinking focuses on a general mathematical foundation for ecology. Fundamental to this approach is the insight that interactions between entities (e.g., organisms or populations) determine the dynamics of higher levels (Patten 1982). This emphasis leads to graph theoretic analyses of component interactions. The approach generates, for example, new indices of functional complexity (Ulanowicz 1983). In addition, the theory argues for the importance of indirect causality, that is, influences that go beyond one-on-one competition or predation interactions (Patten 1982). Indirect causality may require important changes in our approach to community structure and ecosystem processes by

emphasizing interactions rather than component behavior. In general, Network Theory develops a set of concepts for organizing ecological understanding rather than generating testable hypotheses.

The fourth line of development emphasizes the juxtaposition of theory and testing. Formalized by Allen and Starr (1982), it shares with Evolutionary and Network approaches a direct dependence on General Systems Theory (e.g., Simon 1962) but differs in seeking empirical tests of predictions. It shares with the Empirical Approach a commitment to ecological data and analysis and the generation of testable hypotheses (Allen, O'Neill, and Hoekstra 1984) but differs in developing a comprehensive conceptual framework. Emphasis has been placed on beginning with a specific observation set (Allen, O'Neill, and Hoekstra 1984; O'Neill et al. 1986) and taking advantage of the hierarchical structure that emerges. This fourth approach has been particularly useful in applying hierarchical implications at larger scales such as the landscape (Urban, O'Neill, and Shugart 1987) and biosphere (O'Neill, in press).

SOME PRINCIPLES OF HIERARCHY

At the core of the four lines of development is a body of principles begun in the 1960s (Simon 1962; Whyte, Wilson, and Wilson 1969; Pattee 1973) as an approach to analyzing complex systems. The chief insight was that systems often contain an endogenous organization, a hierarchy of levels. The investigator can take advantage of this organization to isolate behavior that can be studied by classic approaches.

Hierarchical organization results from differences in process rates. Complex systems, such as ecosystems, operate over a wide spectrum of rates. Behaviors can be grouped into classes with similar rates that constitute levels in the hierarchy. Phenomena on a given level will be relatively isolated from lower and higher levels. Lower levels have relatively rapid rates and appear as background static or variability that is filtered or averaged out at the level of interest. Higher-level behavior is relatively slow and appears as constant from the level of interest, that is, as a set of constraints or boundary conditions on the phenomenon of interest. The hierarchical organization permits one to dissect phenomena out of the total complexity of the system. Studied on the appropriate time and space scale, the phenomenon can be viewed as the behavior of a relatively simple system and approached with traditional scientific methods.

There is a clear analogy between this conceptual framework and a controlled experiment, say, at the population level. Here we would "control" higher-level behaviors such as temperature and light by keeping them constant. We handle lower-level "noise" by averaging across many individuals. In this way we try to isolate a single level and a simple set of phenomena.

One consequence of this hierarchical structure is that behavior must be explained on three adjacent levels (O'Neill 1966; Koestler 1967). The focal level is the level of interest in a particular study. The focal level changes as the research problem changes and may be the population in one study and the landscape in another. Once the appropriate focal level is identified, dynamics are explained by looking to the next lower level. For example, if we are focusing on a population, then behavior is explicable in terms of the interactions of its components, that is, individual organisms at the next lower level. The significance of behavior, its functional or adaptive relevance, is explicable by reference to a higher-level system. Thus, if we are focusing on the individual level, sexual behavior finds its significance in the persistence of the population. To date, all of the hierarchical developments in ecology have found insight in this Triadic structure (Allen and Starr 1982; Patten 1982; Salthe 1985).

Dynamics at a particular level are structured by what happens at higher and lower levels. Higher levels impose constraints or boundary conditions, for example, temperature or precipitation. The level of interest is constrained to operate within the bounds set by the system of which it is a part. An intuitive example might be a consumer whose growth is constrained by the productivity of the ecosystem.

Lower levels impose additional limitations, termed “initiating conditions” by Salthe (1985). An intuitive example is the flight speed of a flock of birds that is limited by the speed of individual birds in the flock. Initiating conditions represent a type of constraint that is imposed on a higher level by its components. A level can only display behavior that is the feasible resultant of its components. An ecosystem cannot fix atmospheric nitrogen if there are no nitrogen fixers within that ecosystem.

Current theories vary in the extent to which they rely on the concept of constraint. But constraint appears to be a useful concept in explaining ecological dynamics. Developments in aquatic ecology clearly reflect a growing awareness of how hydrodynamics impose scaled constraints on the planktonic level of organization (Denman and Platt 1976; Harris 1980). Similarly, Carpenter (in press) shows that food-web dynamics are constrained by time scales imposed by top carnivores.

Current developments in hierarchy share this sparse set of philosophic concepts. The hierarchical concepts themselves are nothing new. They are Neoplatonic and can be found in Plotinus (ca. 250 A.D.) and Proclus (546 A.D.). They have been rediscovered periodically throughout the history of Western culture. It is interesting to note that, although the theories share these concepts, they differ on the reality of hierarchical structure. Salthe (1985) stands at one extreme with a stated commitment to concrete reality. He is talking about *the* hierarchy of life. Other authors (Webster 1979; MacMahon et al. 1978, 1981) seem to agree with the concreteness of hierarchical levels, at least implicitly. Network Theory seems neutral on the point, beginning its analysis with an existing network of interactions rather than considering the reality of the defined network. Allen (in Allen and Starr 1982) and O'Neill (in O'Neill et al. 1986) share the view that the ontological question is a moot point for the scientist. We begin with phenomena viewed in a particular observation set. If a hierarchical structure can be detected, then the system can be treated as hierarchical and the principles of the theory will be expected to apply.

EFFECTS OF THE NEW AWARENESS OF SCALE

The shared set of philosophic concepts has an intuitive appeal but is thin on hypotheses. It is a new way of looking at systems rather than a set of equations and theorems. In fact, for many ecologists, hierarchical considerations appear more as a conceptual framework than as a predictive theory. It is in the development of derivative mathematical theories yielding specific predictions, in the stimulation of new field and laboratory investigations, and in the generations of testable hypotheses that the current concern for scale will find its fruition. However, it is already becoming clear that the conceptual framework itself will prove valuable to ecology, and I would like to review some of the more notable applications.

The first and simplest application has been an increased consciousness of the extent to which our models and measurements are scale dependent. It is easy to view hierarchy as nothing more than insightful experimental design. But this becomes increasingly hard to maintain as more and more scale problems are identified even in the work of insightful experimentalists. The archetypic example involves aquatic ecologists who towed their nets in random transects trying to measure plankton that were lined up in turbulence cells like beads on a string (Abbott, Powell, and Richardson 1979). Only with the development of fine-scaled measurement and spectral analysis did the effect of scale on their measurements become apparent (Levasseur, Therriault, and Legendre 1984).

A similar story occurred in stream ecology. Streams were analyzed for nutrient efficiency, comparing inputs and outputs for a reach of stream. Only with the development of the scale-free measures of nutrient spiraling (Newbold et al. 1983) did it become apparent that the existing measures of efficiency were inadequate, being critically dependent on the dimensions of the reach being measured.

Yet another instance is recounted by Gingerich (1983). He reviews paleontological studies comparing rates of morphological change in darwins (change by a factor of e per million years, where e is the base of the natural logorithm). Recent mammal assemblages are abundant, allowing observations every few thousand years. Many minor changes are observed at a rate of about 4 darwins. Older invertebrate assemblages are rare, permitting observation only every million years. Most minor changes are not observed and the rate is given as 0.1 darwins. But in fact the mammals did not evolve more rapidly, and when the data are corrected for the scale bias, the invertebrates probably evolved more rapidly.

Walters (1986) provides an insightful analysis of why fisheries management sometimes fails. The resource is modeled on one scale as a single population over several generations. The fisherman operate at much longer time scales because they are concerned with discounted capitalization of ships and equipment. The result is that the models do not do a good job of predicting the resource, and the fishermen do not act as "logically" as the model says they should to optimize yield.

One of the best tests of a new conceptual framework is its ability to resolve controversies. An example of the utility of hierarchical concepts has emerged from recent controversies over the mechanisms that control aquatic food webs. There is evidence for "top-down" control showing that fish, at the top of the food web, constrain the food web. Other evidence indicates a "bottom-up" control showing that phytoplankton, at the bottom of the food web, control productivity throughout the food web. Hierarchical principles have been found to provide a simple explanation for the conflicting data (Carpenter, in press). Phytoplankton operate on short time scales and represent a lower hierarchical level. They constrain the food web over short time scales and explain much of the intraseasonal variability in the system. Fish operate on longer time scales and represent a higher hierarchical level. They constrain the food web over longer time scales and explain much of the interseasonal variability in the system. Thus, both "top-down" and "bottom-up" controls exist but operate on different time scales, as predicted from their hierarchical position.

The examples could be expanded almost indefinitely. In most fields of ecology, the new awareness of scale has led to new insights, new concepts, and proposed solutions to old and scale-naive dilemmas. The case can be made, even on existing literature, that the concepts of scale and hierarchy have proven their value. Investigators are beginning to take measurements across several scales (Perez et al., in press), to consider how simultaneous constraints from several hierarchical levels can influence community structure (Ricklefs 1987) and geographic distributions (Neilson and Wullstein 1983, 1985; Neilson 1986). However, given the active development of hierarchical concepts, I believe that we have only seen the tip of the iceberg. To convey the true promise of the hierarchical approach, I would like to touch on several current developments, emphasizing how the conceptual development is leading to new and testable hypotheses.

SOME CURRENT DEVELOPMENTS IN HIERARCHY

Spatial Hierarchies

A consideration of scale leads one to question whether an arbitrary circle drawn on the ground will capture the dynamics of all the organisms contained therein. The question suggests a radical Gleasonian approach with each population, or perhaps each life form, operating on a different spatial scale.

If a species, under a particular environmental regime, can win one-on-one competitive interactions with other species, a small-scaled strategy should be selected for. A plant, for example, would tend to become a dominant, shading out competitors and using vegetative reproduction to establish and maintain its spatial position. If an organism outcompetes its immediate neighbors then it gains a selective advantage at this small scale. But if a species loses ninety-nine out of every one hundred interactions, then selective pressures might lead it to operate on a scale hundreds of times larger than the dominant. If the species succeeds in operating at a sufficiently larger scale, it will operate on a different hierarchical level, and hierarchical principles predict that it will thereby isolate itself, no longer directly interacting with the dominant. The species would have to win only on rare occasions and still persist in the environment. This strategy would lead to shorter life cycles, smaller stature, and widely dispersed seeds rather than vegetative reproduction.

According to current ecological theory, plants operating at a large scale would be considered rare and classed as losers in the competitive battle. If persistence is the criterion, however, such plants are very successful. A simple consideration of scale might find a final resting place for St. Rosalia's goat bones. The speculation is interesting because it involves very simple and testable assumptions: the probability of success in competition experiments should be inversely related to the scale at which a species operates and to life history characteristics such as dispersal ability. While such an experiment might make little sense when comparing trees with ferns, it should be feasible in old field communities. Such experiments may permit us to reevaluate competitive exclusion as a scaled phenomenon of greatest interest in greenhouse pots and Ehrlenmeyer flasks. In the field, competition plus scaling strategies may be more relevant for explaining community structure. Consider also whether the thorny question of the distribution of the abundances of organisms is the simple consequence of the distribution of the probability of competitive success combined with scaling strategies to avoid exclusion.

Spatial Scales on the Landscape

A key prediction of the hierarchical concept is that process rates should be grouped into distinct levels. At a particular spatiotemporal scale, interacting components operate at similar rates and are relatively isolated from higher and lower levels that operate at much slower or faster rates. For hierarchical principles to be helpful in analyzing ecological systems, it is necessary to identify such levels in observations of the system. Hierarchical considerations predict that a complex system will not show rates uniformly distributed between the fastest and slowest rates. Rather, the rate processes will be grouped into distinct levels.

Application of time-series analysis to environmental data has already indicated that the required levels can be detected in ecological systems. Van Voris et al.

(1980) and Perez et al. (in press) have demonstrated a number of distinct levels in microcosm systems. Distinct levels have also been clearly demonstrated in aquatic ecosystems (e.g., Stommel 1963).

Krummel et al. (1987) have recently demonstrated hierarchical structuring in spatially distributed systems. They found that small shapes on the landscape had simple outlines, probably determined by human activities. Large shapes had complex outlines determined by a distinctively different set of constraints, such as topography. Processes determining shapes on the landscape fell into only two distinct levels rather than being uniformly distributed at all scales.

Similar-level structures can be detected in land-use data for landscapes. O'Neill et al. (in press) have examined the percentage of a map transect occupied by a particular land use. By replicating the transect it is possible to estimate the variance on the land-use measure. Adjacent sites along the transect are then pooled and the aggregates are assigned to the land-use type occupying the majority of the sites. The aggregation is repeated so that the same land-use data is examined at a set of increasing scales and the variance is calculated at each scale.

Greig-Smith (1957) points out that the sample variance in such pooled data should decrease as the size of the sample (i.e., aggregate size) increases. If land use on adjacent sites is uncorrelated, a plot of log variance against log scale will show a slope of −1.0. Correlations, implying some process operating on the landscape (Levin and Buttel 1986), will lead to slopes lying between −1.0 and 0.0.

O'Neill et al. (in press) found that the variance analysis revealed a hierarchical structure in landscape data. Over some scales, the variance decreased with a slope much less than −1.0 (−0.003 to −0.27 for different landscapes). At adjacent scales, the slopes changed abruptly and approached −1.0. For different landscapes, the analysis showed as many as three distinct levels (i.e., regions of shallow slope) separated by regions of slopes approaching −1.0. The implications of the analysis are that processes determining land-use patterns on the landscape are segregated into distinct spatiotemporal levels as predicted by hierarchical considerations.

Ecosystem Models and Stiff Systems

Aquatic ecosystem models typically assume that consumers are moving through a well-mixed soup of food organisms. Current scale studies invalidate this assumption. Piscivorous fish must operate at large scales relative to planktivorous fish that, in turn, must operate at larger scales than plankton. Hierarchical considerations indicate that dealing with all of these scales in a homogeneous volume of water may be the wrong approach. Fish may not interact with plankton, they may constrain them. The difference is that model formulation is radically changed and requires stiff system models that explicitly consider more than one time scale. Thus the growing concern for scale may result in radically new models of aquatic ecosystems.

Concern for modeling multiple scales leads us to some of the theoretical work being done in hierarchy. If a model explicitly considers two time scales, then a common scenario shows the slower time scale establishing a manifold, that is, a slowly changing trajectory, to which the faster dynamics are asymptotically stable. However, the trajectory may move the system toward unstable regions.

As the system moves toward a major instability, it is a reasonable conjecture that the rate of return to the manifold will decrease as the point of instability is approached. This possibility suggests a way of monitoring large-scale changes, even at the global level (O'Neill, in press). Large-scale changes are difficult to measure directly, and it may not be possible to determine whether a change is good or bad. However, it may be possible to detect whether slow changes are leading the system to a point of instability by monitoring short-term recovery experiments. If recovery time increases, it may indicate that the total system is moving toward instability and remedial action is called for. We are moving toward testing the feasibility of this approach in microcosms. We will look for a pattern in recovery from small perturbations as the system is moved along a temperature/light trajectory toward a known point of instability determined in preliminary experiments.

Nonequilibrium Thermodynamics

A related result is derived from our explorations of nonequilibrium thermodynamics. The theory states that, far from equilibrium, a system will tend toward a state of minimum entropy production. It will approach this state along a manifold described by a potential function. For present purposes, the most interesting aspect of the theory is what happens as a bifurcation point is approached. Far from a bifurcation point, the potential function increases rapidly with deviations from minimum entropy production. Thus, specific exemplars of the system, tending to minimize entropy production, will lie close to the minimum entropy state and close to each other. Near a bifurcation point, the potential function increases slowly and the manifold "flattens." Therefore, a random sample of systems would show greater deviations from the minimum entropy state.

These considerations lead to the conjecture that the variance measured among systems with similar perturbation regimes should be greater for systems near a bifurcation point. Further, the variance should increase through time for systems approaching a bifurcation point. For example, African grasslands close to the line of progressive desertification in the Sahel should show greater variability than similar grasslands with similar climatic variability further to the south. Aspects of this conjecture will be tested in aquatic microcosms where replication is possible, as is manipulation of environmental conditions that determine the state of the system relative to a bifurcation point.

PERSPECTIVES ON FUTURE DEVELOPMENTS

Given the current hectic pace of developments in hierarchy and scale, it is apparent that this will remain an active and fruitful field for some time to come. Because of the kaleidoscopic dimensions of the field, it is impossible to chart the precise course. However, it is interesting to speculate on the possibilities and the major challenges facing hierarchy theorists.

The most obvious challenge is the continued development of methods for measuring and analyzing spatial and temporal patterns. We can expect continued developments in quantifying scales with indices such as fractal dimension (Burrough 1981; Levin and Buttell 1986; Krummel et al. 1987). In terrestrial ecology we can expect continued emphasis on landscape and global scales. In aquatic ecology, we can expect new approaches to modeling and continued insight on the implications of hydrodynamic and food-web constraints. I am particularly anxious to see an explicit wedding of empirical insights with theoretical developments in hierarchy.

Understanding scaled ecological systems will require translation of information between scales (O'Neill 1979) and methods to relate findings at different scales (O'Neill, in press). Considerable effort has already gone into understanding scale translations (e.g., Allen, O'Neill, and Hoekstra 1984), but much work remains to be done. Important aspects will be the effects of aggregating dynamic behavior at finer scales (Gardner, Cale, and O'Neill 1982; Cale, O'Neill, and Gardner 1983) to higher levels, the use of scale functions to translate across scales (Milne et al., in press), and the explicit use of hierarchical principles for extrapolation (King 1986).

We can expect active development of the Network Approach to hierarchy. At present, I am aware of four books in preparation that provide a comprehensive and forceful presentation of this approach. We can look forward to this approach providing significant new insights into the way populations interact to cause ecosystem dynamics.

At present, hierarchical principles constitute a loosely integrated set of insights on scale phenomena. The conceptual framework is based on the inductive observation that complex systems often show a hierarchical structuring of rate processes. The concepts show their greatest utility in synthesizing available information and in reconciling apparent dilemmas in both theory and measurement. As illustrated by numerous examples in this paper, many workers find the principles valuable in investigating and explaining ecological systems. Others find the conceptual framework difficult to apply and call for development of mathematical theories that will allow precise and objective derivation of predictions.

The challenge is to progress from the present generalizations to theory in the sense of systematic principles and methods. This progress will be most useful if it is accompanied by mathematical theory that permits rigorous derivation of testable hypotheses. As a result, we can expect to see many aspects of the conceptual framework developed into specific theories. Such a development would greatly extend the influence of the hierarchical concept.

The most important challenge facing hierarchy theorists is the timely development of testable hypotheses. However, even before a systematic theory is achieved, we can expect the strong empirical interest in scale to result in a rapid development of field and laboratory testing of the implications of current concepts. We will see the development of large-scale measuring instruments such as FTIR (Fourier Transform InfraRed) being used to test hierarchical concepts in the field (Gosz, pers. comm.). In short, I think we are entering a period of great excitement and activity that will permanently alter the way we conceptualize and study ecological systems. We can remain optimistic that the current interest in questions of scale will stimulate efforts to develop a more precise mathematical theory that will facilitate even more rapid progress in the future.

ACKNOWLEDGMENTS

The author's research and preparation of this manuscript was supported in part by the Office of Health and Environmental Research, United States Department of Energy, under Contract No. DE-AC05-84OR21400 with Martin Marietta Energy Systems, Inc., and in part by the Ecosystem Studies Program, National Science Foundation, under Interagency Agreement BSR-8021024 with the United States Department of Energy. I would particularly like to thank George Sugihara and Steve Carpenter, who helped clarify many points through their thoughtful review of the manuscript.

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Chapter 11

Physical and Biological Scales of Variability in Lakes, Estuaries, and the Coastal Ocean

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What is meant by "scale"? Why is it an important concept in ecology? Why does scale play a particularly prominent role when one speaks of "coupling"? Can one make nontrivial, general statements, if phrased in terms of scale alone, that apply to several seemingly different systems? Can other generalizations that highlight "scale" and "coupling" help us understand why some ecological systems differ so greatly from others? I shall address aspects of these questions here, with particular emphasis on results from lakes, estuaries, and the coastal ocean. I begin with some elementary notions, then review how scale considerations enter the coupling between physical and biological systems in the size scale regime between 100 m and 100 km—a regime of great ecological interest and the scale of most lakes, estuaries, and the coastal ocean. Other papers in this volume focus on, for example, terrestrial systems and the general question of how large, complex systems are structured; I end, then, by advancing some speculations about these and other areas I have neglected. Finally, some publications on theory in biological oceanography (and related disciplines) have recently appeared: one is nearly a tutorial (Platt, Mann, and Ulanowicz 1981) and the other assays the use and prospects for ecosystem theory (Ulanowicz and Platt 1985). I therefore largely avoid the topics that these authors have addressed so well.

ELEMENTARY CONSIDERATIONS

Intuitively, one speaks of the spatial scale of a problem as the distance one must travel before some quantity of interest changes significantly. Two adjacent parcels of water separated by 1 mm are likely to have very similar concentrations of