S. A. Levin T. M. Powell J. H. Steele (Eds.)

Patch Dynamics

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FOREWORD

A century from now, humanity will live in a managed—or mismanaged—global garden.

We are debating the need to preserve tropical forests. Farming of the sea is providing an increasing part of our fish supply. We are beginning to control atmospheric emissions. In a hundred years these separate aspects will need to be integrated into a single management system. We shall use novel farming practices and genetic engineering of bacteria to manipulate the methane production of rice fields world-wide. The continental shelf, especially off Asia, will be developed to provide food, energy, and, probably, living space. The capture of any remaining wild marine animals will be regulated like deer hunting.

To make such intensive management possible will require massive improvements in data collection and analysis, and especially in our concepts.

A century hence we will live on a wired earth. Like the weather stations that form a network over the land's surface, the oceans of the next century will have a three-dimensional lattice of sensing stations. The crust of the earth will also receive the same comprehensive monitoring now devoted to weather. Thus earth, air, and sea will be continuously sensed and their interactions modeled in order to anticipate major events such as El Niño, hurricanes, earthquakes, volcanoes, and climatic fluctations.

As the peoples of Asia, Latin America, and Africa approach the levels of wealth of Europe and North America, environmental fatalism and modest demands for food will be replaced by impatience with the accidents of nature and intolerance of mismanagement of the environment—particularly the living resources that are the focus of our material and altruistic concerns. The need for careful global management will become irresistible. Our control of physical perturbations and chemical inputs to the environment will be judged by the consequences to living organisms as individual species and as interacting systems. Above all, our human ability to affect life in all sectors, aquatic or terrestrial, brings these aspects together.

The problem is: How can we provide the factual and theoretical foundation needed to begin to move from our present, fragmented knowledge and our limited abilities to a managed, wired—and beautiful—global garden a century from now?

Joel E. Cohen
New York, New York

PART I

COMPARING TERRESTRIAL AND MARINE ECOLOGICAL SYSTEMS

John H. Steele, Steven R. Carpenter, Joel E. Cohen, Paul K. Dayton, and Robert E. Ricklefs

SUMMARY

We have entered a period where the study of the earth as a total system is within the reach of our technical and scientific capabilities. Further, an understanding of the interactions of earth, sea, and air is a practical social necessity. These interactions encompass physical, chemical, and biological factors. The biological or ecological components are critical not only as parts of these processes, but as a major and direct impact on man of the consequences of global changes in the system. Yet the possible nature and direction of ecological change is the most difficult aspect to predict and to relate to the other, physical and chemical, processes.

So far the terrestrial and marine sectors[1] have been considered separately. There can be good reasons for this lack of integration. The practical logistics (ships versus jeeps) are one reason for this separation. The organization of research institutes and of the federal funding exacerbates the dichotomy. But the critical question is whether the science itself requires this division. A workshop in Santa Fe in 1989 was held to address this question specifically and to propose measures to bring the components together. The need for such a meeting was evident from the discussions. The participants agreed that they all acquired new and useful ideas from the exchange of information and concepts. More significantly, these discussions revealed many topics that required and would benefit from more detailed and extensive consideration.

The scientific interests and excitement of generalizing across sectors was the dominant theme. For example, is the correct comparison between the longest-lived components—trees and fish—rather than at the same trophic level? We were also aware of the societal importance of understanding the very different consequences of human disturbance. Thus, assessments of waste disposal options in each sector of the environment and at local, regional, or global scales demand comparative study. Especially, we were conscious that any real convergence in ideas and integrations of theories would be a long-term process involving the

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[1] It is recognized that freshwater coastal estuarine environments are of intrinsic importance and particularly significant in these comparisons. In the following text, "terrestrial and marine" is often used as a shorthand for the complete range of systems.

removal of institutional and funding barriers. There was no doubt, however, that the perceived need to view our world as a single system requires ecological theory and practice to achieve a strong common basis.

At this preliminary meeting we sketched some major topics for comparative studies (food web structure, patchiness, biodiversity, etc.) and methods for promoting convergent evolution (workshops, summer schools, paired collaboration, production of texts, etc.). The summer school at Cornell in 1991 was the direct outcome of these discussions. It is intended to be the first in a series that will cover the topics listed in this introductory section, which draws on the report of the 1989 meeting and is intended as background to the subsequent material.

PRESENT STATUS

General concepts such as Global Geoscience presuppose some ability to integrate ideas and research in the aquatic, terrestrial, and atmospheric sciences. Thus, the physics of the atmosphere, the ocean, and even the interior of the earth come together under the auspices of geophysical fluid dynamics, even though the research programs and facilities are quite separate and distinct. Programs are under way to study the fluxes of carbon, nitrogen, and other elements through the atmosphere, ocean, and land interfaces. These fluxes involve interactions that encompass physical, chemical, and biological factors. In particular, various flux rates are determined by ecological conditions. But the ecological components of these global studies are critical not only as part of these processes, but also because they are seen as having direct impacts on our own economic or aesthetic values.

Changes in plant and animal distribution and abundance are seen as the consequence of our large-scale interventions, and these perceived changes provide the basis for societal concerns and actions. Yet the underlying processes that cause ecological changes are the most difficult to identify and to relate to physical and chemical changes on land, in the atmosphere, and in the ocean.

Considering the urgency of the global problems, there is distressingly poor communication among ecologists. Even scientists studying the same habitat from different perspectives—ecosystem or population biology—ask different questions in different languages. For example, a population biologist might study crabs or birds and have no interest in the nitrogen cycling that is fundamental to the local existence of the animals. A worse division separates "pure" and "applied" ecologists. The former carefully avoid situations influenced by man, although agricultural and fisheries biologists ask similar questions of their systems. As a result, they have different professional societies and journals.

But nowhere are differences greater than those existing between terrestrial ecologists and biological oceanographers. They belong to different professional societies. There is less than 10 percent overlap between the memberships of the Ecological Society of America and the American Society of Limnology and Oceanography. Certainly their systems are different, and so are their questions and methods of study. For example, most marine ecologists have no grasp of the ecological diversity of insect species, or of the ubiquitous coevolutionary relations of terrestrial systems. Few terrestrial ecologists have any appreciation of the intricate and dynamic relations between physical and biological factors in oceanic systems.

Recently there has been evidence of better communication among ecologists working in the same general habitats. However, the terrestrial and marine fields seem to be growing further apart. The organization of research and its funding exacerbates this dichotomy. Are there also conceptual reasons for this separation?

Although the atmosphere and ocean are governed by the same dynamics, the processes operate at fundamentally different space and time scales. Probably the most important consequence is that marine adaptations have evolved in situations where the populations are closely dependent on physical features. Pelagic marine populations are faced with ever-changing physical habitats and are motile and usually capable of rapid reproductive responses. This contrasts with terrestrial adaptations, which often respond to much longer time scales and deal with atmospheric variability as short-term noise.

How can such differences be bridged? It is critical that the scientific community become aware of the different perspectives and the various strengths and weaknesses of the several disciplines. The following examples illustrate how the strengths in one discipline could be imported into another.

1) Terrestrial ecologists have long been very effective in developing evolutionary paradigms. Marine systems have equally fascinating but very different evolutionary patterns that could be exploited profitably with theories and methods developed for terrestrial systems.

2) Marine ecologists have developed sophisticated methods to study and analyze physical and biological coupling across space, time, and size scales. These approaches might contribute to a better understanding of atmospheric/biotic relations of dispersal and behavior at boundaries.

3) Terrestrial and freshwater ecologists have a considerable body of knowledge and theory about foraging behavior and biology. This has led to increased understanding of the role of specialists and generalists in food web dynamics. Marine research could apply some of these theories to the foraging of higher-order predators.

4) Marine studies of patch dynamics as a mix of physical processes and biological behavior are well developed. Many of these concepts would be appropriate to problems in the terrestrial realm on large time or space scales—especially climate-related phenomena.

5) Terrestrial workers have a long history of controlled (or intrusive) field experiments. Manipulations of intertidal situations have been undertaken for 50 years but only recently have been applied to benthic populations. Experimental control of pelagic systems is very difficult but can be used to test carefully posed hypotheses.

6) Freshwater processes are intensively studied. These aquatic ecosystems are capable of controlled (and uncontrolled) manipulation. Although questions of mobility and of scale appear to separate them from marine and terrestrial systems, freshwater studies should provide opportunities for conceptual and technical links.

Finally, we need to be reminded that there are many common issues and questions. Cross-system comparisons include boundary layer communities in different fluids; maintenance of pattern at different temporal and spatial scales; and the role of disturbance, ecotones, succession etc.

MAJOR THEMES

Why Are Marine and Terrestrial Ecology Different?

Marine and terrestrial researchers function in different institutional and granting situations. But their divergent approaches appear to arise from perceived differences in the physical environments and in the manner these affect organisms and biological interactions. Biological oceanographers, in particular, view the physical characteristics of the marine environment as primarily responsible for pattern in biological communities, relegating the intrinsic pattern-generating capacities of biological systems to a minor role. Terrestrial ecologists, while recognizing the dependence on the physical background, emphasize that dynamical properties of populations and communities generate pattern within ecological systems independently of the physical environment.

Biological interactions in the ocean, such as predation, are viewed as important; but the major determinants of spatial and temporal variation in biological populations and processes are usually considered to be imposed by corresponding patterns in the physical system, especially variations in temperature, salinity, light, and nutrients. In particular, the spatial and temporal scales depend on the pertinent scales of variation in the physics. Most of the energy in the marine environment is stored in physical forms—temperature gradients and water movement. Thus, fluid and thermal properties of water dominate these biological systems.

Terrestrial ecologists stress the storage of energy in biomass and organic detritus and so decouple biological and physical components to some degree. The influence of the atmosphere on temporal patterns is moderated by the storage of biomass. Furthermore, spatial variation is under primary control of topography and soil, whose temporal variation (without human influence) is of very long scale compared to both atmospheric and marine processes of similar spatial scale. It is usually assumed that the dynamics are mainly demographic interactions between populations. For example, time lags in the response of populations to environmental changes can initiate population cycles, but their periods and amplitudes depend on biological characteristics. Finally, terrestrial systems are considered to be strongly organized by evolutionary interactions. Host specialization, mutualism, mimicry complexes, and other evolved arrangements among species are thought to be far more prevalent in terrestrial than in marine systems, where consumers are seen as more generalized (algal-coral symbioses notwithstanding). Evolutionary ecology is predominantly a terrestrial discipline.

While biological components of marine and terrestrial systems are subject to the same general processes, the expressions of these processes, especially as a function of space and time scales, differ greatly due to the physical nature of each environment. This fact has reinforced the separation of ecosystem studies but also offers the potential for evaluating and testing general theories of ecosystem processes that could predict these major differences between ecological sectors.

Dimensions for Comparisons

No single "axis" can bring together the contrasts among marine, terrestrial, and freshwater ecosystems. For example, the contrasts between systems dominated by sessile and mobile organisms are at least as marked as those between terrestrial and aquatic regimes. The two-dimensional structure of sessile systems is determined mainly by topography, while mobile systems are subject to the three spatial dimensions of hydrodynamics.

"Pelagic" organisms in air or water are influenced by the temporal scales in each medium. At all spatial scales, temporal change is slower in the ocean than in the atmosphere. In particular, the major eddy systems responsible for much of the variability in each environment have very different scales. Atmospheric eddies (high- and low-pressure systems) are about 1,000 km in diameter and move a distance equal to their diameter in two or three days. Ocean eddies are much smaller (ca 100 km) and can move this distance in about 30 days. Consequently, the weather fluctuations of the two environments differ by an order of magnitude in both temporal and spatial scale.

Parallel distinctions exist for major biotic processes. In mobile systems, patterns are set by passive advection and active migration, and the use of these alternative mechanisms depends on the relation between biological and physical scales in each environment.

In the sessile components of systems or of life cycles, spatial pattern depends heavily on biogeographic ranges and on *in situ* competitive, predatory, and mutualistic interactions. Succession sets the tempo of community variation. Thus, the mobile-sessile axis in the context of environmental scales can integrate seemingly disparate features of different environments. This axis must include "boundary-layer" communities whose patterns are determined by both topography and hydrodynamics.

Studies in freshwater ecology provide remarkably clear examples of the perspectives that derive from pelagic and benthic ecology. Recently two parallel workshops (supported by NSF) were convened to assess progress in lake and stream ecology. In the lake workshop report, predator-prey interactions and temporal variability were the major issues, with only one chapter dealing mainly with spatial patterns. At the stream workshop, disturbance, spatial heterogeneity, and biogeography were dominant topics and only two chapters dealt with interspecific interactions.

Another "axis" received significant attention at the Santa Fe workshop—the scales of body size, turnover time, and trophic status. In aquatic systems, the size of organisms and population turnover time increase up the food chain while unit growth rate (Rmax) decreases. In terrestrial systems, body size and turnover time often decline up the food chain while Rmax increases. Compare phytoplankton and trees. These opposite trends have important implications for stability and temporal variability. They are especially relevant to the degree and manner of coupling or decoupling between physical and biological processes. Thus, in aquatic systems, nutrient enrichment will have an immediate effect but the temporal pattern of subsequent community response can depend on predator turnover time. In contrast, the quasi-cycles of spruce budworm outbreaks appear to be set by the rate of recovery of the forest canopy between outbreaks. Thus, cycling rates are often governed by large biota having slow turnover times but with very different trophic status (forests or fishes) in different systems. The general implications of opposite trends in turnover time with trophic position are worthy of future study in non-linear food chain models.

These "dimensions"—(1) space/time scales of physical processes, (2) mobile/sessile life styles, and (3) size/growth rate/trophic position—provide systematic methods to define the differences between the marine terrestrial and freshwater sectors. The participants consider that they form a basis not only for qualitative comparisons of observations but also for more detailed future conceptual integration.

Common Issues

There are many topics in aquatic and terrestrial research where some common definition of the concepts, or comparisons of data sets, would be useful. Thus one way to illustrate the need for more interaction is to list briefly common issues faced in the study of ocean, terrestrial, and freshwater ecosystems. This list is not intended to be comprehensive.

> Cross-system parameters: What variables should be used to make possible comparisons among different ecosystems?
>
> Biodiversity: How many different species or phyla are there on land and in the sea? Is biodiversity best described by Linnean taxonomy, or would other functional concepts, such as body size, be equally or more useful?
>
> Disturbance: What roles do anthropogenic and natural disturbance play in changing the diversity in different ecosystems?
>
> Dispersal: What is the nature and importance of the movement of organisms across ecosystem boundaries?
>
> Coevolution: What is the importance of coevolution in different environments?
>
> Food webs: At what level of detail are the trophic structure of marine and terrestrial food webs similar—or different?
>
> Patchiness: What are the mechanisms underlying spatial patterns and what are their predictable or stochastic consequences?
>
> Energetic and material balances: How are the dynamics of energy and material flow related to ecosystem structure?
>
> System aggregation: What are the trade-offs in describing ecosystems at various levels of aggregation?
>
> Remote sensing: How can we assimilate the dense data sets from satellites? How do we combine them with *in situ* observations?
>
> Long-term data: What human and natural records are available from aquatic and terrestrial systems, and how do we compare them?
>
> Boundary layers: What are the special fluid dynamic conditions that characterize communities living at the interfaces and utilizing the solid and fluid media?

Scale dynamics: A very general question. How should dynamics on widely different scales be linked in theory or in numerical models?

PRESENT PROGRAMS

The previous sections have illustrated the wide range of common issues and also the difference in scales at which aquatic and terrestrial systems respond. If we are to study the interactions across time scales, then long-term data sets are necessary. At geological time scales, pollen analyses on land show the trends in forest and grassland distribution since the last ice age. In the sea, oxygen isotope analyses of calcareous shells in deep ocean cores demonstrate the temperature changes since the last ice age (and earlier). It is assumed that at the very long periods, we are observing the response of a globally coupled system.

At historical time scales, the long-term data sets are nearly all associated with and affected by human activity—forestry or viticulture on land, fisheries in the sea. Can we compare tree-ring data and fisheries statistics? Are the longer-lived components the main determinants of ecosystem structure? We require long-term studies at the community or ecosystem level. Some of these exist. There are the Hubbard Brook Forest Program (30 years), for example, and the Californian Current Surveys (25 years), which provide both space and time coverage. Can these be compared in terms of ecological processes, scales of variability, response to environmental change?

For terrestrial and freshwater systems, the Long-Term Ecological Research (LTER) network, supported by NSF, is an emerging source of data and ideas for cross-system comparisons. Studies across LTER sites are under way, focusing on the identification of parameters and processes that can be used for quantitative comparisons. At the Santa Fe workshop there was substantial interest in expanding such cross-system studies to include sites that are not part of the present LTER network. It was considered that a major advance would be the inclusion of marine systems in this expansion. There have been comparative reviews, particularly of fishery systems, but a more systematic progress is required. One program on global marine ecosystems (GLOBEC) is being developed with the aim of defining the physical/ecological relations that affect population dynamics for a wide range of scales and a diversity of species. Thus assessment of previous marine data sets and of pending programs in the context of the terrestrial studies would close the information gap among marine, terrestrial, and freshwater systems.

OPTIONS FOR ACTION

What topics require active collaboration by researchers in terrestrial and aquatic ecology? Based on discussion in the 1989 workshop, the following set was selected. It is not exhaustive but represents the range of subjects where significant benefits to science would result from effective interaction of active researchers.

Long-Term Data Sets

A primary requirement is for the different research communities to appreciate the nature of the data available in other sectors, the way in which observations are made, methods of analysis, the underlying hypotheses or conceptual models, and the future plans. This must be the basis for cross-system comparisons of global ideas or specific theories. The LTER network provides timely examples and growing experience with the types of comparison that are needed. It is essential to broaden these efforts by combining them with relevant and appropriate marine studies. Sustained comparisons of marine, terrestrial, and freshwater ecosystems are a major recommendation of the workshop.

Body Size, Trophic Structure, and Community Dynamics

Numerous observers of aquatic food chains have pointed out the steady increase in body size from phytoplankton through herbivorous zooplankton to carnivores. Other observers, at least since Elton in 1927, have remarked that many terrestrial food chains, or portions of these, proceed from very long-lived primary producers such as trees or shrubs to short-lived organisms such as insects and their parasites. Coupled with these patterns of increasing or decreasing body size are many other physiological or ecological variables such as rate of growth and length of life. These divergent patterns are often cited as the basis for the very different dynamics of each system.

At the same time, patterns in the topological structure of food webs have been discovered in recent decades that seem to transcend these distinctions between aquatic and terrestrial ecosystems. For example, the fractions of top, intermediate, and basal species appear to be independent of total species numbers. These fractions do not seem to differ significantly between the two kinds of systems.

How is topological structure invariant for systems with very different dynamics and scale relations? Do food webs with increasing body size respond to perturbations differently from those with decreasing body size? These questions are of considerable theoretical interest. They are also of practical importance, in view of our concerns about anthropogenic perturbations at global and local scales.

Methods of Analysis of Community Structure

General comparisons are very dependent on the methods for collecting data on community structure and on techniques of analysis. The geographical extent of a community and the position of its boundaries are difficult to define because the species inhabiting a particular place extend or contract their ambit at a wide range of scales from the diurnal to seasonal, to successional, to evolutionary periods. The underlying processes are very different in each environment, including passive dispersal patterns determined by physical dynamics, active migration, and alteration of the environment as well as adaptation to it. The common usage of terms such as *population*, *community*, and *ecosystem* for descriptions in the different sectors can conceal significant differences implicit in underlying concepts.

Interdisciplinary studies could usefully focus on techniques for measuring scale relations and defining the dimensions of populations and the coupling and exchange between communities. These couplings have practical consequences in terms of the definition of fish stocks, the design of nature reserves, and the identification of "damage" from pollution and other disturbances to natural systems. They are also important to our understanding of the role of evolutionary dynamics and speciation in marine and terrestrial systems.

The products of these studies would deal with comparisons of analytical techniques, examples of analyzed systems, scales for definition of community structure, and the consequences for community development and evolutionary processes.

Experimental Manipulation of Ecosystems

Large-scale experiments have been remarkably successful in resolving controversy and achieving insights that would take far longer through observational or laboratory scale experimental studies. Whole lake manipulations are a good example. Evolving statistical and modeling techniques can provide a rigorous foundation for detecting change in large unreplicated experiments. Freshwater and terrestrial habitats provide virtually all the examples of such controlled large-scale experimentation. In the open sea, such direct experiments are not practical. The consequences of extreme over-fishing can be viewed as very large exclusion experiments and can provide valuable insights into community responses. But over-fishing obviously does not allow rigorous definition of cause-effect relations, particularly in the context of natural variability.

Partial manipulation in fjords has been carried out. Mesocosms (enclosed volumes up to 3000 m^3) have been used, but the value of this approach and the interpretation of results have been controversial.

It would be valuable to have comparisons of the opportunities for, and the limitations on, manipulations at various scales, methods of analysis, and interpretation of results from these different "experimental" approaches. The potential for future work would be considered. For example, whole estuary experiments may be both feasible and critically important for predicting impact on near-shore regions—both land and sea.

Disturbance

The general role of disturbance is of very great interest. The term is difficult to define exactly. Disturbances include coarse-grained, infrequent events such as hurricanes, landslides and fires, as well as finer-scale events such as tree falls, ant mounds, and badger diggings. Predation in a very broad sense can be an important disturbance by changing the size and age frequency of the prey or by altering the spatial mosaic. The effects of disturbance have become an important component in the study of terrestrial, freshwater, and benthic systems. While these effects on the patch dynamics of two-dimensional systems are dramatic and ubiquitous, there may not be a comparable effect on ocean planktonic systems. Extreme alterations by man in density of fish stocks have no detectable link to observed fluctuations at lower trophic levels. Are these differences a matter of definition of "disturbance," of the data sets, or of different ways in which each system responds to irregular forcing? This topic—the modes of response to disturbance—would be a valuable focus of comparative and collaborative workshops.

Origin and Maintenance of Diversity

It has been suggested that diversity at the species level is generally greater on land but at the phylum level is larger in the sea. Such divergent patterns, if confirmed, require examination of the process responsible for their origin and maintenance. Major issues include the degree to which local diversity is determined within the context of the local physical environment, as contrasted with rates of species production resulting from migration of populations between regions. Another important issue is the relationship between local and regional species diversities that are coupled by the turnover of species between habitats (beta diversity). If marine communities are delimited primarily by physical processes and terrestrial (and benthic) communities exhibit greater influence of species movement and habitat selection, one might expect to find different patterns of beta diversity and perhaps differences in the influences of various processes and local and regional diversity.

Such comparisons would likely reveal gaps in our understanding of diversity and elucidate general patterns and the processes responsible for them. The inclusion of paleontologists would contribute an important historical perspective.

Patch Dynamics

In all environments, it is recognized that spatial and temporal variability—patches and population outbursts—are not merely noise but essential features of the food web dynamics ensuring adequate feeding rates and reproduction. However, methods of observation and analysis differ significantly between environments. In the sea, continuous spatial records are obtained from ships, and spectral analysis is used to define the biological patterns and compare them with physical observations. Moored recording systems provide comparable temporal data. Satellite data now extend the scales and display the complex interactions of physical and biological dynamics. For obvious logistic reasons, such methods cannot be used on land, and in turn different methods of analysis and description are used. As with other aspects, the primary focus in the open sea is on the physical forcing, whereas on land the ecological interactions are considered most important. Freshwater and benthic communities provide significant examples with alternative and sometimes conflicting explanations.

Aggregations of organisms imply that, locally, the system is far from a general equilibrium state. The behavioral mechanisms by which aggregations are formed and the consequences for the dynamics of the populations are important topics. At present, terrestrial and marine studies of these phenomena are conducted independently. The theoretical descriptions are quite separate. This is a major topic where useful comparisons can be made.

Boundary-Layer Communities

Exploring ecological processes may be most meaningful if contrasts are made among communities that reside within similar physical settings. In a moving fluid (water or air), the "boundary layer" is that region adjacent to the boundary (e.g., seafloor or forest floor) where there is a gradient in velocity perpendicular to the boundary due to the drag of the surface on the flow. All boundary layers are similar in structure but differ in their thickness, the shape of the velocity profile (the shear), and the mixing characteristics, all of which are functions of the flow velocity, fluid viscosity, and, in some flows, the roughness of the boundary. Communities residing within a boundary layer may be defined at several spatial scales. In the ocean, for example, a relatively thick boundary layer forms over the seafloor, due to steady, large-scale ocean circulations; thinner boundary layers form over local features, such as a rock ledge in an otherwise sandy bottom; and even thinner boundary layers form over organisms (e.g., kelp blades and mussel beds) that come into direct contact with the flow. Similar scale changes occur for desert, grassland, or forest systems.

Organisms residing within boundary layers in air or in water have many common problems. For example, erect plants and animals must be able to withstand fluid drag without being damaged, attached organisms may have spores or larvae that disperse in the fluid and must somehow make it back down to the surface again, and organisms that feed on suspended material must live in fluid regions with a high suspended food flux. The specific adaptations of organisms on land or on the seabed will differ because of the much lower fluid viscosity of air versus water. Fluid velocities tend to be much larger and mixing processes much faster in air than in water. Contrasting the ecology of boundary-layer communities living in different fluids should provide meaningful insights into the coupling between physical and biological processes in the evolution of population and community characteristics.

Scaling Up and Scaling Down

The problem of scale interactions is now a central theme in ecology. The advent of satellite observations has enlarged the range of spatial scales over which ecologists can describe their systems. On land this has increased the scales at which patterns are observed. In the oceans the reverse is true. We now see complex patterns at 1 - 100 km scales, where previously we assumed relative uniformity. Thus, one of the dichotomies separating land and sea studies is removed. One problem in both regimes is to assimilate the small-scale heterogeneities into descriptions of larger systems. The patchiness in the observations and the non-linearities in the processes do not permit simple averaging. Are there emergent properties? Can the fine structure of ecological processes be parameterized into the larger biochemical relations required by regional, or even global, studies of flux dynamics? What are the corresponding time scale changes?

Once again, the general questions are similar even though the detailed methodologies differ. If we are to have a comparative discipline permitting us to appreciate the effects of change at different scales from short-term episodic events to decadal climate trends, then we need to understand the range of responses available in the biosphere and especially the ways in which these responses occur at quite different scales from those of the forcing processes.

MECHANISMS FOR ACTION

Fostering new perspectives that integrate marine and terrestrial points of view will require a breaking down of traditional intellectual and institutional barriers. To some degree this may be accomplished by enlightened scientists and innovative funding. But major shifts in any discipline are more likely when students are encouraged to pursue new directions. We require the establishment of specific mechanisms involving faculty and students from both marine and terrestrial backgrounds.

The specific topics and options discussed in previous sections deal with very diverse aspects of ecology where there are overlaps or, more frequently, gaps in our understanding of common features in different environments. The topics cover the need for systematic data comparisons and availability of different analytical methods, as well as theoretical or conceptual issues. Various mechanisms for achieving a more integrated view will be required.

First, the conduct of field research is best carried out by the groups or institutes specializing in each sector. Thus, we do not recommend new field programs. This does not mean that such research groups or individuals will not benefit from interaction with colleagues in the other sectors. Quite the opposite. We have noted that such interactions are notoriously absent, restricting the sources of ideas for analysis and for generalization.

Secondly, these deficits are longstanding, being based on the separate organization and funding of research in each sector. Integration will not be achieved by a single large conference or symposium. Such large meetings tend to exacerbate rather than remove the separation of interests. So the need is to bring together relatively small groups over a relatively long period of time, allowing sustained interaction.

Thirdly, progress in increasing the dialogue should involve those near the start of their careers as well as the more senior researchers. The latter may be the generalists, but they are also often set in their separate ways.

Lastly, the federal agencies should be brought in, not only because their funding is the basis for action, but also because their present structures are significant factors in maintaining the separate directions. The need for restructuring is recognized in the emerging patterns of inter-agency support for global change research. An involvement of program managers would be very helpful in ordering specific project developments to take account of cross-system integration.