Comparison of Terrestrial and Marine Ecological Systems

Report of a Workshop held in Santa Fe, New Mexico

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1 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. The purpose of the workshop was to address this question specifically and, as appropriate, 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. Thus, the meeting was considered a success as a specific scientific event. More significantly, these discussions revealed many topics which required and would benefit from more detailed and extensive consideration. The time for this meeting was too short both to educate all the participants and to make detailed plans for further progress.

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 removal of institutional and funding barriers.

At this first, 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.) We must work out more specific plans and determine funding sources.

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.

2 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

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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.

auspices of geophysical fluid dynamics; even though the research programs and facilities are quite separate and distinct. Programs are underway to study the fluxes of carbon, nitrogen and other elements through the atmosphere, ocean and land interfaces. These fluxes involve interactions which 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 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 which 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 which 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% 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 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 between 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. As a result of discussions at the meeting, the following examples emerged of strengths in one discipline which 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 which 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.

3 Major Themes of the Meeting

3.1 Why are marine and terrestrial ecology different?

Marine and terrestrial researchers function in different institutional and granting situations. But their divergent approaches appear to rise 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, differs 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.

3.2 Dimensions for Comparisons

No single "axis" can bring together the contrasts among marine, terrestrial and freshwater ecosystems that were apparent to the workshop participants. 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 2 or 3 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 what the workshop defined as "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 present 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.

3.3 Common Issues

During the discussion many specific questions were raised which occur in aquatic and terrestrial research and 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 tradeoffs 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?

4 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 underway focussing on the identification of parameters and processes which can be used for quantitative comparisons. At the 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 between marine, terrestrial and fresh water systems.

5 Options for Action

At the workshop four subgroups were asked to choose topics requiring active collaboration by researchers in terrestrial and aquatic ecology. After discussion in plenary 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.

5.1 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.

5.2 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.

5.3 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.

A workshop would usefully focus on techniques for measuring scale-relations, 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 the workshop 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.

5.4 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 modelling 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 provide valuable insights into community responses. But overfishing 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 3,000 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 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.

5.5 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.

5.6 Origin and Maintenance of Diversity

A workshop would address the differing patterns of diversity in marine and terrestrial environments. 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 which 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.

A third consensus was that 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.

The discussion at the workshop reviewed mechanisms at different levels; a program for collaboration between individuals in distinct fields; workshops on topics outlined in the previous sections; summer schools over a period of years; an institute devoted to cross-sectoral syntheses.

(a) Support for interdisciplinary programs is always difficult. It is likely that, from the projected workshops, more detailed comparative projects will arise for data analyses and theoretical studies. A funding mechanism for such collaboration should be an integral part of the longer term workshop sequence.

(b) As a preliminary proposal we could envisage a series of two workshops per year for five years. The options suggested in the previous section could form a basis for such a proposal subject to more discussion and definition than was possible at this preliminary meeting.

(c) These topics could be formulated in terms of a series of summer schools lasting 5–10 weeks with at least 10 "staff" and 10 "students". Some of the staff and also visiting lecturers could stay for shorter periods. The core activities would include extended lecture/seminar series on, say, two topics with a leading speaker for each series. A major output could be research reports from students. The lectures could be published as reports — or more formally, since there is a need for texts dealing explicitly with these intersectoral comparisons.

(d) The concept of an "ecological institute" is being considered elsewhere. The ideas developed at this workshop could — and should — form a central theme in such discussions.

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