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Chapter 16

Epistemology, Experiments, and Pragmatism

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Introduction

In retrospect, what we now call complex interactions encompass several of the major advances in aquatic ecology. Some examples include the trophic-dynamic concept (Lindeman 1942), the multidimensional niche (Hutchinson 1957), size selective predation and the size efficiency hypothesis (Hrbacek et al. 1961; Hrbacek 1962; Brooks and Dodson 1965), the keystone predator concept (Paine 1966), and optimal foraging theory (Werner 1977). Recent advances offering similar benefit include the microbial loop (Riemann and Sondergaard 1986; Scavia and Fahnenstiel this volume; Porter et al. this volume), the ontogenic niche (Werner and Gilliam 1984; Crowder et al. chapter 10; Stein et al. chapter 11), chemical induction of antipredator morphological, behavioral and life history traits (Havel 1987), behavioral responses to predation (Kerfoot and Sih 1987) and the trophic cascade argument (Carpenter et al. 1985). The preceding chapters offer many specific examples of complex interactions in aquatic communities. Others will certainly appear in the near future. Chapters 10-14 develop both the general state of current understanding and the specific priorities for future work in this area of ecological research.

The goal of this chapter is to facilitate and accelerate the development of as yet unknown new ideas by offering a synthesis of current knowns and our best guesses about potentially productive directions for future work. Reasoning from theory and collective experience, we offer some epistemological perspectives with regard to studies of complex interactions. In addition, we make some specific suggestions about the institutional, logistic and financial arrangements that can enhance the creative potential of research activities.

Why Study Complex Interactions?

One respondent to the workshop invitation asked, "Why complex interactions? I'm still trying to figure out the simple ones!" The point was well taken. There are at least two major reasons why we cannot forego work on complex problems until all of the simple ones are resolved.

The primary reason for work on complex problems is that many of the specific questions may simply pale to insignificance (or be incidentally solved) as we learn more of the general mechanisms that structure aquatic communities and regulate their function. In other words, the big picture will emerge before each of the numbered spaces is filled. As argued from the perspective of hierarchy theory (Allen and Starr 1982; Allen et al. 1984; O'Neill et al. 1986; Frost et al. chapter 14), a more effective concept of scale allows understanding of what can and what cannot be resolved.

We have neither the time nor the talent to pursue our understanding of complex ecological interactions exclusively through reductionism. New insights will best, if not solely, derive from an effective hybridization of appropriately scaled concepts and methods.

The second reason for work on complex questions is the urgency of application-aquatic ecology must be closely allied with the management of both water quality and fisheries. That is both a desirable result of basic research and a societal obligation of the National Science Foundation. Success must be viewed in the larger, ultimate context of the success of ecology as a discipline. We might well profit from the example of molecular biology, where disciplinary proximity to applications in medicine has allowed a valuable synergism in generating support for and productivity of basic research. Our proximity to environmental issues and aquatic resource management offers similar potential. Redfield and Flanagan's message (Preface, this volume) is clear-be creative, collaborative, and do not avoid applied issues.

Temporal Patterns and Interaction Strength

Analyses summarized in this volume argue that a major effort should focus on the relationship between temporal and/or spatial pattern and the strength of interactions in lake communities (Bartell et al. chapter 7). As is apparent in the deliberations of the food web group (Crowder et al. chapter 10) and the habitat interactions group (Lodge et al. chapter 12), in the results of mesocosm experiments (Neill chapter 3) and in the larger context of whole lakes viewed on a historical scale (Carpenter chapter 8), surprising and apparently unpredictable responses arise from temporal and spatial heterogeneity in the existence or strength of key interactions.

The perspective of Paine's strong interactions (Paine 1981) and a recent review comparing terrestrial and aquatic community responses to predation (Murdoch and Bence 1987) show that some of the most important linkages result in local extinctions. It follows that what cannot be seen in an initial, descriptive study may turn out to be the most important components of a set of complex interactions. It follows, too, that the apparent variability of populations and communities serves as evidence that linkage strength is variable.

The large and growing number of surprising responses of natural systems to experimental manipulation (Walters 1986) suggests that the equilibrium assumptions of conventional population and community ecology and food web theory may be misleading, if not wholly inappropriate (Crowder et al. chapter 10). While it is difficult to design for surprises, it is apparent that confining an experimental treatment series to the range of observed variation within a given system may not reveal the major mechanisms responsible for the current variation. The factors that determine community composition are not necessarily those that regulate interspecific interactions. The most informative surprises usually express change of at least fivefold to tenfold in response variables such as organism size, survivorship, percent composition of an initially dominant species, etc. Thus, a rule of thumb for experimentalists searching for indicators of linkage strength is to plan for at least a 10X range in treatment conditions and to be prepared for surprises in the results.

Surprising responses from manipulative experiments may result from scale dependence of system response in microcosms, mesocosms, etc. Miniaturization may retain a representative physico-chemical context for studying complex interactions; however, the organisms of interest cannot be rescaled. This may lead to amplification of the interactions (Neill chapter 3) and a subsequent misinterpretation of their relative importance in larger systems. This scaling problem suggests that examination of complex interactions through manipulative experiments be performed in a series of different sized enclosures in order to develop scaling rules for extrapolation to lakes and reservoirs.

Results measured across order-of-magnitude treatment ranges may also be of broader theoretical importance. Normally well-behaved, deterministic dynamic systems can exhibit aperiodic, unpredictable behavior when pushed (e.g., through manipulation) to specialized regions of parameter space (May and Oster 1976, Gleick 1987). Environmental, ecological, or energetic constraints may decrease the likelihood of naturally functioning systems entering these chaotic parameter regions. Careful experimental design integrated with appropriate models may provide a powerful combination for further elaborating complex interactions in communities and testing important theoretical concepts.

Ecological systems often manifest multiple causality (Hilborn and Stearns 1982). The same phenomenon (e.g., change in mean size) can result from different mechanisms (e.g., size selective mortality or change in resource supply). Future work on complex interactions will reveal many more cases of multiple causality. Analyses of direct and indirect pathways may effect a fusion of population and ecosystem paradigms in the arena of aquatic community ecology. For example, the large-scale perspective of biogeochemical budgets offers relatively poor predictability of community composition, as does the species- level resolution of population ecology. Yet biogeochemical processes such as zooplankton excretion, the function of microbial loops, and littoral and benthic detrital processing strongly influence nutrient supply rate ratios to phytoplankton (Lodge et al. chapter 12). Population interactions-predation and competition-may then regulate composition of the assemblage. Each of these processes typically operates on different spatial and temporal scales; budgets on the annual and whole lake scale for biomass of entire trophic levels, while the population processes include seasonal to instantaneous time scales operating at the level of habitats, species, and life history stages. Reports of the topic groups (Chapters 10-14) identify a diversity of major research questions. It is apparent, however, that scale issues appear in each of many perspectives and therefore merit the attention of major research effort.

Hierarchical perspectives that help develop some general rules or guidelines for experimental work on multiple time-space scales are sorely needed. Because lakes offer such a wide range of conditions, they offer opportunities to develop concrete examples of scale dependent phenomena and applications of hierarchy theory. The deliberations of Frost et al. (chapter 14) offer some general guidelines, but the specific examples of conjecture and testing remain to be developed by creative researchers.

Ecological applications of hierarchy theory (O'Neill et al. 1986) draw heavily on terrestrial examples and the results of incisive experimental studies in the rocky intertidal (Paine 1980). Both are essentially two-dimensional and long-term relative to the dynamics of a planktonic community. One summer of phytoplankton turnover is analogous to thousands of years of forest dynamics. Thus, the multidimensional problems of lakes and the range of important temporal scales that operate in aquatic communities demand special and specific attention. The potential range of scales is clearly demonstrated in the contrasts of the as yet immeasurably rapid rates of the microbial loop (Porter et al. chapter 13), long-term observational studies (Mills and Forney chapter 2), and the view of centuries hybridized from empiricism and simulation by Carpenter (chapter 8).

Recruitment Research: An Example, Opportunity, and Imperative

One of the major themes in this volume is the evidence of the linkage of fishes to microbes and phytoplankton. As clearly argued by Persson et al. (chapter 4), limnology has paid little attention to the role of fishes in

aquatic communities. That oversight is now obviously important. As an example of the need for further work on food web linkages and their role in complex interactions, we take one research theme, recruitment, and develop it more explicitly.

Understanding the causes of variability in recruitment of early life history stages of fishes has been identified as a key problem by both applied and basic research interests (May 1984, Rothschild 1986). Obviously, the predictive power of that understanding will enhance management capability of the fisheries profession. Much the same magnitude of variability is expressed by many marine and freshwater invertebrates. In the larger ecological context, Strong (1984) demonstrates that density vague regulation of populations and community interactions is evident in many aquatic and terrestrial systems.

A panel formed by the U.S. National Academy of Science identified the recruitment question as the foremost research priority in fish ecology (Rothschild 1986). Similarly, the National Oceanic and Atmospheric Administration and the Biological Oceanography Program of NSF have recently sponsored major research initiatives designed to help resolve the unknowns associated with the recruitment question.

One of the key questions identified through the Complex Interactions Workshop is the recruitment problem, although in the context of complex interactions, recruitment issues are more often expressed through the complexity of effects arising from changes in trophic ontogeny (Werner and Gilliam 1984). Resolution of both cause and effect with regard to variation in recruitment of fishes would greatly advance our understanding of aquatic community ecology. The recruitment process is known to be limited by a nested hierarchy of abiotic and biotic constraints. Autecological constraints dictate the presence or absence of a species. Variable, stochastic weather effects play a major role in the production and relative survival of gametes and early life stages. Species interactions such as predation, competition, disease, and parasitism subsequently determine most of the mortality of a cohort within the first few months of life. Both density dependent and density independent components are involved and interact on multiple spatial and temporal scales. Although the majority of attention has focused on fishes, virtually any species that exhibits pulsed reproductive effort and highly variable survivorship in early life history stages can evoke similar ecological effects. Thus, the same principles of trophic ontogeny and size structured interactions apply to many planktonic taxa (such as *Chaoborus* and many copepod species), as well as to a diversity of littoral and benthic invertebrates (chapters 10-12).

As the case for fishes is best known, their example will serve to illustrate the imperative for research. Year class strength in fishes is highly variablea basic and oft-confirmed observation. Much of what we know about recruitment variation has derived from studies of fish populations manipulated through exploitation. As developed in a subsequent section on epistemology and experimental approach, big treatment effects expressed in recruitment responses have been a major source of insight.

The consequences of variable recruitment can be transmitted over long time scales (many years) and expressed throughout aquatic food webs. For example, a strong year class of planktivorous fishes can alter the composition of the zooplankton (Crowder et al. chapter 10; Mills and Forney chapter 2; Persson et al. chapter 4). As a result of altered species composition and biomass of zooplankton, effects cascade at smaller scales through altered selectivity and grazing rates into the phytoplankton and the microbial loop (Riemann and Sondergaard 1986; Kitchell and Carpenter 1988; Stockner and Porter chapter 5; Scavia and Fahnenstiel, chapter 6). As developed in several chapters of this book, fish effects are dependent upon and expressed at many levels of the community and vary in response to recruitment variation.

Variation in recruitment of a long-lived piscivorous species may evoke an even more extensive and long-lasting effect, but with opposite manifestations at each successively lower trophic level. The storage effect (Warner and Chesson 1985) of a strong and successfully recruited year class of piscivores can last a decade or more and will continue to be expressed in the composition and function of the aquatic community. This level of regulation and feedback is expressed in the opposite way at each lower trophic level, can completely alter planktonic community structure, and may account for up to 50% of the variance in primary production (Carpenter and Kitchell 1987; Carpenter et al. 1987). The key component in these cases is the cause of recruitment variation. The manifestations of variable recruitment afford an opportunity to examine amplification or attenuation of ecological signals through networks of populations connected by competitive or predator-prey interactions that vary through space and time.

Virtually every plausible cause for recruitment variation has been advanced and championed (May 1984). The arguments range across density independent mechanisms (e.g., storms, asynchrony in the seasonal plankton bloom relative to early life stages), simple starvation, strong competition, predation, and all possible interactions among the above (Rothschild 1986). Each is credible and none are unequivocally tested. Depending on the species in question, some mechanisms may be more important than others. Generality may emerge from the many research efforts currently directed to this issue but community ecology can neither wait for the answers nor do without them. In fact, we must view recruitment variation in the community context if we are to make progress. Variable recruitment is both the effect of species interactions and the cause of community changes. Understanding the causes, effects, and feedbacks of recruitment variation is a critical nexus of understanding complex interactions in aquatic systems.

Lake systems offer a unique opportunity for developing the requisite

research on this issue. They are, in general, less subject to the confounding advective effects of marine systems. They offer relatively discrete and, therefore, quasireplicate systems for development of independent tests. Diversity at the level of species, life histories, and trophic guilds is variable among lakes-but usually in predictable ways (Tonn and Magnuson 1982)and offers a gradient of potential interactions. Similarly, the range of morphometry, productivity and sizes offered in lake systems allows development and testing of ideas pertinent to the questions of habitat interactions, resource limitation, and scale.

Opportunities for natural experiments abound. Strong or weak year classes are often correlated within a regional setting; thus, the opportunity for independent replication is readily available. Controlled experimentation on recruitment can be accomplished through cooperation with fisheries management agencies. Many lakes are regularly manipulated by stocking policy and other large-scale fisheries management practices designed to alter specific fish populations and/or composition of the fish community. Exploitation regulations can effect substantial changes in the size and species composition of the fish assemblage. Piscicides are regularly used to remove undesirable fishes. The resultant communities and their interactions offer a full range of treatment conditions from zero to high density fish populations, and a set of intermediates that would allow evaluation of colonization responses, founder effects and understanding of the shape of response curves as community development proceeds.

In small systems, manipulation at the species or trophic level are easily achieved, while in large systems (e.g., the Laurentian Great Lakes) analogous manipulations are underway and can serve as a basis for tests of scale effects (Kitchell and Carpenter 1987; Scavia and Fahnenstiel chapter 6). Natural experiments such as winter- or summer-kills occur regularly in some systems and intermittently in others. Recolonization and the development of a fish species assemblage occurs through natural immigration processes and/or through the action of fisheries agencies.

Thus, the ontogenically changing role of fishes as predators and competitors is amenable to experimental analysis at temporal and spatial scales pertinent to complex interactions in natural communities. A diversity of opportunities exists for collaboration with management agencies in developing a suite of manipulative studies that can reduce the costs of largescale experimentation. The resultant convergence of basic and applied interests is an obvious advantage.

The Case for Opportunism

Planning exercises such as this workshop should be complemented by arguments on behalf of serendipitous opportunity. Community ecology has long taken advantage of natural experiments and an opportunistic response to major natural catastrophes in order to develop understanding or generate hypotheses complementing those derived from controlled experimentation. Manipulations performed by lake managers offer similar opportunities.

Many classes of natural experiments are available in lake systems. Winter-kill lakes have been used as a means for sorting among the effects of autecological constraints and species interactions (Tonn and Magnuson 1982). Some of the most dramatic insights derived from the history of aquatic community ecology stemmed from the introduction of exotic species. Some examples include alewife in coastal ponds (Brooks and Dodson 1965), peacock bass in Gatun Lake (Zaret and Paine 1973), Nile perch in Lake Victoria (Balon and Burton 1986), and the sequence of sea lamprey. alewife and Pacific salmon in the Great Lakes (Kitchell and Crowder 1986). Other invasions such as those of the Eurasian water milfoil, Hydrilla, water hyacinth, rusty crayfish, and grass carp have had equally potent and instructive effects in developing our understanding of littoral zone communities (Carpenter and Lodge 1986). At the smaller scale, experimental approaches substantially enhance understanding and predictive power when dominant or rare members of an extant community are manipulated (Paine 1980, Bergquist and Carpenter 1986, Neill chapter 3, Persson et al. chapter 4).

Most invasions or introductions have had little ecological consequence (Diamond and Case 1986); however, the spectacular effects of those that have been successful demand attention to the future and will challenge the very best of ecological theory (Balon and Burton 1986). Ecological principles have been successfully employed to forecast the outcome of some introductions (Kitchell and Crowder 1986), but most are poorly anticipated and fully expressed before ecologists can offer either advice to management or contributions based on firm understanding.

From the lessons of history, we can be confident that exotic species will continue to appear in lake systems. We can also see that a planned rather than reactive approach will recognize these perhaps unwanted introductions as an opportunity to learn. Clearly, our understanding of rules for community composition have been augmented by the lessons of previous invasions. It follows that invasions to come may be equally if not more instructive. Lake systems offer the obvious value of replicates in time and space for this next in a series of potentially instructive mishaps.

Epistemology and the Experimental Approach

No single experimental or analytical approach seems uniquely appropriate to the evaluation of complex interactions. There is, however, some guidance from the principles of hierarchy theory. Given the number and kinds of unknowns and the frequency of unexpected results that derive from



FIGURE 16.1. A conceptual diagram of experimental protocol for evaluating complex interactions. The current state and maximum response of a community are first determined by a big treatment experiment. Rate of response, shape of the response curve, and interactions of system components are subsequently determined via factorial experiments. Only two of potentially many system state variables are depicted.

research on lake communities, it follows that a sequential or hierarchical treatment protocol would accelerate our rate of discovery.

Lessons learned from the introductions of exotic species (see previous section) or large-scale biogeochemical perturbations (Schindler and Fee 1974; Schindler et al. 1985) clearly demonstrate big effects from big treatments. These lead to an understanding of the dimension of potential community response and allow inferences about the relative importance of

specific mechanisms as the system changes state. Thus, a first approach to gaining understanding would involve a plan for applying big treatment effects and anticipating big responses. The major merit and goal of this approach is to dimension the limits of possible community responses as a first estimate of the compensatory capacity of the system under study.

In Chapter 10, arguments are advanced against working outside the realm of observed variation. One of the perspectives of a hierarchical view is that system structure can best be understood by defining system limits (O'Neill et al. 1986). We argue that some of our major conceptual advances (e.g., the keystone predator concept) derived from an approach based on big treatment manipulations, that the lessons of exotic species include many unexpected responses, and that even well-planned experiments evoke most informative surprises (Neill chapter 3). We should plan for and initiate this type of manipulation as a first step.

We recognize, however, that the big perturbation approach offers less understanding of the transient behavior of complex interactions as expressed at the temporal and spatial scales of natural variability. Toward an understanding of those questions, we suggest a factorial or gradient design within the range of variation exhibited under large perturbations. This would allow sufficient replication to elucidate mechanisms, clarify the components of variability, quantify directional change, and detect nonlinearities. Thus, the mechanistic understanding required for adequate prediction and testing would be best derived by first conducting a big manipulation experiment designed to dimension the response capacity of the community, followed by factorial or gradient experiments focusing on certain components of the reduced matrix of possibilities (Fig. 16.1).

Although experimentalists (acting on the advice of good statisticians) might choose to develop a factorial design as a first approach, the lessons of history suggest that a big treatment experiment followed by gradational treatments will maximize our progress. That evidence lies in the many mesocosm and pond studies where the major contribution of the research was evoked in only a small fraction of the treatment units (Hall et al. 1970, Neill chapter 3). Judicious monitoring of community structure following natural or planned manipulations represents an alternative to the combined manipulation and gradient experiments previously outlined. Estimates of the variance associated with community components through space and time permit the development of neutral models (Caswell 1976) aimed at quantifying the relative importance of different ecological interactions (Harris and Griffiths 1987). The ability of these variously scaled models to explain portions of the monitored variance in community structure may reveal the scale dependence of interaction strength. Development, application, and analysis of these models may provide a means for identifying the scales at which various phenomena, identified and measured in the laboratory, apply in nature.

One of the workshop synthesis groups discussed experiences with un-

expected results that arose during their research programs. Their consensus was that major conceptual insight occurs as a revelation. The template for creativity is usually opened by conflict, paradox, or contradiction. The catalysis of innovation is generally unpredictable, but usually associated with an alternative offered by abandoning the constraints of conventional wisdom, by the insights of a colleague trained to a different world view, or by an accident. While it remains impossible to plan for creative insights, we can recognize that thinking at a different scale and interaction with scientists of different traditions are common correlates. Our recommendations at the close of this chapter emphasize development of the kinds of opportunities and institutional support that may provide the requisites of creativity.

Many of our most informative surprises have derived from unexpected perturbations in complex systems (Walters 1986). These revealed the constraints of response potential (O'Neill et al. 1986). We suggest that assessing the extreme scenarios of community response would be a most appropriate first step. That helps define the determinants of community structure. Analysis of variation around the mean condition can follow. That provides understanding of the regulators of community structure. Given the finite lifetime of most research grants and the low funding probability of a renewal to clean up the details, we argue that our understanding of response patterns will best derive from a bold initial step and a wellplanned follow through. Progress may be further enhanced if this kind of protocol can be employed in an institutional setting that maximizes the prospect for conceptual insight and collegial interaction.

Fostering Creativity

The proliferation of pages in print has a negative effect on the kinds of creative endeavor required to better understand complex interactions. A logical consequence of the information explosion is that individual researchers will choose and/or be forced by time constraints into increasing specialization. This tendency is counter to the kinds of expansive thinking that may help resolve large, complex problems. In fact, specialization in ecology tends to promote refinement of the status quo, which is antithetical to the development of fundamentally new ideas-the charge of the National Science Foundation!

How can this contradiction be resolved? We argue that efforts to promote interdisciplinary collaboration and training are required. Research initiatives should maximize learning rates through pairings of theorist and experimentalist, molecular microbiologist and plankton ecologist, fisheries biologist and limnologist, etc. In a similar way, studies that combine two or more scales of investigation should prove fruitful. For example, the patchiness of planktonic and littoral habitats could profit from the view of those who sample on the scale of minutes and meters if properly juxtaposed with the view held by those whose perspective is of whole lakes and years to decades. This hypothetical combination can take the real world shape of collaboration among algal ecologist, fish ecologist and paleoecologist.

The greatest rates of progress on complex interactions will arise from polythetic approaches. The various approaches to limnological research differ in the space and time scales which they address as well as in their degree of realism, detail, and complexity (Fig. 16.2). All models employ simplification to achieve insight, and so are low in realism, detail, and complexity. However, models offer great flexibility with respect to time scale. Laboratory microcosms achieve somewhat greater realism than models, but generally operate on restricted time scales of hours to months. A somewhat longer range of time scales is addressed by field mesocosms, which offer relatively more realism, detail, and complexity. Whole-lake results are the standard of realism, detail, and complexity to which all other approaches must be compared. However, field experiments at large spatial and temporal scales are rather rare (Strayer et al. 1986). Paleolimnology is the only consistent source of integrative data at time scales of decades to centuries, but such data span a great range of levels of realism, detail, and complexity (Binford et al. 1983).

Aquatic ecologists are asked by society to provide information for management decisions that usually focus on time scales of years to decades. Models, paleolimnology, and whole-lake studies are the only approaches that directly address these time scales. However, a number of constraints



FIGURE 16.2. Relationships among possible approaches to analyzing lake systems with respect to time scale on which each approach can be applied, and the degree of realism, detail, and complexity of each approach.

on whole-lake studies also dictate important roles for work in microcosms and mesocosms. Multiple causality is ubiquitous, and the methods for separating and quantifying contrasting causal mechanisms dictate smallscale, reductionistic studies (Hilborn and Stearns 1982). Yet, small-scale studies alone are not sufficient for forecasting behavior of larger systems, because small-scale studies cannot fully determine which causal pathways will predominate at larger scales. One of the great challenges of ecology is to understand how information from models, small-scale experiments, and paleoecology can be translated into inferences and predictions about long-term lake dynamics. Integrative studies combining several approaches and scales will be needed to resolve this problem.

"In My Lake..."

We begin this section by refusing to concede that each lake is different from all others. That may seem unnecessary to those who have not attended a national limnological meeting but the phrases "In my lake..." and "But in my lake..." should sound disturbingly familiar to those who have. From certain research perspectives, the individuality of lakes is an interesting property and an asset (cf. Persson et al. chapter 4). We feel, however, that studies of complex interactions will advance most rapidly if we can develop ways to understand basic mechanisms before testing their generality in the vast range of lake types. In fact, we argue that the test for site effects, while an important consideration, is subordinate to derivation of a mechanistic understanding.

Methods must be developed that permit extrapolation of interaction strength across systems of different scale. No rigorous criteria for valid comparison across differently sized systems have been established. Investigators invoke names (i.e., microcosm, mesocosm, pond, lake) that carry implications of structure, complexity, and scale; nevertheless, these names remain attached to fuzzy concepts that continue to frustrate the development of theory and promulgate the uniqueness of individual study sites.

We have attached high priority to the collaborative, interdisciplinary approach. Given the dispersion of aquatic ecologists, we conclude that research initiatives will be most effective if specialists can be aggregated by common interest at a subset of common sites. We envision development of facilities that will focus people and research problems, thereby reducing the unnecessary duplication of analytical facilities and monitoring effort that accompanies limnological work on each of many lakes. Thus, the overhead of research enterprise can be minimized and the creativity of scientists more effectively focused on important research questions.

Based on discussions during the workshop, at least four general kinds of sites seem necessary: arctic or alpine lakes, natural north temperate lakes, southern reservoirs, and tropical lakes. This ensemble would offer the full range of physical and latitudinal gradients of interest. Each site should include:

- 1. Multiple lakes, some monitored, others available for large-scale manipulation.
- 2. Administrative infrastructure and permanent staff to coordinate and maintain the facility.
- 3. Capacity for smaller-scale manipulative studies as might be conducted in pond systems, large limnocorrals, or mesocosms.
- 4. Laboratory facilities, housing, and appropriate local support staff as necessary to accommodate independent investigators.

Coordination among sites would permit tests of hypotheses across trophic or geographic gradients. An example would compare the magnitude of food web effects in natural oligotrophic lakes with those derived from similar manipulations in eutrophic reservoirs (see Crowder et al. chapter 10). Results of these kinds of comparative tests would serve as a basis for developing more rigorous tests for site effects and create some perspective on the merits of the argument that "In my lake..."

In much the same fashion as oceanographers share cruise opportunities, independent investigators interested in a particular aspect of complex interactions would be encouraged to pursue their expertise under the umbrella of ongoing or planned large-scale manipulations. Again, as in the case of shipboard collegiality, the synergism of informal interactions among juxtaposed scientists provides opportunities for new ideas and creative exchange that minimize the inefficiencies of isolated competition and the constraints of traditional wisdom.

These arguments seem familiar to those of us who have pleaded the case for a new colleague or support to a field station. Our goals differ in that the focus of these facilities would be ongoing and intended large-scale manipulations. We hold that a system of experimental lake sites is extremely valuable to aquatic ecology and deserving of the same kind of institutional support that has been provided for research vessels, high energy physics installations and biotechnology centers. More importantly, such a system is requisite for most efficient and rapid progress in developing our understanding of aquatic communities, their variability, and their potential as public resources.

Additional Opportunities

The general goals above can also be facilitated by a number of more modest programs.

1. Provide more flexibility in the grant process.

a. Fund collaborative efforts appropriate to the disciplinary diversity of the problem.

b. Fund studies for longer periods than the traditional two or three years when such longer time scales are appropriate to the problem.

c. Provide extensions of up to 12 months which would allow time for data interpretation and development of renewal requests in phase with the annual cycle of field research.

2. Provide more support for interaction and collaboration.

a. Provide grant supplements to allow travel for consultantships and collaborations.

b. Support general planning workshops (such as the Notre Dame workshop) at about 5-year intervals.

c. Support annual series of special topic conferences in aquatic ecology similar to the Gordon Conferences.

3. Create opportunities for broader training.

a. Support training workshops on new techniques or approaches (e.g., microbial methods, phytoplankton taxonomy, applications of new theory, etc.).

b. Provide a greater number and diversity of fellowships for graduate students (e.g., to support travel and yearlystipends to learn new techniques and perspectives at a different institution; to support summer work learning new techniques; to support the development of curricula that broaden students' training).

c. Provide postdoctoral and midcareer training for scientists seeking to learn a new subdiscipline and/or collaborate with workers in another discipline.

Summary

Complex interactions involve multiple causal pathways plus multiple spatial and temporal scales. Any complex interaction may have seasonal, biogeochemical, predator-prey, behavioral, and/or evolutionary components. Because of their multifarious nature, complex interactions are not dealt with effectively by any one of the established world views (epistemes) of aquatic ecology. For example, the taxocene approach (phytoplankton communities, fish communities, etc.) is inadequate because it neglects trophic structure, while the trophic level approach is often too aggregated to cope with variable life histories and most interspecific interactions. Consequently, progress on complex interactions will require new, or at least synergistic, combinations of the well-established epistemes. Complex interactions also require polythetic approaches. We argue that the most rapid progress will come from sequential research designs that proceed from strong manipulations at large scales to finer grained experimental programs designed to elucidate and compare individual mechanisms. In some cases, broadly-trained investigators and/or interactive teams will be needed to accomplish such research plans.

Funding effective work on complex interactions poses a significant

challenge. Intense competition for research support engenders conservatism which favors work within the boundaries of conventional wisdom, rather than the novel juxtapositions of perspectives, disciplines, and methodologies that are needed to study complex interactions. Specific suggestions for new kinds of funding and greater flexibility in the granting process were contributed by many workshop participants and are summarized herein.

Finally, we must find ways of training researchers to recognize and account for the effects of scale. Many forces, including intra-disciplinary competition and the explosive growth of the literature, contribute to specialization. The resultant factionalization leads to an emphasis of small problems, diminishing ecology's standing relative to the disciplines with which it must compete for funds.Innovative programs are needed that teach scientists to seek appropriately scaled approaches and foster the receptiveness to other perspectives essential for progress on the most important basic and applied questions that face aquatic ecology.

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References

- Allen, T. F. H. and T. B. Starr. 1982. Hierarchy: Perspectives for ecological complexity. Chicago: University of Chicago Press.
- Allen, T. F. H., R. V. O'Neill, and T. W. Hoekstra. 1984. Interlevel relations in ecological research and management: Some working principles from hierarchy theory. USDA Forest Service General Technical Report RM-110, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, 11 pp.
- Balon, E. K., and M. N. Burton. 1986. Introduction of alien species or why scientific advice is not heeded. Env. Biol. Fish. 16:225–230.
- Bergquist, A. M., and S. R. Carpenter. 1986.Limnetic herbivory: effects on phytoplankton populations and primary production. Ecology 67:1351–1360.
- Binford, M., E.Deevey, and T. Crisman. 1983. Paleolimnology: An historical perspective on lacustrine ecosystems. Ann. Rev. Ecol. Syst. 14:255–286.
- Brooks, J. L., and S. I. Dodson. 1965. Predation, body size, and composition of plankton. Science 150:28-35.
- Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. BioScience 35:634–639.
- Carpenter, S. R., and J. F. Kitchell. 1987. The temporal scale of limnetic primary production. Am. Nat. 129:417-433.
- Carpenter, S. R., J. F. Kitchell, J. R. Hodgson, P. A. Cochran, J. J. Elser, M. M. Elser, D. M. Lodge, D. Kretchmer, X. He, and C. N. von Ende. 1987.

Regulation of lake primary productivity by food web structure. Ecology 68: 1863–1876.

- Carpenter, S. R. and D. M. Lodge. 1986. Effect of submersed macrophytes on ecosystem processes. Aquat. Bot. 26:341–370.
- Caswell, H. 1976. Community structure: a neutral model analysis. Ecol. Monogr. 46:327–354.
- Diamond, J., and T. J. Case. 1986. Ecological Communities. New York: Harper and Row.
- Gleick, J. 1987. Chaos. New York: Doubleday.
- Harris, G. and F. B. Griffiths. 1987. On means and variances in aquatic food chains and recruitment to the fisheries. Freshwat. Biol. 17:381–386.
- Havel, J. E. 1986. Predator-induced defenses: A review. *in*: Predation: Direct and Indirect Impacts on Aquatic Communities, ed. W. C. Kerfoot and A. Sih. Hanover: University Press of New England.
- Hilborn, R, and S. C. Stearns. 1982. On inference and evolutionary biology: the problem of multiple causes. Biotheoretica 31:145–164.
- Hrbacek, J. 1962. Species composition and the amount of zooplankton in relation to the fish stock. Rozpr. Cesk. Acad. Ved Rada Mat. Prir. Ved. 72:1–116.
- Hrbacek, J., M. Dvorakova, V. Korinek, and L. Prochazkova. 1961. Demonstration of the effect of the fish stock on the species composition of zooplankton and the intensity of metabolism of the whole plankton assemblage. Verh. Int. Ver. Theoret. Angew. Limnol. 14:192–195.
- Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Harbor Symp. Quant. Biol. 22:415–427.
- Kerfoot, W. C., and A. Sih. 1987. Predation: Direct and Indirect Impacts on Aquatic Communities. Hanover: University Press of New England.
- Kitchell, J. F., and S. R. Carpenter. 1987. Piscivores, planktivores, fossils and phorbins. *in*: Predation: Direct and Indirect Impacts on Aquatic Communities, ed. W. C. Kerfoot and A. Sih. Hanover: University Press of New England.
- Kitchell, J. F., and S. R. Carpenter. 1988. Food web manipulation in experimental lakes. Verh. Internat. Verein. Limnol. 23:351–358.
- Kitchell, J. F., and L. B. Crowder. 1986. Predator-prey systems in Lake Michigan: model predictions and recent dynamics. Environ. Biol. Fishes 16:205–211.
- Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. Ecology 23:399–418.
- May, R. M., ed. 1984. Exploitation of marine communities. Berlin: Springer-Verlag.
- May, R. M. and G. F. Oster. 1976. Bifurcations and dynamic complexity in simple ecological models. Am. Nat. 110:573–599.
- O'Neill, R. V., D. L. DeAngelis, J. B. Waide, and T. F. H. Allen. 1986. A Hierarchical Concept of Ecosystems. Princeton: Princeton Univ. Press.
- Paine, R. T. 1966. Food web complexity and species diversity. Am. Nat. 100:65–75.
- Paine, R. T. 1980. Food webs, linkage interaction strength, and community infrastructure. J. Anim. Ecol. 49:667–685.
- Riemann, B., and B. Sondergaard. 1986. Carbon dynamics of eutrophic, temperate lakes. Amsterdam: Elsevier Scientific Publishers.
- Rothschild, B. J. 1986. Dynamics of marine fish populations. Cambridge: Harvard University Press.
- Schindler, D. W. and E. J. Fee. 1974. Experimental Lakes Area: Whole-lake experiments in eutrophication. J. Fish. Res. Bd. Canada 31:937–953.

- Schindler, D. W., K. H. Mills, D. F. Malley, D. L. Findlay, J. A. Shearer, I. J. Davies, M. A. Turner, G. A. Linsey, and D. R. Cruikshank. 1985. Long-term ecosystem stress: The effects of years of experimental acidification on a small lake. Science 228:1395–1401.
- Strayer, D., and J. S. Glitzenstein, C. G. Jones, J. Kolasa, G. E. Likens, M. J. McDonnell, G. G. Parker, and S. T. A. Pickett. 1986. Long-term ecological studies: An illustrated account of their design, operation, and importance to ecology. Pub. No. 2 of the Inst. of Ecosystem Studies, NY Bot. Garden. 38 pp.
- Strong, D. R. 1986. Density vagueness: abiding the variance in the demography of real populations. *in*: Ecological Communities, ed. J. Diamond and T. J. Case, 257–268. New York: Harper and Row.
- Tonn, W. M., and J. J. Magnuson. 1982. Patterns in the species composition and richness of fish assemblages in northern Wisconsin lakes. Ecology 63:1149–1166.
- Walters, C. 1986. Adaptive management of renewable resources. New York: MacMillan.
- Warner, R. R., and P. L. Chesson. 1985. Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. Am. Nat. 125:769–787.
- Werner, E. E. 1977. Species packing and niche complementarity in three sunfishes. Am. Nat. 111:553–578.
- Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. Ann. Rev. Ecol. Syst. 15:393–425.
- Zaret, T.M., and R.T. Paine. 1973. Species introduction in a tropical lake. Science 182:449–455.