

CHAPTER 9

Scaling Issues in Experimental Ecology *Freshwater Ecosystems*

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EXPERIMENTS HAVE CONTRIBUTED SUBSTANTIALITY TO OUR UNDERSTANDING of ecological processes in aquatic and terrestrial ecosystems (Hairston 1989; Resetarits and Bernardo 1998). Their use has been particularly effective in studies of freshwater ecosystems (Lodge, Blumenshine et al. 1998), in part because many key processes in aquatic habitats operate at scales that lend themselves to experimentation. Informative experiments have been conducted at scales ranging from test tubes and liter-sized containers to whole lakes and streams. Whole-ecosystem manipulations have had substantial advantages for experimental work (Carpenter et al. 1995), but such large-scale experiments also have some significant drawbacks and can not always be used to investigate ecological phenomena. Effectively tailoring the scale of freshwater experiments to the questions and habitats being addressed is a critical component of advancing the understanding of aquatic ecosystems.

Microcosms play a critical role in applying an experimental approach to a full range of freshwater habitats and ecosystems (Daehler and Strong 1996). Microcosms cannot, however, incorporate the complete range of organisms, habitats, or processes that are important in freshwater ecosystems. Ecologists must be conservative and clever in extrapolating the results of experiments in containers to natural ecosystems. In some cases researchers can realistically simulate natural phenomena in their experiments to gain an understanding of ecological processes. Such realistic simulations are not the only situations that can help to explain ecological phenomena, however. Important insights can be gained in experiments that examine gradients of scale that represent critical

ecosystem features or that generate realistic results in situations where such results might not be expected.

Our goal in this chapter is to present an overview of the varied approaches to gaining information from freshwater experiments. We discuss important scaling issues that must be considered in the design and interpretation of experiments that simulate natural ecological processes. We also consider examples of how driving factors have been evaluated without experiments using environmental gradients or using unrealistic experiments.

Experimental studies of freshwater systems regularly incorporate considerations of spatial and temporal scales (Frost et al. 1988). In some cases, the scales of observation used realistically simulate processes operating in natural systems. For example, the spatial scales that are critical to some aquatic organisms can be represented realistically in test tubes or containers of a few liters in volume. Others require mesocosms 1 to 5 m in diameter and several meters in depth, a size that is manageable in many natural habitats. Some of the important interactions involving phytoplankton, for example, appear to be incorporated realistically in containers 1 m³ in volume or less (Reynolds 1997). Of course, not all freshwater ecosystem organisms or processes can be realistically represented in practical container experiments.

Time scales representing many aquatic ecosystem processes can also be incorporated into mesocosm experiments. Experiments to evaluate a wide range of freshwater processes can be carried out over less than one week. The direct effects of zooplankton on phytoplankton can be assessed over the course of a few days, a period over which in-container conditions are not expected to differ markedly from in-lake conditions. As with spatial considerations, though, there are important freshwater ecosystem processes that take a substantial period of time to play out, a length of time that is difficult to handle experimentally. Some experiments certainly involve time periods that are too long or too short and containers that are too small, but there are many cases where microcosm experiments can be conducted over temporal and spatial scales that are realistic for freshwater ecosystems.

Not all of the interacting elements of aquatic ecosystems can be expected to be fully represented even in very large mesocosm experiments, however. Under-represented elements include important components of aquatic communities (e.g., fishes and macrophytes), major physical features of aquatic habitats (e.g., mixing patterns and

thermal structure), and the complete range of interacting habitats in aquatic ecosystems (e.g., pelagic and benthic regions). That is not to say that worthwhile insights can only be gained from reasonably scaled experiments, however. We will discuss cases where useful insights can be derived from unrealistic conditions.

As suggested previously, the potential to manipulate entire natural ecosystems directly is a substantial advantage for experimental work in freshwater habitats (Carpenter et al. 1995). Several highly successful experiments have been conducted on whole lakes or streams to evaluate fundamental ecosystem processes or responses to stress (e.g., Peterson et al. 1985; Schindler 1990; Brezonik et al. 1993; Carpenter and Kitchell 1993). These experiments have provided important insights into basic system characteristics that can be extended to ecosystems that have not been manipulated.

Whole-ecosystem experiments have their own limitations, too, in terms of their replication (e.g., Carpenter et al. 1989; Stewart-Oaten et al. 1992), in their ability to control for natural variability in important system drivers, and in their capacity to include processes occurring in their surrounding watersheds. It may also be difficult to conduct large-scale experiments over a period of time necessary for the influence of an important factor to propagate through an ecosystem. For example, fish populations were only reduced after several years in a lake acidification experiment because only young fish were affected by the pH depression (Schindler et al. 1985). It must also be considered that, due to the complex nature of interactions within aquatic ecosystems, what is intended as a single stress, such as acidification, may actually generate a number of stresses operating on the manipulated ecosystem. The specific factors generating a particular ecosystem response may not be simple to determine (Frost et al. 1999).

Experimental manipulations in containers can be particularly effective in conjunction with whole-ecosystem experiments to help understand the mechanisms operating in aquatic ecosystems (Frost et al. 1988). Also, because only a limited number of entire aquatic ecosystems can, or should, be manipulated experimentally, systematic considerations of scale are essential for extending information from the few experimental manipulations that are practical to developing a full understanding of natural ecosystem function.

SCALE CONSIDERATIONS WHEN CONDUCTING FRESHWATER EXPERIMENTS

The complexity of freshwater ecosystems limits how effectively experimental conditions can be expected to represent natural situations. There are many critical factors that must be considered when attempting to draw inferences about natural phenomena from experiments, particularly those in mesocosms. In this section we present an overview of some of the factors that must be considered in the design of experimental systems.

There are some variables for which scaling issues are not an obvious factor in the ways that they are imposed in experiments. Examples include temperature or the concentration of a chemical constituent like N, P, or H. Such variables have been termed "intensive" (e.g., Denbigh 1964) and contrast sharply with distinctly scaling variables such as space or time, which are termed "extensive." Intensive variables should be incorporated extrinsically into the design of an experiment but they function quite differently from extensive variables.

Space and time are two obvious scaling factors that must be considered in the design and interpretation of any experiment. Experiments that are conducted over too long a time or in too small a container have obvious limitations in their ability to simulate natural conditions. Understanding how to define "too," however, can often be a problem. Concerns about space and time may seem so obvious as to be trivial, but one does not have to delve very deeply into the ecological literature to see how comfortable some investigators seem to be with drawing inferences from artificially scaled experiments (e.g., Wilbur 1997). It is valuable to consider the ways that spatial and temporal factors that constrain an experimental system can have major influences over the inferences that can be drawn about ecological systems.

Freshwater experiments can be conducted over time periods that are either too short or too long. Leibold et al. (1997) attribute different patterns of experimental versus naturally occurring phytoplankton-zooplankton relationships to the short duration of experiments that have investigated these relationships, regardless of the size of the unit in which experiments were carried out. They attribute these differences to a reduced scope of possible outcomes in enclosure experiments due to the reduced potential for changes in community composition, and thus ecosystem function. Most freshwater experiments have been conducted

with a relatively short duration. In a recent review, Lodge, Blumenshine et al. (1998) found a geometric mean of experiment durations of 29 days in 327 studies. In short experiments, an absence of longer-term processes and indirect effects can accentuate the role of direct interactions (Ives 1995; Diehl and Kornijow 1997; Leibold et al. 1997; Sarnelle 1997). Although some experiments have attempted to evaluate the influence of experimental duration (Lodge, Blumenshine et al. 1998) or the generation times of study organisms (Ives et al. 1996), the relationships of these variables with physical and biological complexity remain unclear.

Some experiments are also too long. When enclosure effects increase over time, such as the growth of periphyton on chamber walls, the differences between a mesocosm and a natural system will magnify as an experiment proceeds. Temporal factors such as the life spans of keystone organisms and the growth rates of important system components are critical experimental considerations.

The size of enclosures can influence experiments in a variety of ways. Enclosures can operate through direct effects on physical conditions and by constraints on the movement and behavior of larger organisms. The walls of an enclosure can have dramatic impacts on experimental conditions by exaggerating the influence of attached organisms relative to natural situations in lakes and streams (Bloesch et al. 1988; Lyche et al. 1996). Enclosure effects can also exclude processes from freshwater experiments that are important in natural settings. For example, mixing patterns and thus the horizontal and vertical diffusion of heat and material, turbulence, light penetration, nutrient sources, and nutrient concentration can be substantially altered by enclosure effects (Bloesch et al. 1988). Other factors, such as seasonal weather cycles, physical disturbances, or colonization will be very different in enclosures than in lakes or streams (Polis et al. 1996). Many organisms, particularly large fishes, may not survive in enclosures and, even if they survive, their behavior can be substantially influenced by container conditions. Community responses to treatments will be constrained to those processes that can operate within the size of an experiment's enclosure. If large-scale processes operating in natural systems outweigh those that occur at smaller scales, some fundamental community and ecosystem patterns, along with responses to perturbations, will differ markedly between enclosures and natural settings.

Enclosures may limit the complexity of biological patterns and processes that can operate in experiments. Direct interactions may be

accentuated by spatial constraints in enclosures relative to natural settings. For example, a reduction of spatial heterogeneity favors observing direct effects of predation and competition because potential refuges and alternative food resources are diminished in simplified enclosure habitats (Sarnelle 1997). The isolation of lake habitats, communities, and ecosystem processes can be major artifacts of experimental enclosure design. Such components of lake and stream ecosystems do not function independently of each other. Although benthic and pelagic communities are often studied in isolation, even in natural settings, they are linked through competition for light and nutrients (Sand-Jensen and Borum 1991). Interactions of separate freshwater habitats must be a fundamental consideration of any experimental design, and of its evaluation.

Experiments dependent on including a full range of producer communities are particularly subject to difficulties when all habitats are not fully represented. For example, the contribution of benthic algae to whole-lake algal biomass and production may be substantial. Lodge, Blumenshine et al. (1998) suggest that the percent of whole-lake primary production due to benthic algae is higher in shallow lakes and may range from 35 to 95 percent of lake primary production for lakes with mean depth < 6m. The high surface area:volume ratios in most enclosure designs relative to lake habitats will exaggerate the importance of benthic communities. Studies that explicitly focus on pelagic organisms and processes may employ short experimental duration (days) or manual removal of periphyton on enclosure walls to compensate for wall effects (e.g., Bloesch et al. 1988; Hansson and Carpenter 1993; Lyche et al. 1996; Chen et al. 1997). In some instances, growth of periphyton on enclosure walls has been quantified to evaluate compensatory patterns of benthic and pelagic algal responses to nutrient additions (Hansson 1988; Mazumder et al. 1989; Blumenshine et al. 1997). Increases in near-surface phytoplankton with nutrient enrichment can also reduce light penetration and concentrate primary production in surface waters (Hansson 1988). Limitations on the spatial distribution of producer communities in an experiment must be a fundamental consideration in its interpretation.

The distribution of nutrients and the importance of different nutrient sources, particularly from distinct freshwater habitats, must be considered in any experiments where the level of primary production is an important factor. The full range of natural mechanisms of nutrient delivery and

uptake can be difficult to simulate in many enclosure designs. For example, nutrient inputs from allochthonous sources are important in many smaller lakes, but whether nutrients are derived from surface runoff, subsurface inputs, or other routes will affect spatial distribution of algal communities (e.g., Cole et al. 1990). In well-lit, lake-bottom communities, epipelagic algal mats affect sediment oxidation patterns and the release of phosphorus to the overlying water column (Carlton and Wetzel 1988). At higher nutrient-loading rates, increases in phytoplankton may retard production of light-limited benthic algae. Thus, in nutrient manipulation experiments, water-column nutrient-addition rates, duration, and benthic algal substrate type and area will interact to affect how and where algae accumulate in enclosures (Blumenshine et al. 1997). Investigations of the effects of nutrient additions, or other factors that act on lake production, need to consider whether enclosures are intended to simulate only open water communities in isolation or whether the effects of benthic communities are being considered as influencing phytoplankton responses to nutrient manipulations.

Enclosure can limit the potential for the inclusion of ecosystem feedback processes in experiments. Feedback processes are essential features of an ecosystem's behavior that account for much of its basic structure and function (DeAngelis et al. 1986). Feedback can be strongly influenced by scaling factors in experimental manipulations. For example, Forrester (1987) characterized major shifts in the behavior of living systems as signaling the displacement of control from one feedback configuration to that of another. Ulanowicz (1991) described at least eight properties of autocatalytic feedback that are nonmechanical in nature. Feedback can be viewed as an emergent property of ecosystems related to size, in the sense that, with an increase in the scale of observation, comes a greater likelihood that all the components of a feedback loop will be included. Failing but one member, a feedback loop loses its identity, along with associated properties, and becomes but a linear concatenation of a process. An enclosure that does not include all feedback loop components is incapable of incorporating realistic elements of ecosystem behavior.

Ulanowicz's (1991) considerations on feedback have special relevance for ecological experiments in enclosures. It is usually impossible to include representatives of all the elements of an ecosystem in a contained space. Furthermore, the limited spatial extent of enclosures can affect certain processes, such as feeding and predator avoidance, so as to

preclude these interactions from the dynamics. Thus, with ever smaller mesocosms comes the growing likelihood that species components or processes that are elements of a feedback loop will be excluded from the community. As a result, the associated feedback control will be excluded from the dynamics of the experiment and, following Forrester's (1987) observation, the behavior of the enclosed system might come to depart significantly from that of the natural system it is intended to simulate. The influence of starting conditions that are specific to experimental enclosures may also result in different trajectories of experimental and natural systems, suggesting different controlling factors and therefore raising the potential for errors with extrapolations to natural situations (Bloesch et al. 1988).

Experiments intended to examine particular ecosystem processes may have special limitations. In experiments to examine how grazing by herbivores modifies algal assemblages (reviews in Brett and Goldman 1997; Leibold et al. 1997), herbivore grazing pressure is commonly manipulated through initial stocking, sieving grazers from enclosures, or indirectly by manipulation of plantivorous fish. Sieving may unintentionally remove some nontarget plankton, such as larger algae (Bloesch et al. 1988), and result in weaker contrasts in grazer assemblages between treatments especially with respect to body size (Cottingham et al. 1997; Persson 1997). Sieving may also represent an important export of nutrients from nutrient-poor systems. In some enclosure experiments where grazing pressure has been modified by the manipulation of planktivorous fish, results have typically compared well with patterns in natural lake communities (e.g., Mazumder et al. 1989; Hansson and Carpenter 1993; Vanni et al. 1997). This may occur because of the inclusion of fish effects on nutrient cycling, such effects being absent in experiments that rely on sieving. Grazer-manipulation experiments can be conducted in a variety of ways and must be interpreted with specific cautions that are in some ways similar to those in other freshwater experiments.

The use of fish in enclosures is another experimental design that can be difficult to extrapolate to natural settings. Lakes differ substantially in the composition or abundance of their fish assemblages much more than simply in terms of fish presence or absence. The effects of fish predation on prey communities in lakes may operate over a gradient of fish-predation pressure (Blumenshine et al. 2000). Interannual differences in weather conditions can affect over-winter survival or spring recruitment of fish and their prey. A limited range of seasonal effects in enclosure experiments

could, for example, overemphasize the importance of predation for prey communities, thus masking the importance of other processes.

An additional consideration for enclosures involves the spatial distributions of fish that are often dictated by behavioral interactions of predator and prey species. Some aggregative or refuge-use patterns in response to the presence or absence of a predator may be observed in relatively large enclosures, but patterns observed in natural settings may operate on larger spatial and temporal scales than can be observed in enclosures (Eklov 1995). Other organisms may be concentrated in particular lake habitats such that predator-prey interactions and their resulting community patterns may be expected to extrapolate well to enclosure experiments. Lodge, Stein et al. (1998) were able to realistically compare snail, crayfish, and pumpkinseed sunfish distributions in littoral communities from laboratory aquaria and field cages to distributions within lakes. Predator and prey variability patterns on a whole-lake scale are linked with factors on spatial and temporal scales that would not be incorporated in most enclosure experiments and support the suggestion that enclosures enhance direct interactions relative to indirect factors that occur in natural systems in equilibrium (Diehl and Kornijow 1997; Englund 1997; Sarnelle 1997). A primary challenge for freshwater experiments is not only to determine which processes control the patterns of interest, but to resolve the spatial and temporal boundaries of each process and to determine why these change with scale (Fisher 1994).

ASSESSING RESPONSES IN FRESHWATER EXPERIMENTS

The responses in an experiment can be assessed with variables that reflect very different scales of resolution. The degree to which organisms in a community are identified separately, or the degree of taxonomic aggregation (e.g., to species, genera, families, etc.), are critical scale considerations when assessing how an ecosystem responds during experimental manipulations (Frost et al. 1988). In some ways this can be considered as parallel to space and time in the design of an experiment but taxonomic aggregation is fundamentally different from spatial or temporal scales of an observation. The extent of taxonomic aggregation is frequently driven by an observer's experiences and perspectives. Its extent has important consequences for the ways in which system processes are perceived.

Two examples of different kinds of taxonomic aggregation illustrate how levels of aggregation can provide very different kinds of information about an ecosystem. When evaluating the primary-producer community in a lake, an investigator can assess the biomass present for each of the 30 or more species that are likely to occur in the algal community present in a liter of water. Alternatively, the photosynthetic potential of the same community can be evaluated by quantifying the total amount of chlorophyll present in the same liter. Obviously, knowing all about the species present in the producer community provides much more detailed information than does quantifying total chlorophyll. The effort necessary to obtain this detailed information, however, is much greater than that needed to measure total chlorophyll and there are many assessments of producer communities in fresh water for which the chlorophyll concentration provides all of the information that is needed. Moreover, it appears that predictable and understandable responses by phytoplankton, even to fairly major nutrient additions, are those that are closer to the total chlorophyll measurements than to assessments of individual phytoplankton species (Cottingham and Carpenter 1998).

Responses to nutrient additions contrast with the effects of acidification for zooplankton (Frost et al. 1995) and for phytoplankton communities (Schindler et al. 1985). In response to acid additions, individual species provide much stronger responses than aggregated variables like total biomass or production. For example, in a paired-basin, whole-lake acidification experiment, some individual zooplankton species showed dramatic declines with acidification (figure 9.1). At the same time other zooplankton species increased substantially as pH decreased (figure 9.2). Increases by some species were sufficiently large that they masked declines in the total biomass of major groups of zooplankton or in the entire zooplankton community (Frost et al. 1995). Different responses at different levels of aggregation were quite evident in these responses. An integrated measure of zooplankton community composition provided by a similarity calculation comparing the relative biomass of the members of the zooplankton communities in the treatment and reference basins showed an early response to acid effects (figure 9.3). In contrast, the difference in total zooplankton biomass between the treatment and reference basins responded at a later stage of the experiment and never exhibited as substantial a difference as the similarity index (figure 9.3). Phytoplankton species showed a similarly higher sensitivity to acid effects than total algal biomass or production (Schindler et al. 1985).

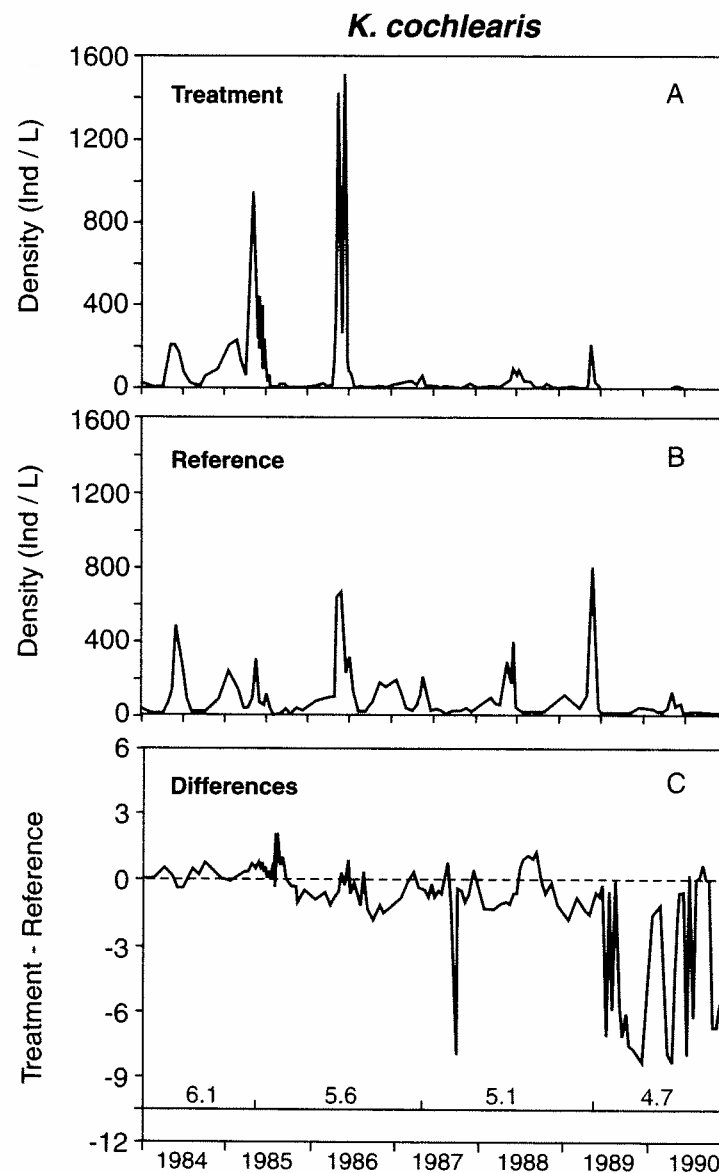


FIGURE 9.1 Abundance of *Keratella cochlearis*

Abundance of *Keratella cochlearis* in Little Rock Lake from 1984 to 1990 in (A) the treatment basin and (B) reference basin, and (C) differences between the log₁₀ (treatment abundance + 1) and the log₁₀ (reference abundance + 1). (From Gonzalez and Frost 1994) Ind = individuals.

This contrast between responses to two different forms of ecosystem stress illustrates important ways that ecosystem responses can be

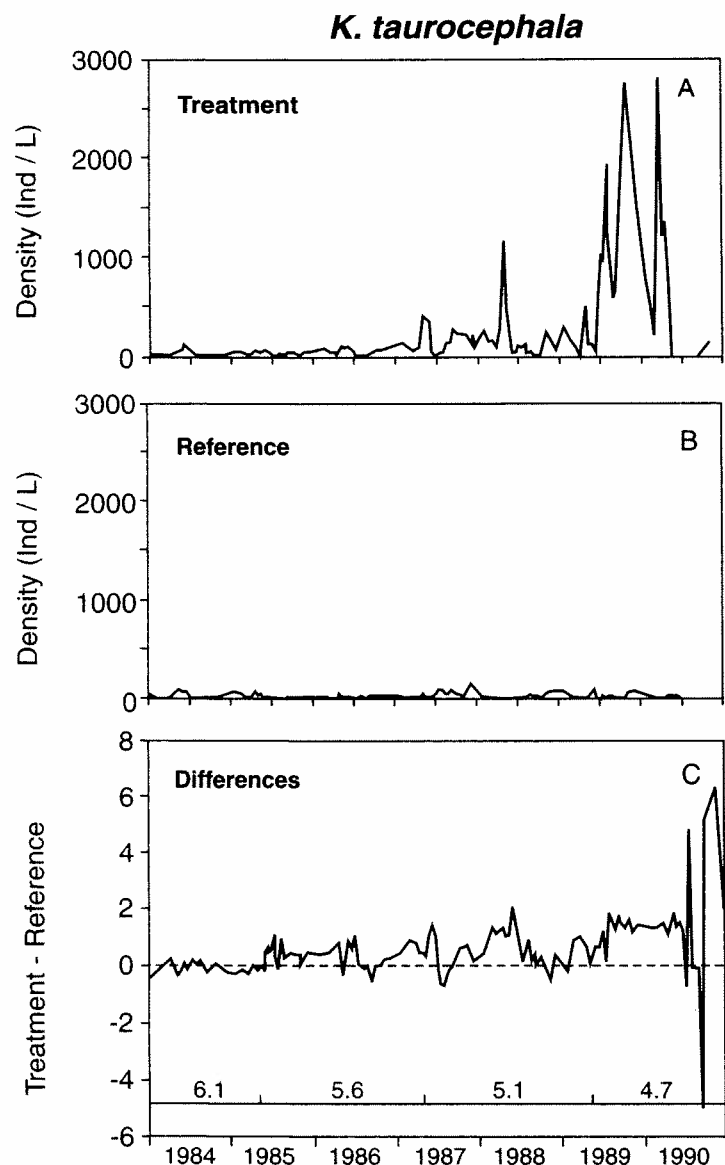


FIGURE 9-2 Abundance of *Keratella taurocephala*

Abundance of *Keratella taurocephala* in Little Rock Lake from 1984 to 1990 in (A) the treatment basin and (B) reference basin, and (C) differences between the $\log_{10}(\text{treatment abundance} + 1)$ and the $\log_{10}(\text{reference abundance} + 1)$. (From Gonzalez and Frost 1994) Ind = individuals.

perceived quite differently. In attempting to optimize the amount of information that can be obtained in evaluating ecosystem processes in

experiments of any scale, there are important choices that must be made in terms of how to best evaluate a community's response.

A need to understanding human effects on ecosystems is a driving factor in much present-day environmental research. In assessing human effects, the choice of an appropriate aggregation scale has strong potential for maximizing understanding, particularly in optimizing the information obtained from sampling efforts that are limited by financial resources. In assessing ecosystem stress, investigators have to consider which level of aggregation provides the best way to assess system condition, options that range from individual species to the total mass of organisms performing an ecosystem function. In choosing an effective indicator, sensitivity to stress must be weighed against the variability that a variable would exhibit in a habitat if no stress were present (Frost et al. 1992). Both sensitivity and variability will differ among variables that aggregate different numbers of taxa. Functional compensation limits responses to stress by aggregated zooplankton variables (Frost et al. 1995). Not all species are sensitive to a stress, however, and a variable at an intermediate level of

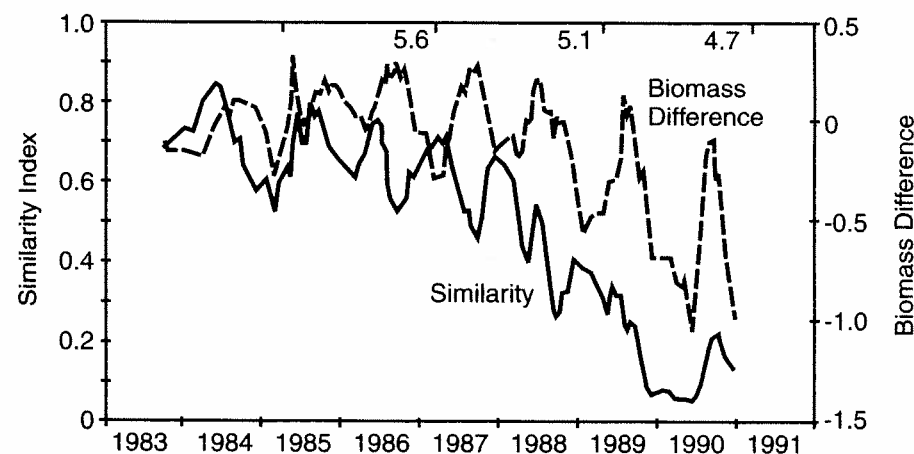


FIGURE 9-3 Zooplankton Species Similarity and Biomass Difference

Similarity in species composition and differences in total zooplankton biomass between the treatment and reference basins of Little Rock Lake calculated for all sampling dates between 1983 and 1991. Both were smoothed using five-point moving averages. Similarity was calculated following Inouye and Tilman (1988). The differences in biomass were calculated following Stewart-Oaten et al. (1986) as $\log(\text{Treatment Biomass}) - \log(\text{Reference Biomass})$. Original biomass units were $\mu\text{g/L}$. (From Frost et al. 1995)

aggregation might provide a more generally detectable response to a variety of stresses than would individual species. The consideration of different levels of aggregation itself can generate important insights into basic ecosystem properties (Frost et al. 1995).

EXPLICIT TESTS OF SCALING GRADIENTS

Some evaluations have been undertaken to investigate directly the effects of different scales of experimental treatments on perceptions of fundamental ecosystem processes. In some cases, these studies have involved direct experimental manipulations that have compared driving factors along distinct gradients to reveal important ecological principles. Some investigations have also used mathematical models to evaluate gradients of experimental conditions. Using either approach, researchers have developed understandings of the roles of key environmental factors.

A clear example of using a gradient of different forms of enclosures comes from estuarine studies. Petersen et al. (1997) conducted experimental tests on the effects of the size and the configuration of experimental enclosures. They employed two series of enclosures. The first had a constant depth as volume changed from 0.1 to 1.0 to 10 m³ while the second had the same shape, with a constant radius:depth ratio of 5.6 across the same range of volumes (figure 9.4). Using these series, they were able to demonstrate that gross primary productivity in Chesapeake Bay was limited by different ecosystem features during different seasons. During spring when nutrients were abundant, productivity per unit surface area or per unit light energy received was constant across the enclosures with a constant shape (figure 9.5a), consistent with the control of productivity by the availability of light. In contrast, during summer when nutrients were low, productivity was constant per unit volume and increased per unit area in the enclosures with greater depth (figure 9.5b), consistent with nutrient limiting conditions. The summer pattern in the enclosures was shifted toward spring conditions when nutrients were added to enclosures. During fall, enclosures exhibited patterns with elements of those seen during both spring and summer suggesting a combination of light and nutrient limitation (figure 9.5c). The different controlling factors in Chesapeake Bay were revealed from these evaluations of gradients of small enclosures. Similar patterns are likely in freshwater studies.

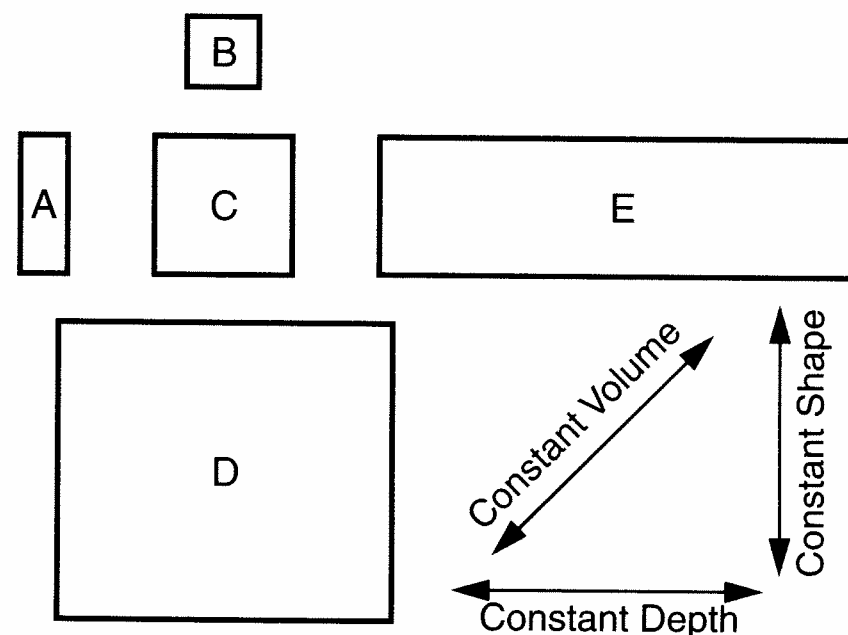


FIGURE 9.4 Experimental Ecosystem Size and Shape Experiment

Scale diagram of relative sizes and shapes of cylindrical experimental ecosystems viewed from the side. Constant-depth series (A, C, E; depth = 1 m) and constant-shape series (B, C, D; radius/depth = 0.56) intersect at the intermediate 1-m³ C mesocosms. A and B both have a volume of 0.1 m³; D and E both have a volume of 10 m³. Three replicates of each mesocosm type were constructed. (From Petersen et al. 1997)

In a modeling exercise, Englund (1997) examined how enclosure size affects the interpretation of predator-prey interaction patterns, and the mechanisms generating these patterns. His models suggested that the size of enclosures in predation experiments that allow prey to move in and out of the experimental unit affects the perceived importance of particular mechanisms such as prey behavior or direct predation compared to underlying predator-prey interactions. Prey movements had less effect on prey densities in larger enclosures, whereas predation mortality was independent of experimental-unit size.

The effects of an herbivorous zooplankter, *Daphnia*, on a natural community of microzooplankton were compared across two different-sized mesocosms and in a whole-lake setting where a fish kill provided a natural experiment (Sarnelle 1997). *Daphnia* effects varied substantially with the type of experiment. The magnitude and direction of *Daphnia* effects on microzooplankton depended on the experimental setting. Not surprisingly, and perhaps reassuringly, results in the larger mesocosms

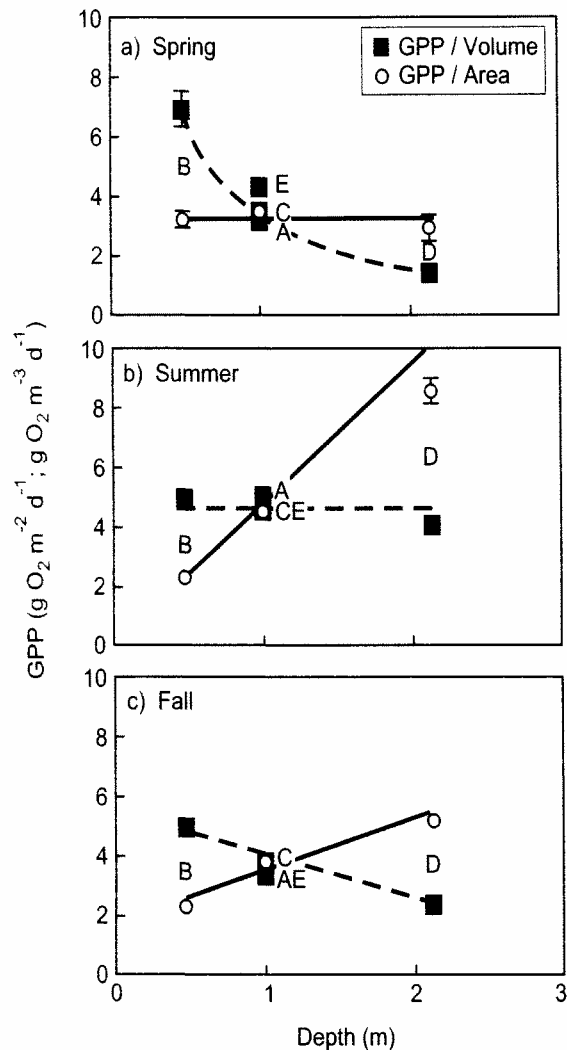


FIGURE 9-5 Primary Productivity in Size and Shape Experiment

Gross primary productivity averaged over prenutrient pulse period for each dimension of mesocosm in spring, summer, and fall experiments (GPP). GPP is expressed both per unit volume (closed squares) and per unit area (open circles). In (a), the dashed line through GPP per unit volume is from equation 6 in Petersen et al. (1997). Note that this describes a hyperbolic relationship between GPP per unit volume and depth. In (b), the continuous line through GPP per unit area is from equation 9 in Petersen et al. (1997). Continuous and dashed lines in (c) are lines of best fit. Error bars are ± 1 SE of the mean. Bars are excluded in cases where the error is smaller than the diameter of the symbols. (From Petersen et al. 1997)

were most similar to those that occurred in the whole lake. Understanding the reasons for such scale-induced differences can reveal fundamental aspects of the nature of interactions among different ecosystem components.

Finally, considering a different sort of gradient, Gonzalez and Frost (1994) tested the extent to which zooplankton responses during a whole-lake acidification experiment could be predicted by standard laboratory bioassays. Two rotifer species had responded markedly to acid additions in Little Rock Lake, Wisconsin. *Keratella cochlearis* populations decreased with acidification (figure 9.1) but *K. taurocephala* abundance increased dramatically (figure 9.2), becoming the dominant rotifer species at the lowest pH stage of the experiment. Laboratory assays were not at all effective at predicting in-lake responses, however. Assays were able to predict that *K. cochlearis* would decline, but only when increased acidity was combined with reduced food availability. Laboratory experiments with feeding *ad libitum* demonstrated no sensitivity by *K. cochlearis* to acid levels. For *K. taurocephala*, responses differed even more sharply between the lake and the laboratory. Laboratory assays suggested that *K. taurocephala* population growth rates would be diminished under acid conditions. They gave no indication of its eventual tremendous proliferation in the lake's treatment basin during experimental acidification. Certainly predictions based upon these laboratory experiments were of limited utility in predicting responses when a whole lake was acidified.

The extreme differences reported between laboratory and lake conditions emphasize how difficult extrapolations from artificial to natural conditions can be. At the same time, systematic consideration of scale differences in experimental systems can reveal much about ecosystem conditions. Even the work that demonstrated the difficulties of predicting in-lake effects from laboratory bioassays (Gonzalez and Frost 1994) was also able to confirm that the shifts occurring with acidification in the treatment basin were driven by indirect, food-web related mechanisms rather than the direct effects of acidification (Webster et al. 1992). Scaling issues have a bearing on the numerous aquatic experiments that make use of enclosures but they are not considered explicitly in much of this work (Petersen et al. 1999), even to the point that many papers do not report the dimensions of the enclosures used in the experiments. Enclosure experiments are essential in increasing the basic understanding of ecosystem function but they can be much more

useful if they consider scale issues directly as the examples we have provided demonstrate.

LESSONS TO BE LEARNED FROM UNREALISTIC EXPERIMENTS

Experimentalists frequently attempt to simulate natural ecosystems in order to evaluate fundamental processes, but realistic experiments do not provide the only opportunity to develop an understanding of factors controlling ecosystems. Allen (this volume) illustrates some very different ways that realistic and unrealistic experiments can be used to understand ecosystem processes. In a simple dichotomy, the assumptions underlying experiments can be classed as realistic or unrealistic. Likewise, the results of experiments can be categorized as reasonably representative of natural conditions or not. When realistic assumptions generate reasonable results, experiments can be used to evaluate the effects of factors that have been manipulated as reflecting close-to-natural conditions. Such situations can be replicated in a systematic fashion to evaluate the effects of a factor being manipulated. This is the standard situation that is usually sought in experimental work.

A less obvious source of insights can also derive from unrealistic assumptions in experiments. If results clearly do not represent natural situations, an experimenter has results that are highly predictable but not very useful. For example, if the oxygen is exhausted from a mesocosm, it is not surprising if fish do not survive. Unexpected results, however, can provide very important insights into fundamental system-organizing processes. The mud minnow, *Umbra limi*, does not die in chambers from which oxygen has been exhausted if there are bubbles present because it is capable of gathering oxygen from bubbles that are typical under ice in many mud-minnow habitats (Magnuson et al. 1983). This result has helped to explain the overall distribution pattern of fish communities in lakes across northern Wisconsin (Tonn and Magnuson 1982). It also illustrates critical tradeoffs that occur between adaptations to extreme environments and survival capabilities in interactions with other species. The mud minnow's unusual ability to survive oxygen stress allows it to prosper where other fishes can not. Mud minnows are, however, extremely vulnerable to the effects of oxygen-stress-intolerant fishes when oxygen is present. Mud minnows dominate only in habitats with oxygen stress. A fish experiment without oxygen may have seemed

unrealistic but it revealed the mud minnow's unusual adaptations to a unexpectedly wide range of habitats.

Experiments that are too long but that continue to produce realistic results can serve as other examples of surprising situations that have the potential to provide insights into the nature of ecosystem processes. In such cases, ecosystem processes are much more resilient to the time-related effects of an experiment than would originally have been anticipated.

One major justification for the use of simple experimental systems is their ability to eliminate variables to determine the degree to which unnatural conditions can result in natural behavior. This situation parallels what occurs in successful system modeling. For example, axenic cultures can be used to assure that nutrient uptake or formation of a particular compound is caused by a particular alga alone and not by associated microbes or by microbe-algal interactions. Information on single and paired algal cultures has been useful in explaining dominance shifts in more complex systems that contain multiple species of algae, bacteria, and grazers (Rose et al. 1988).

Properties controlled by a dominant process can be easier to predict, repeat, and model than properties that result from several interacting processes. For example, in interlaboratory testing of Standardized Aquatic Microcosms (SAMs) (Taub 1993; American Society for Testing and Materials 1996), nitrate depletion in controls was highly reproducible, and fairly easy to model, whereas the time for recovery from CuSO_4 toxicity was more variable between experiments, and more difficult to model (Swartzman et al. 1990; Taub 1993). The CuSO_4 recovery process depended on the balance of many variables (e.g., growth of the least sensitive algal species, production of dissolved organic matter, and development of alkaline conditions) and, whereas the sequences of recovery were similar in different experiments (Conquest and Taub 1989), the time of recovery was highly variable (Meador et al. 1993). Experimental work can be used to develop an understanding of ecosystem processes by evaluating simple phenomena rather than mimicking a natural system.

In natural temperate ecosystems, the intensity of light and its spectral distribution undergo highly predictable diurnal and seasonal changes. In many indoor microcosm facilities such as the SAMs, however, light is supplied on an on/off basis for the same number of hours per day and at the same intensity throughout an experiment. In spite of the simplification of the light regime, SAM communities underwent sequences similar to spring algal blooms, zooplankton blooms, and

summer "clear-water" phases in a 63-day experiment (Taub 1993). The mechanism driving these phenomena, as demonstrated in a simulation model, involved nutrient dynamics and toxicants that delayed nutrient uptake by the algae and shifted the overall alga cycle (Swartzman et al. 1990; Conquest and Taub 1989). These results suggest that the natural light cycle (varying intensity during the day and increasing duration from spring to summer) was not required to generate typical seasonal behavior. Indeed, many aquatic microcosm facilities have not attempted to supply light in a realistic manner. In other situations where the effects of different light regimes have been tested experimentally, however, they have been linked with the overall structure of freshwater phytoplankton communities (Litchman 1998). Different ecological processes appear to vary in their sensitivity to light regimes but light conditions must be considered as a factor in many enclosure-experiment designs.

If a model system is developed so that specific simple properties or purposes are met, artifacts do not have the same effects that they would if a system were designed to simulate natural situations. This is analogous to a physics experiment that explores the properties of an object moving on a frictionless plane. As long as the properties of the plane are reasonably frictionless, the experimental results can be informative, although they do not completely simulate a natural system, and ideal conditions cannot be met. Taub (1969a, 1969b) examined the behavior of three gnotobiotic ecosystems that contained (1) a single species of alga, (2) that species with a single protozoan grazer species, and (3) the alga and grazer with three species of bacteria. Some responses of the systems were reasonably similar. Of course, the outcomes could have been different if container size, light intensity, nutrient levels, and so on had been different. These experiments were not intended to replicate natural systems but to use fundamental principles to explore the behavior of ecological systems. Experimental systems can be heuristic even when they do not mimic natural ecosystems.

FRESHWATER VERSUS ESTUARINE EXPERIMENTS AND ECOSYSTEMS

This chapter's arising from a workshop on scale considerations in experiments sponsored by the Multiscale Experimental Ecosystem Research Center (MEERC) warrants some direct comparisons between estuarine and freshwater systems. Contrasts between these habitat types reveal how different controlling variables are emphasized in manipulative

work in estuaries and fresh water but also illustrate some features common to experiments in both habitats.

Critical chemical factors provide some of the sharpest contrasts between estuarine and freshwater experiments. Ionic strength, and its variability, is one of the defining differences between estuarine and freshwater ecosystems. Fresh water typically contains only limited amounts of dissolved salts, whereas estuaries can have much larger amounts of salts, and they can be quite variable. Estuarine experiments must consider salinity as a controlling variable for a wide range of processes, whereas it is a minor factor in most freshwater manipulations. Salinity is characterized by mass, which does not lend itself to the same types of scale considerations as extensive variables such as time or size.

Another chemical factor, the concentration of hydrogen ions, generates major differences both among and within freshwater ecosystems but only exhibits minor differences within estuaries. The pH of freshwater habitats has figured extensively in investigations of critical processes in lake ecosystems (e.g., Schindler et al. 1991), but pH is not typically given special consideration in estuarine studies. Of course, other intensive chemical variables such as the concentrations of N or P are critical in both freshwater and estuarine ecosystems, but these intensive variables too are not subject to the same scale considerations as extensive variables.

Nutrient levels have certainly figured prominently in MEERC programs and other estuarine research, but considerations for estuaries do not typically extend to oligotrophic conditions. Are there any modes of behavior in oligotrophic aquatic ecosystems that are not found in relatively more productive estuaries? One fundamental difference may be an absence of mutualistic or positive feedback interactions among organisms. Such relationships can be fairly common in nutrient-poor environments (e.g., tropical oceans, open-ocean gyres, and oligotrophic lakes and wetlands) where algal-invertebrate symbioses occur, in sponges (Wilkinson 1987; Frost 1991) and corals (Reisser 1992), and where periphyton-carnivorous plant interactions (Knight and Frost 1991; Ulanowicz 1995) exist; they are relatively rare in estuaries.

Most important perhaps, freshwater and estuarine ecosystems differ in their degree of openness or their connection with surrounding ecosystems. Many freshwater ecosystems occupy a concave topography, that is, they are situated at a low point of the surrounding landscape. Gravity tends to bring not only water into such systems but also nutrients, sediments, and detritus that have been washed off the surrounding watershed. As a result,

lakes tend to become progressively more eutrophic and experience directional succession over time. Estuaries also serve as traps of nutrients, sediments, and toxins (Odum 1970), but they are fundamentally different physical habitats than lakes. Long-term trends in conditions in estuaries may exhibit different or less directional trends over time than in lakes and other freshwater ecosystems because estuaries are open to the sea. Differences in the degree of openness of estuaries and freshwater habitats may lead to fundamental differences in the ways that microcosms relate to natural freshwater and estuarine ecosystems.

These differences do not suggest, however, that there are not common processes and problems in freshwater and estuarine ecosystems. Controls over primary production by nutrients or light (Petersen et al. 1997) and the combined potential influence of bottom-up and top-down processes on food webs (Carpenter and Kitchell 1993; Micheli 1999) are two obvious examples of phenomena that characterize both habitat types. Similarly, human-generated eutrophication is a major problem in both habitats (Paerl 1988). Eutrophication is driven primarily by P inputs in freshwater ecosystems but by N in estuaries (Paerl 1988), of course, again reiterating fundamental differences between estuaries and fresh water. Most important, however, some techniques for extrapolating from experiments to understanding the functioning of natural ecosystems are applicable in fresh water and in estuaries.

COMMENTS

The points that we have raised have shown that a number of cautions must be borne in mind when evaluating freshwater ecosystems by experiments. Care in interpretation is necessary even when experiments are conducted in whole ecosystems and certainly when they are carried out in enclosures. At the same time, we have presented ample evidence for the diverse ways that the fundamental understanding of ecosystems depends upon experimental work that is typically conducted in enclosures. Some experiments can be designed to reasonably simulate natural ecological processes. Other experiments that have been conducted under conditions that are far from realistic can still be useful when they systematically evaluate gradients of experimental effects or when they produce surprisingly realistic results. A wide range of differently scaled experiments that are interpreted with proper care is essential for increasing the general understanding of ecosystem patterns and processes.

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