
CHAPTER 5

Getting It Right and Wrong *Extrapolations Across Experimental Scales*

Michael L. Pace

EXPERIMENTS IN ECOLOGY ARE CRITICIZED FOR MANY SINS ranging from poor designs (Hurlbert 1984; Underwood 1994) to irrelevance (Peters 1991; Carpenter 1996; Resetarits and Bernardo 1998). These criticisms reflect, in part, a significant concern about relating experimental results to ecological reality. Simply put, how do we use what we learn in experiments? Ideally, experiments reveal interactions, expose underlying mechanisms, and support or refute models. There remains, however, a critical problem about how to relate even the best experiments to the ecological systems of ultimate interest, because results may include scale-dependencies that do not extrapolate.

In considering this problem, two general types of experiments can be distinguished. In one case, a question is tested using a contrived population, community, or ecosystem in a laboratory or quasi-laboratory setting. The Ecotron facility in the Centre for Population Biology at Silwood Park in Ascot, England, is a good example of such a system (Lawton 1996). Here, artificial ecosystems have been created and replicated to carry out controlled experiments that focus primarily on generality, testing key concepts and theoretical models. Extrapolation to a specific field situation is not a direct goal. The hope is for experimental results to be indicative of general interactions and so help illuminate important mechanisms operating in nature, perhaps in a diversity of systems. A second general class of experiments has a more system-specific focus. In these experiments the emphasis is on quasi-realistic conditions. Typically, natural assemblages of organisms are used. These experiments are often referred to as "field experiments." A primary goal of these experiments is extrapolation. The hope is that significant regulatory

factors and interactions revealed in the experiment will generalize to the field (i.e., nonexperimental) situation.

A key element in the evaluation of "field experiments" and in the translation of experimental results to understanding is the issue of extrapolation. A number of questions are relevant. How do we extrapolate results? Can we scale up results of experiments conducted at small scales to larger scales of interest? How do treatments imposed in experiments relate to variability observed in natural systems? What ecological interactions create artifacts in experiments, thereby inhibiting extrapolation? These are crucial questions, particularly for what I have labeled "field experiments," because these studies have direct extrapolation as a primary goal. Surprisingly little emphasis, however, is placed on the problem of extrapolation. For example, the general questions posed above about extrapolation of experimental results are not directly treated in recent philosophically oriented texts on ecology (e.g., Peters 1991; Shrader-Frechette and McCoy 1993; Pickett et al. 1994) or in works on experimental ecology (e.g., Hairston 1989; Wilbur 1997). For most research reporting field experiments, consideration of extrapolation is at best relegated to a few paragraphs of discussion. Extrapolation is rarely the subject of a more formal analysis. The neglect of extrapolation, therefore, is a serious blind-spot in experimental ecology. Without understanding the context and limitations of experiments, we cannot build a predictive science.

The goal of this chapter is to explore the concept of extrapolation in the context of experiments. The focus is on aquatic experiments that manipulate nutrient loading and predation and assess responses at the community and ecosystem levels. I begin by defining extrapolation and providing an example of successful extrapolation. This result illustrates the utility of comparative frameworks in extrapolation. I then compare responses of plankton in enclosures and corresponding whole lake experiments to evaluate if enclosure experiments predict responses at the ecosystem level. I evaluate lake ecosystem processes related to success or failure in extrapolation. I argue that experimental research is best done simultaneously with research carried out on the object of interest (i.e., the population, community, or ecosystem of concern) in order to promote ongoing comparisons between experimental results and field observations. Specifying scales of interest and a more careful evaluation of extrapolation should enhance experimental research and facilitate the evaluation of results obtained from multiple approaches.

SUCCESSFUL EXTRAPOLATION: AN EXAMPLE

Extrapolation has a specific meaning in statistics—"to estimate the value of a variable outside its . . . range" and a more informal meaning in common use—"to infer (that which is not known) from that which is known; conjecture" (*Random House Dictionary of the English Language*). Experimentalists think in terms of both meanings. Experimental conclusions are used to infer significance of a process in the field. The first meaning of extrapolation also has significance, however, because an objective may be to project the value of a variable measured in an experiment to the natural situation where the range of variation may be greater than observed in the experimental unit.

To explore ecological extrapolation, it is useful to begin with an example. A nutrient fertilization experiment was carried out in mesocosms at the Marine Ecosystems Research Laboratory (MERL) of the University of Rhode Island. The MERL tanks were amended with nitrogen, phosphorus, and silica over a concentration range from no loading to 32 times the background value (Nixon et al. 1984; Oviatt et al. 1986). Hobbie and Cole (1984) measured the responses on planktonic bacteria in these enclosures and found, not surprisingly, that bacterial production increased in correspondence with nutrient loading and primary production. Bacterial production was a strong, linear function of primary production based on means from each enclosure (figure 5.1). Cole et al. (1988) subsequently compared these results with data drawn from the literature for a wide variety of aquatic systems that covered a gradient of trophic conditions. Does this relationship extrapolate either quantitatively or qualitatively to reflect the general pattern of primary and bacterial production? The answer is yes on both counts. The bacterial-primary production relationship derived from the MERL tanks is the same as the relationship derived from field studies in marine and freshwater systems (figure 5.1).

The relationship observed in the MERL tanks extrapolates to the general situation. The MERL tanks, in terms of pelagic bacterial production, are representative of a class of systems observed in nature. What is the basis for this successful extrapolation? First, the microbial system in the 13 m³ MERL tanks contained at any time > 10¹³ bacteria, and there were on the order of 50 to 200 generations produced over the six-month course of the experiment (Hobbie and Cole 1984). Thus, the time and spatial scales of the experiment were "large," and so, unlike the outcome of many

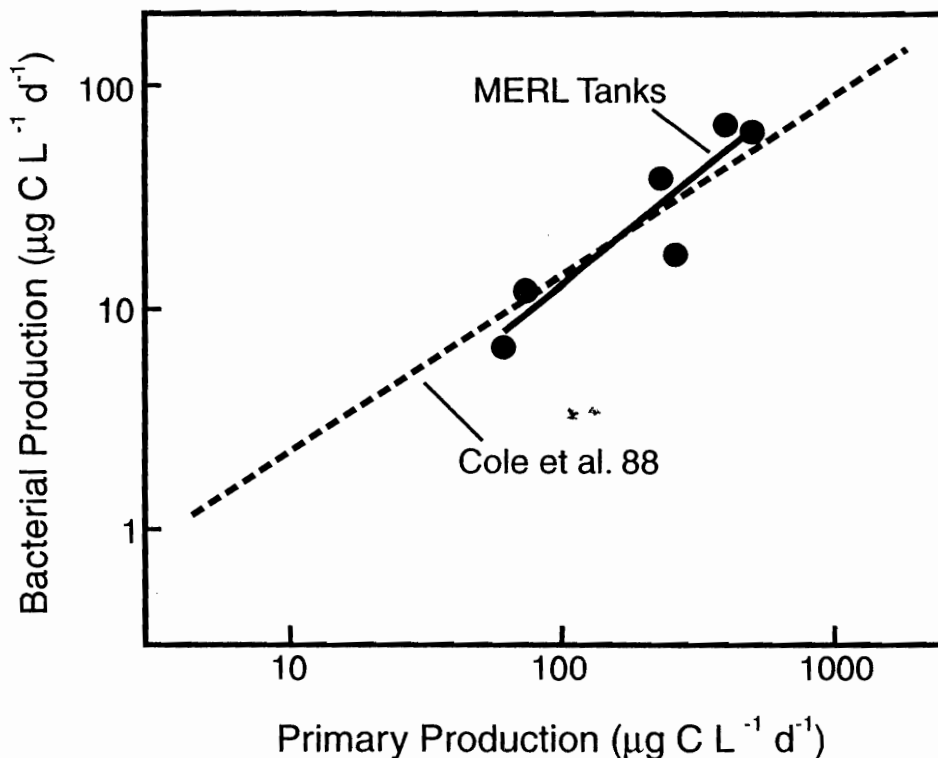


FIGURE 5.1 *Production and Scale*

Relationships between primary and bacterial production in MERL (Marine Ecosystems Research Laboratory) enclosures in comparison with a general relationship derived from the literature by Cole et al. (1988). Each point on the graph is the mean for a tank along a nutrient-loading gradient as measured by Hobbie and Cole (1984). Lines are least square regressions.

experiments (Tilman 1989), the observed response is not a transient. Second, the MERL systems were designed to realistically simulate estuarine systems in a number of ways—including water exchange, temperature, mixing, and light regimes (Oviatt 1981, 1994). These regimes yield realistic patterns of phytoplankton primary production when compared to the adjacent estuary (Keller 1988). Thus, the MERL systems are most similar to the “field experiments” I discussed earlier in that considerable effort was made to create realistic conditions.

A third reason for successful extrapolation was that the experiment created a significant gradient of two major factors regulating bacterial responses—nutrient loading and primary production. Thus, the noise associated with variation in time and space within a particular system was small when compared to the response over the larger scale of comparison created by the experiment. Large manipulations are often most successful at revealing regulatory factors but, unlike the MERL situation, are difficult to create in many small-scale field experiments.

For bacterial production and other processes (Nixon 1992; Kemp et al. 1997), the MERL nutrient fertilization experiment serves as an example for how to assess extrapolation of results. A comparative framework based on a broad empirical relationship (bacterial production; Cole et al. 1988) made the evaluation possible by providing a context for the results.

COMPARATIVE FRAMEWORKS

Comparative analyses provide one foundation for extrapolation. Ecosystem studies can be helpfully organized along gradients of either processes or properties. Limnologists have developed a set of comparative frameworks for this type of analysis. The most significant process that organizes comparisons of lake studies is nutrient loading. For example, productivity of many trophic groups including phytoplankton, bacteria, zooplankton, benthos, and fish are strongly correlated with nutrient loading in lakes (Peters 1986). The lake framework, however, extends well beyond nutrient inputs. Some additional lake gradients include physical and geographic features related to lake size, landscape position, latitude, and shape. In addition, the loading of dissolved organic carbon is emerging as an important gradient for comparisons among lakes (Morris et al. 1995; Williamson et al. 1999). Oxygen dynamics (Nürnberg 1994), sulfate concentrations (Caraco et al. 1989), and fish community structure (Brooks and Dodson 1965) represent other features of lakes that are useful for organizing variation. A similar list could be developed for estuaries as well as other types of ecosystems. In the case of estuaries, the list, at a minimum, would include nutrient loading, estuary size and shape, tidal range, mixing regimes, freshwater input, and human population density in the watershed.

Further development of these comparative frameworks is an important challenge. Comparative frameworks are not only essential for extrapolation; they are also a foundation for theory. They represent major patterns for explanation. Of equal importance, integration of these frameworks provides a means to developing richer and deeper theory (Pickett et al. 1994). Current lake research provides an example of integration as a new focus develops on the interactions of nutrients, food web structure, and dissolved organic carbon (Carpenter and Pace 1997; Carpenter et al. 1998). Comparative analyses of many other ecosystem

types lag behind lake research. Again considering the case of estuaries, the lack of comparative analysis is partly due to logistic difficulties, but is also related to a dominance of site-specific studies in estuarine research.

EXTRAPOLATION AND LAKE ENCLOSURE EXPERIMENTS

One way to directly assess extrapolation is to compare similar manipulations done over different experimental scales. I have participated in experiments with colleagues that have considered how nutrient loading and food web structure regulate the abundance and variability of various trophic groups in lakes. Our group has conducted experiments in 45 L plastic buckets (Pace and Funke 1991), 2 m³ plastic bags (Cottingham et al. 1997), and whole lakes (Carpenter and Kitchell 1993; Carpenter et al. 1996; Pace and Cole 1996; Carpenter et al. 1998; Pace et al. 1998). These experiments were all conducted in the same set of lakes located at the University of Notre Dame Environmental Research Center in Gogebic County, Michigan. Here, I compare how well short-term enclosures with fixed manipulations extrapolate to responses observed in whole lake experiments. In addition, results of a longer nutrient loading experiment in enclosures are compared with a similar series of whole lake nutrient additions. In the lakes and experiments reviewed below, the cladoceran, *Daphnia*, was an important grazer and consisted of a mixture of two species, *D. rosea* and *D. pulex*, that were aggregated in counts and biomass estimates. These species are referred to collectively for convenience in this chapter as *Daphnia*.

Short-term Enclosures and Whole Lake Experiments: Responses of Heterotrophic Microbes to Fixed Treatments

Heterotrophic microorganisms including bacteria, flagellates, and ciliates tend to increase strongly in abundance across lake productivity gradients (e.g., Bird and Kalff 1984; Porter et al. 1985; Gasol and Vaqué 1993). Predation by crustacean zooplankton, especially on protozoa, can also be significant and potentially regulate the abundance of these organisms. For example, in one of our study lakes, Pace and Vaqué (1994) measured daily mortality rates of heterotrophic flagellates and ciliates due primarily to *Daphnia* in the range of 0.5–1 and 0.2–0.6 d⁻¹ respectively. These mortality rates are comparable to expected in situ growth rates. Thus, measurements

of rate processes indicate that resources and predators are potentially significant in determining the abundance of heterotrophic microbes.

We examined resource and predatory control as well as their interaction in two enclosure experiments (Pace and Funke 1991). These studies were conducted during 1988 and 1989 in two adjacent lakes, Paul and Peter, that are described in Carpenter and Kitchell (1993). The experiments were intentionally short term (4 d) and small scale (45-L enclosures) in order to avoid substantial changes in the manipulated factors (*Daphnia* and nutrients) over time. Bacteria responded positively to nutrients in both experiments—roughly doubling in abundance. *Daphnia* had no effect on abundance and actually increased bacterial productivity in one of the two experiments. Flagellates and ciliates responded positively to nutrients in three out of four cases and negatively to *Daphnia*. Reductions of flagellates by *Daphnia* were stronger in the presence than in the absence of nutrients resulting in significant or marginally significant interactions (Interaction P's = 0.002 and 0.06).

In a series of whole lake experiments beginning in 1991, we manipulated the fish communities of three lakes to create food web structures that either promoted (East and West Long lakes) or suppressed (Peter Lake) the dominant zooplankton grazer, *Daphnia*. A fourth lake (Paul) served as an unmanipulated reference. The three experimental lakes were subsequently fertilized with inorganic nitrogen and phosphorus beginning in 1993. Nutrient loads were at a constant ratio (N:P > 30:1 by atoms), but daily loading rate varied annually to represent a range of enrichments (summarized in Carpenter et al. 1998).

How well did the responses observed in the enclosure studies compare with the whole lake results? Enclosure results provided correct and incorrect predictions (table 5.1). For example, bacterial production increased in response to whole lake nutrient additions, and *Daphnia* had a strong negative effect on the dynamics and average abundance of ciliates. These results were in accord with extrapolations from the enclosures (table 5.1). Bacterial abundance, however, did not increase in the fertilized lakes, a result in contradiction with results from the enclosures (table 5.1). Instead, only specific growth rates (i.e., growth rate per cell) increased with nutrient loading (Pace and Cole 1996). In the enclosure experiments, flagellates increased with nutrient additions in 1 of 2 cases but did not increase in the whole lake experiments. Similarly, ciliates increased in response to nutrients in both enclosure experiments while increases with lake fertilization were observed in only one case (table 5.1). Negative

TABLE 5•1 *Responses of Heterotrophic Microbial Groups to Short-term Enclosure and Whole Lake Manipulations*

Group	Increases in Response to Nutrients		Declines in Response to <i>Daphnia</i>	
	Enclosure	Lake	Enclosure	Lake
Bacteria				
Abundance	2/2	0/3	0/2	0/3
Production	2/2	3/3	0/2	1/3
Flagellates	1/2	0/3	2/2	1/3
Ciliates	2/2	1/3	2/2	2/3

NOTE The responses are presented as number of significant increases in response to nutrient addition and significant declines in response to zooplankton over total cases. In the enclosure experiments, responses were judged significant if $P < 0.05$ for nutrient and zooplankton treatments in a factorial analysis of variance (significant interactions noted in text). In the whole lake experiments, responses were judged significant if t-values associated with time series model fits for the variables, phosphorus loading, and *Daphnia* biomass, exceeded 1.96 (approximately, $P < 0.05$).

responses by flagellates and ciliates to *Daphnia* in the enclosures were also evident in the lakes but were not observed as consistently.

In general, lake responses were more variable than those observed in the enclosures. This is not surprising given the limitations on dynamics and potential shifts in community structure imposed by design of the short-term enclosure experiments. Increasing enclosure size and experimental time might lead to better extrapolation as found by Sarnelle (1997) in experiments with *Daphnia galeata mendotae* and microzooplankton, but as discussed next, dynamic responses and potential artifacts can complicate longer-term enclosure experiments.

Long-Term Enclosures and Whole Lake Experiments: Dynamic Responses of Planktonic Communities

Before fertilizing the experimental lakes, we conducted an enclosure experiment to test the efficacy of the projected range of nutrient loads. Phosphorus (P) and nitrogen (N) were added at four levels (ranging from 0–2 $\mu\text{g PL}^{-1}\text{d}^{-1}$ at an N:P ratio of 25:1 by atoms). Across this nutrient loading gradient, half the enclosures were sieved weekly with a plankton net to remove large zooplankton. After conducting this enclosure experiment, we fertilized two basins in the same lake where the experiment was performed over the same range of loads. This allowed comparison of the longer-term enclosure results with whole lake results.

In the unsieved enclosures, algal biomass measured as chlorophyll a was similar to whole lake values when loading was $< 1 \mu\text{g PL}^{-1}\text{d}^{-1}$ but was very low relative to the whole lake responses at the highest loading (figure 5.2). This suppression can be attributed to the changes in the dominant zooplankton grazers, *Daphnia*. In enclosures, *Daphnia* dominated the zooplankton, and biomass was very high relative to the lake even at low loadings (figure 5.2). In the sieved enclosures, *Daphnia* biomass was reduced at nutrient loadings $< 1 \mu\text{g PL}^{-1}\text{d}^{-1}$ relative to the unsieved enclosures and corresponded more closely to lake conditions (figure 5.3). However, at the highest nutrient loading, weekly sieving was not sufficient to suppress *Daphnia*. Chlorophyll a was much lower in this treatment than observed in the lake at the same loading (figure 5.3). Although *Daphnia* was effective at suppressing phytoplankton in the whole lake experiments as documented elsewhere (Carpenter et al. 1996, 1998), the effect of *Daphnia* grazing was exaggerated in the enclosures.

Why did *Daphnia* achieve a higher biomass in the enclosures? Predation pressure was probably much lower in the enclosures as there were no fish and few invertebrate predators. The very high biomass of *Daphnia* even in unfertilized enclosures (figures 5.2, 5.3) supports this contention. Lack of predation, however, is not a complete explanation, because in one of the experimental basins, East Long, planktivory was also very low (Carpenter et al. 1998). Increased food may have promoted higher populations. Enclosures have large plastic surface areas relative to their volume, and these surfaces became enriched with periphyton (Blumenshine et al. 1997) that *Daphnia* is capable of browsing (Horton et al. 1979). In addition, recent studies have emphasized stoichiometric limitations in terms of C:P ratios for zooplankton (Hessen 1992; Sterner et al. 1993; Elser et al. 1996). The large increase in *Daphnia* populations at the lowest phosphorus loading (figures 5.2, 5.3) may partly reflect a release from poor food quality and severe phosphorus limitation. The same process should have occurred in the whole lake experiments but may have been less pronounced given losses of phosphorus from the surface of the stratified lake via sedimentation relative to the greater potential retention of phosphorus within enclosures on surfaces.

These comparisons of responses are based on mean values. A second and perhaps more important issue is variability. How well do enclosure experiments represent the variability at the whole lake scale under similar manipulations? Here, we can compare two metrics (chlorophyll a and bacterial production) measured in similar ways in the whole lake and

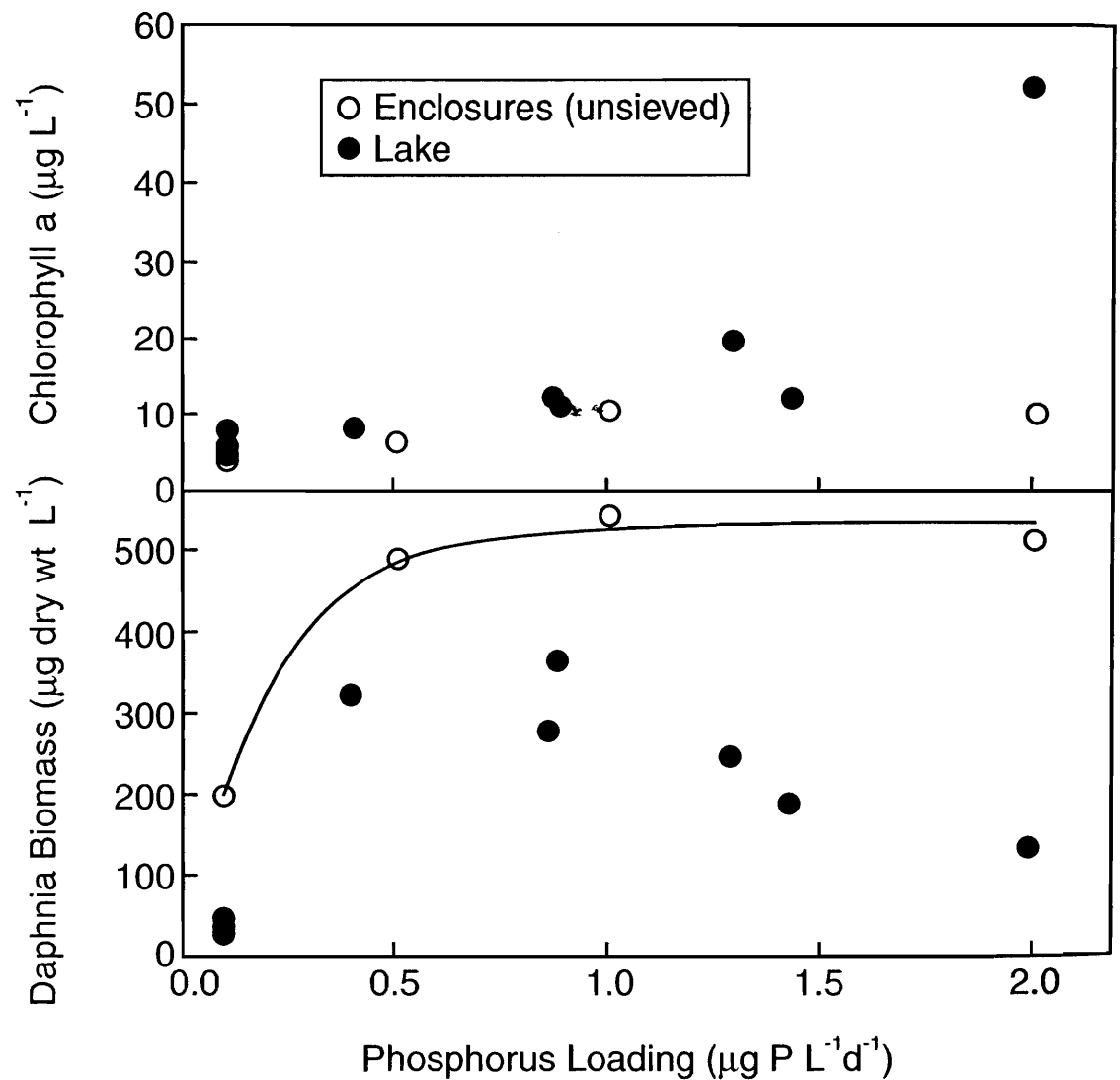


FIGURE 5.2 Enclosures without Grazer Removal versus Lakes

Comparison of unsieved enclosures and lake means in Long Lake across a similar range of nutrient loadings. Means for enclosures are derived from triplicates of each loading treatment (Cottingham et al. 1997). Summer season means for Long Lake are for the East and West basins from 1991 to 1995 (Carpenter et al. 1998). The line fit through the enclosure points for *Daphnia* biomass is an exponential model with the form $y = a(1 - e^{-bx})$.

enclosure experiments. The box plots in figure 5.4 represent major percentiles for data from all the enclosures as well as the Long Lake observations over a comparable range of nutrient loadings (except for lake bacterial production because of missing data at the highest nutrient load). The range of chlorophyll a was 1 to 70 $\mu\text{g L}^{-1}$ in the enclosures versus 3 to 350 $\mu\text{g L}^{-1}$ in the lakes. Enclosures tended to have lower chlorophyll and less extreme blooms relative to the whole lake experiments as suggested by differences in the 75th percentiles of the distributions (figure 5.4) and the differences in the ranges noted above. Limitations on phytoplankton

biomass in enclosures are consistent with strong grazing by *Daphnia*. Similarly, the range of variation of bacterial production was lower in the enclosures relative to whole lake experiments (figure 5.4). Grazing by *Daphnia* had important effects on bacteria in the whole lake experiments (Pace and Cole 1996), but bacteria were even more strongly suppressed in the enclosures (Pace and Cole 1994).

The enclosures provided reasonable representations of lake responses in terms of mean chlorophyll at nutrient loads in the range of 0 to 1 $\mu\text{g P L}^{-1}\text{d}^{-1}$, but only when *Daphnia* was consistently removed. *Daphnia*

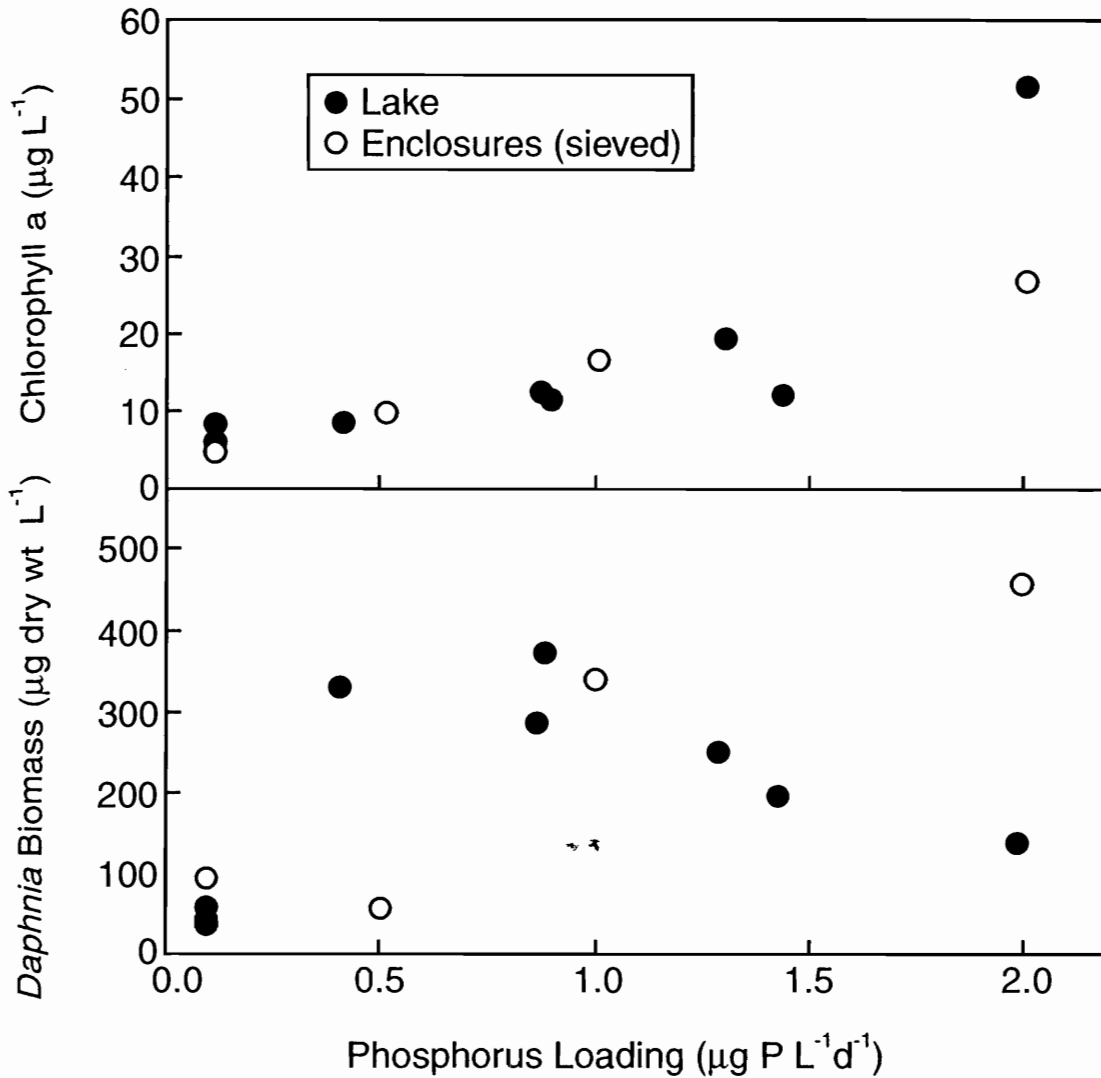


FIGURE 5.3 Enclosures with Grazer Removal versus Lakes

Comparison of sieved enclosures and lake means in Long Lake across a similar range of nutrient loadings as in figure 5.2.

populations, however, dominated enclosures, reducing variability and exaggerating grazing effects relative to the whole lake when not removed or when nutrient loading was high. This comparison indicates the difficulty of representing food web effects in enclosures because of potentially unrealistic population dynamics by a critical grazer. The problem is of greater interest than implied simply by the comparison of these experiments. Interpretations of the interactions of nutrient enrichment, grazer effects, and food chain length on algae are derived from patterns in data drawn from both whole lake and enclosure studies (e.g., Sarnelle 1992; Mazumder 1994). If grazing effects are generally magnified in enclosures, analyses should attempt to determine whether enclosures yield different patterns than lake data. In the studies by Sarnelle (1992) and Mazumder (1994), algal responses to nutrient loading and total phosphorus-chlorophyll relationships were similar for enclosures and whole lake experiments, suggesting similar grazer effects, but the specific issue of *Daphnia* abundance in enclosure versus lake experiments was not analyzed.

I have used the whole lake experiments as a standard for assessing extrapolations of the enclosure experiments. The problem could be extended to address whether the whole lake experiments are representative of a larger collection of lakes or if the results are idiosyncratic. Such an analysis is beyond the scope of this chapter. Previous comparisons, however, of the experimental lakes with patterns observed among lakes at a regional scale suggest the experiments accurately represent nutrient loading and grazing effects on phytoplankton (Carpenter et al. 1991; Kitchell and Carpenter 1993). Other studies demonstrate that lake size has a critical effect on many lake processes including mixing, thermocline depth, water clarity, and mercury contamination of fish (e.g., Fee et al. 1996; and studies summarized in Schindler 1998). It may be possible to develop scaling rules to extrapolate results observed in smaller lakes to larger lakes but the evaluation and understanding of differences along lake size gradients is still developing.

Limnologists are well aware of many problems with enclosure studies, including but not limited to uncertainties about mixing and sedimentation (Vanni et al. 1997; Schindler 1998), fish mortality (Threlkeld 1987), excessive predation (O'Brien et al. 1992), and wall growth (Blumenshine et al. 1997). Despite discussions of these problems by the authors noted, potential artifacts from enclosure studies are often glossed over because they complicate papers and undercut inference. This

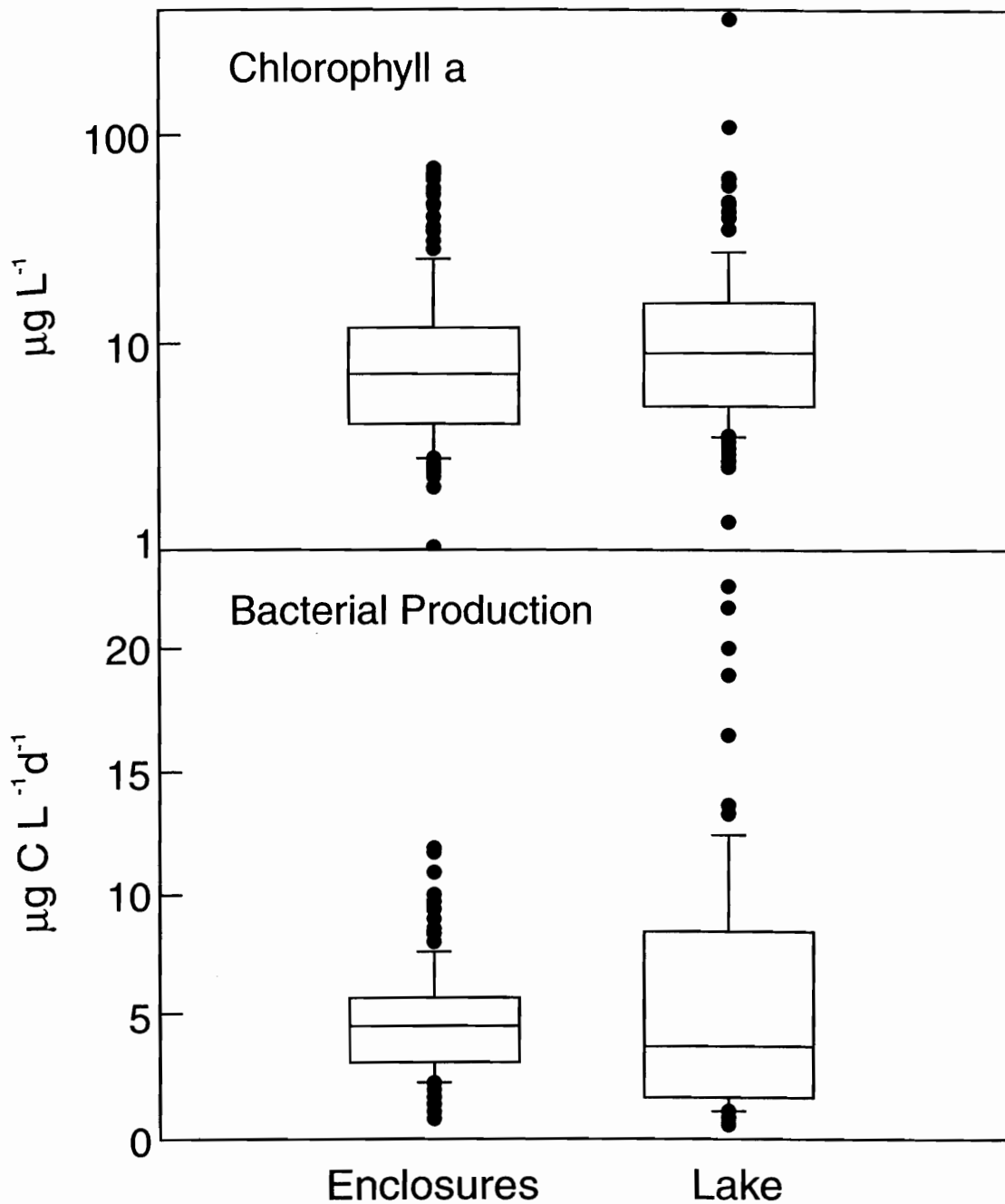


FIGURE 5•4 *Variability in Productivity*

Box plots illustrating the variability in chlorophyll a and bacterial production in the enclosures and lakes over a similar range of nutrient loadings. Upper and lower bars are the 95th and 5th percentiles respectively. Boxes illustrate the 75th (upper line), median (mid-line), and 25th (lower line) percentiles. Points are values less than the 5th percentile or greater than the 95th percentile. Lake data are based on all observations for the years 1992 to 1995 and enclosure data include all observations from the enclosure experiment. Note that the bacterial production box for the "lake" probably underestimates the true variability in this variable, because no comparable data are available from the year with the highest nutrient loading (1995).

tendency to minimize problems leads to a body of experimentation of questionable utility that cannot be readily extrapolated—hardly a desirable situation for a science called upon to make critical predictions about changing ecological systems (e.g., Lubchenco et al. 1991).

Some experiments, of course, do extrapolate well and the point is not to condemn all manipulative, small-scale experiments. For example, phytoplankton are consistently stimulated by additions of inorganic phosphorus and nitrogen whether the experiment is performed in bottles, bags, big tanks, or lakes. This result agrees with knowledge of phytoplankton physiology and the pattern of nutrient limitation in aquatic systems. The general challenge is to translate qualitative and quantitative experimental results to the system of interest.

This challenge becomes more difficult and the potential for misleading results probably rises as the number of ecological interactions (e.g., a food web complex) addressed by an experiment increases. One difficulty here is that manipulations done at different experimental scales may not be equivalent. The whole lake manipulations considered above include numerous interactions between fish and zooplankton that are not included in the enclosures. For example, fish in the study lakes undergo variable recruitment that may result in periods of high or low predation pressure on zooplankton (Post et al. 1997). Under some circumstances (e.g., when planktivores are abundant), fish may also influence nutrient recycling via their migrations between shore and open-water habitats (Schindler et al. 1993). These effects are not simulated by the zooplankton removal methods we used in the larger enclosure experiment. So, the actual ecological interactions manipulated in the lake versus enclosures may be different. Thus, comparisons of the type presented in this chapter must be considered cautiously.

Lakes may represent optimal systems at this point for testing how well small-scale experiments extrapolate to predict the behavior of ecosystems and the shortcomings and advantages of these types of experiments. There is a rich and building literature of whole lake manipulations as well as manipulation experiments done in various kinds and sizes of enclosures. Food web experiments have been especially prominent in lake studies recently and comparisons have been undertaken (e.g., DeMelo et al. 1992; Brett and Goldman 1997). Further analyses, however, are warranted to consider issues such as the comparability of manipulations, the effects of enclosure size, the realism of treatments and responses when compared to whole lake results, and the variability of the same

experiment repeated at the whole lake level (e.g., Lodge et al. 1998). One such analysis comes from Schindler (1998) who reviewed his experiences with experiments at numerous size scales (i.e., bottles to whole lakes) over more than thirty years. He found numerous problems arising from studies using bottle and enclosure experiments that could have lead to incorrect scientific conclusions and “erroneous management decisions” (Schindler 1998:331) without additional work at the ecosystem level.

SCALES OF INTEREST, SOFT EXTRAPOLATION, AND CONTEXT

One key to improving experimentation in ecology in general, and to better incorporate research on scaling in particular, is to constantly question how results contribute to solving problems at the ultimate scale of interest. This means first and foremost that the scale of interest must be made explicit. For lakes, one pertinent scale for predictions is the summer season mean and variance of particular lake properties such as nutrient levels, chlorophyll concentrations, nuisance algae, acidity, fish recruitment, and toxin body burdens. Another scale of interest is often regional. Some properties of interest at this scale are distributions of acid lakes, presence or absence of desirable fish species, number of lakes with fish exceeding a toxic advisory limit, and number of lakes occupied by an invader. There are many other scales and many other properties and problems of interest—the point is scientists must be specific and tailor research efforts accordingly.

Not being explicit about ultimate scales of interest leads to “soft extrapolation.” By this I mean a vague analysis of how to generalize or hope to generalize results from a particular study. Soft extrapolation is a malady of practice. We tend to rationalize this malady by offering up our scientific contributions as pieces of a larger puzzle, and like many undesirable behaviors, we become habituated to it. For example, a common dodge is to say a particular research result will contribute to models without ever specifying what the models are or how the result might specifically improve a given model. By this means (and others), we avoid confronting the scale of interest by not projecting results against independent measures or frameworks. We avoid the hard job of extrapolation.

Experiments like those done in the Ecotron or in laboratory-like settings must also consider the issue of extrapolation but in a different form. In these types of experiments the goal is generality. The hope is that general mechanisms uncovered in these experiments will apply to a wide variety of systems. Thus, the goal is breadth of extrapolation not specific quantitative prediction. Still, to avoid soft extrapolation, general experiments of this nature should strive to specify the domain over which the results may apply and methods for testing that applicability.

Research that helps evaluate and identify scaling relationships should help with the problem of extrapolation as long as it does not facilitate the soft version. There is a tendency to use the concept of scale in an "I'm okay; you're okay" fashion. Levin (1992) notes that while there is no correct scale for a specific system or problem, that "does not mean that all scales serve equally well." We tend to use mantras like "it's a matter of scale" or "but the scales are different"; these should not serve as a means of perpetuating soft extrapolation. On the contrary, appreciation of scaling-dependencies should promote extrapolation. Again, standards and practice in research are important for improving the science.

Finally, context is critical when considering extrapolation. Soft extrapolation may evolve from an incomplete or poorly defined context for a research program. Obviously, context is related to the scale of interest, but more than just specifying the scale, ecologists need an appreciation for the population, community, or ecosystem of interest. As ecological science becomes more technical and information more extensive, specialization ensues. These developments, while deepening understanding, may also act to limit synthetic perspective.

COMMENTS

Most experiments in ecology are done at scales of time and space far below the scale of interest. This means that experimental results must be extrapolated, but the methods for doing so remain poorly understood. Comparison of enclosure and ecosystem experiments reveals cases of both getting it wrong and getting it right. Thus, experiments can both inform and mislead. The statistical rigor of a well-designed, misleading experiment is not very useful. More careful attention to the problem of extrapolation should improve experimental research and facilitate

scaling-up results. The metrics for extrapolation need development and attention. These metrics include comparative frameworks, large-scale experiments, observations from the system of interest, as well as models. Combining these with experiments has been proven and will prove to be effective. A keen sense of ecological systems remains a powerful ally. As technological ability and sophistication of the science increase, we must remember that synthesis and integration are the means to encompassing complexity. This requires scientists capable of seeing beyond the laboratory bench and computer screen to the vistas of the natural world.

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