Ecosystems (1998) 1: 323–334

ECOSYSTEMS

WHOLE-ECOSYSTEM EXPERIMENTS

Replication Versus Realism: The Need for Ecosystem-Scale Experiments

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ABSTRACT

The results of bottle and mesocosm experiments were compared with those obtained in whole-ecosystem experiments at the Experimental Lakes Area. Unless they can be cleverly designed to mimic major ecosystem processes and community compositions, smaller-scale experiments often give highly replicable, but spurious, answers. Problems with appropriate scaling are difficult to deduce without direct comparisons with whole-ecosystem experiments. Reasons are many, but include inappropriate spatial scales to include whole communities, in particular predators and nocturnally active animals; temporal scales that are too short to assess accurately the response of slow-responding organisms and biogeochemical processes; and elimination of key littoral–pelagic and catchment–lake interactions. Identical studies of limnological processes in lakes of a large range of sizes reveals that scaling correction is also necessary when extrapolating from small lakes to large ones. Accurate management decisions cannot be made with confidence unless ecosystem scales are studied.

Key words: mesocosms; ecosystem experiments; Experimental Lakes Area; spatial and temporal scales.

INTRODUCTION

Most ecological experiments involve isolation and manipulation of a small part of an ecosystem, for example in bottles or mesocosms in the case of aquatic ecosystems. Results are then directly extrapolated to whole ecosystems [in the sense of Likens (1992)] or even larger systems. My experience with aquatic experiments at several scales is that such extrapolation is often questionable, for important features of whole lakes and their communities are usually missing. Although this is partly a function of size, microcosms and mesocosms also typically lack the complexity of whole ecosystems, so that such features as air–water and sediment–water exchanges and the activities of wide-ranging organisms are not included. Others have reached similar conclusions about the representativeness of mesocosms (Frost and others 1988; Benndorf 1990; Carpenter 1996; Englund 1997; Peterson and others 1997; Lodge and others forthcoming; Pace forthcoming). Indeed, as I shall discuss, many of the results from experiments in small whole lakes need to be corrected for differences in hydrodynamics, gas exchange, and other processes in order to be properly extrapolated to larger lakes (Fee and Hecky 1992; Fee and others 1996).

In several previous articles, I have compared results from long-term experiments done in small

Received 26 March 1998; accepted 14 May 1998.
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whole lakes with results from mesocosms or microcosms (Schindler 1988, 1990; Levine and Schindler 1992). However, discussions with participants at the recent ecosystem experiment workshop (Jasper National Park, Alberta, 14–17 November 1997), several recent papers on the subject (Carpenter and others 1998; Lodge and others forthcoming; Pace forthcoming), extensions of my experience to community studies in mountain lakes (Paul and Schindler 1994; McNaught and others unpublished), recent studies of scaling over a range of lake sizes (Fee and Hecky 1992; Fee and others 1996), and reviewer comments that I read as subject matter editor for articles in this volume have motivated me to update my views. I believe that the pivotal role of spatial and temporal scales in ecosystem experiments is underappreciated, yet critical to the advancement of ecology. In particular, whole-ecosystem experiments appear to be losing favor because they often cannot be exactly replicated and are expensive and difficult to execute, leading many ecologists to favor smaller scales in order to obtain the satisfaction of statistical confidence.

Over the past 31 years, I have conducted experiments with aquatic ecosystems at several spatial and temporal scales, including short incubations in small bottles, in situ mesocosms of several sizes, and whole-ecosystem experiments of several types [reviewed by Schindler (1988)]. Although each of the scales has proved important in our attempts to understand in-lake processes and catchment–lake interactions, each has shortcomings. This became apparent as we used mesocosms to forecast and fine-tune whole-lake experiments. Conversely, we have used whole lakes to calibrate and verify that smaller-scale experiments were properly representing the interplay of ecosystem-scale processes to an extent where results could be extrapolated with confidence to ecosystem-scale issues [for example, see Schindler (1988, 1991) and Levine and Schindler (1992)]. I believe that such calibration is one of the most important roles for whole-lake experiments, for in most ecosystems, experiments must be restricted to small scales. For reasons that are difficult to anticipate, smaller-scale experiments often yield erroneous conclusions about community and ecosystem processes. Others, working in other aquatic ecosystems, have drawn similar conclusions (Carpenter 1996; Lodge and others forthcoming; Pace forthcoming). In some cases, elaborate measures have been devised to make mesocosms simulate even rather simple ecosystem-scale processes accurately, for example in the Marine Ecosystem Research Laboratory (MERL) estuarine facility (Nixon and others 1984; Oviatt 1994; Santschi 1985). As Pace (forthcoming) has emphasized, knowing the spatial and temporal scales to which an experimental result can be extrapolated with confidence is very important to ecology.

The following discussion is based largely on results at the Experimental Lakes Area (ELA), which was one of the first facilities to be devoted primarily to ecosystem-scale experiments. The reason for the facility was a very simple one: those responsible for managing large and important water bodies were reluctant to risk large sums of money on management schemes that had been tested only in short-term bottle or mesocosm experiments. Small whole lakes were seen as a necessary intermediate step (Johnson and Vallentyne 1971). But, because lakes and resources were limited, we often used smaller experiments as pilot studies for whole-lake experiments, providing the basis for the following discussion.

Importantly, I believe that managers and politicians in today's conservative, economically oriented, resource-hungry society are even harder to convince to act in an ecologically responsible manner than those of 30 years ago, making it more necessary than ever to perform experiments at convincing scales. However, the number of whole-ecosystem experiments has declined in recent years. Colleagues in the USA and Europe, as well as elsewhere in Canada, report that proposals for whole-ecosystem experiments have often been rejected by granting agencies because of concerns about replication or high costs. The problem has been exacerbated by investigators who have misrepresented replicated mesocosms as being "ecosystem scale." This may effectively be the case in certain areas that have been highly modified by humans, by eliminating or restricting the movements of large, free-ranging predators that once had important influences on community structure and ecosystem function. Indeed, the highly simplified ecosystems of plot-scale experiments have been the backbone of modern agricultural development (Pimentel and others 1992). In my experience, however, plots or enclosures usually poorly simulate ecosystems with more or less natural assemblages of species at several trophic levels, and with most of their natural functions intact. Whether they are lakes with several species of fish, rivers with migrating fish, or terrestrial systems with large, free-ranging carnivores, important aspects of ecosystem and community functions and responses to perturbation are controlled by "keystone" organisms too large or mobile to confine in experiments that are smaller than ecosystem scale. Below, I shall make the case that replicated or not, ecosystem-scale experiments

are an important step in the extrapolation of ecological understanding to the understanding and management of whole ecosystems. Carpenter (1996) provides additional arguments for experiments at ecosystem scales.

Very Small Scales: Bottle Techniques

A classic use of bottle experiments is to measure photosynthesis in lakes. When the results of such experiments were applied to whole ecosystems, the predictive power was poor (Schindler and Comita 1972; Bower and others 1987). A closer look at the methods revealed a number of logical flaws. For example, traditional ways of measuring photosynthesis and nutrient limitation often employ strings of small, clear glass bottles, filled with lake water containing natural plankton communities and incubated at several depths for several hours. In most older experiments, including my own, the question of transparency of containers to ultraviolet (UV) radiation was not addressed.

We now know that the interpretation of such experiments had many flaws. Communities in bottles incubated near the lake surface are usually less productive than those at slightly deeper depths. This was commonly assumed to be "photoinhibition," caused by exposure to bright sunlight (Vincent and others 1984). Some early experiments where the depth of incubation was varied during the experiment (Marra 1978) gave higher results than did static exposures, but did not trigger widespread attention to a critical question: how natural were the exposures? However, when a whole lake at ELA was spiked with ^{14}C-labeled dissolved inorganic carbon, and uptake by phytoplankton was compared with bottles over several days, it was clear that photoinhibition of the magnitude indicated by bottle experiments did not correlate with whole-lake results (Bower and others 1987).

Epilimnetic mixing, and the resulting exposure of plankton communities to both photosynthetically active and UV solar radiation, is a complex process poorly mimicked by static incubations. For example, detailed temperature profiles indicate that on days with moderate to brisk winds, the epilimnions of lakes at ELA are mixed rather rapidly, so that exposure to high UV radiation would be brief. However, consideration of several thousand temperature profiles spanning several orders of magnitude in lake area indicates that winds are light enough to allow near-surface microstratification to occur on 25%–70% of midsummer days (M. A. Xenopoulos and D. W. Schindler unpublished). When such conditions occur for several days in a row during cloudless conditions, high UV exposure can have devastating consequences for phytoplankton and bacteria trapped above the near-surface thermocline (Milot-Roy and Vincent 1994; Xenopoulos 1997; Xenopoulos and Bird 1997).

Bottle-scale nutrient experiments were also flawed (Schindler 1971, 1988). It is common to inject bottles with small amounts of nutrients before incubation. If injection of a nutrient causes an increase in production over unmodified reference bottles, it is assumed to be limiting in the natural system. In the early days of eutrophication research, it was commonly assumed that limiting nutrients identified by such techniques were those that should be controlled to reduce eutrophication. Bottle-scale nutrient additions indicate what is limiting to phytoplankton at the time of incubation, but do not necessarily indicate the *cause* of the limitation, which may be inputs of other nutrients, toxins, or nonnative organisms. For example, following fertilization of a lake with phosphorus, bottle experiments commonly indicate that nitrogen is limiting. Also, small enclosures can exclude key ecosystem processes. For example, in experimentally fertilized Lake 227, carbon limitation was indicated in bottle experiments following additions of phosphorus and nitrogen, whereas in the whole lake, exchange of CO_2 between the atmosphere and lake water was sufficient to allow algae to multiply in proportion to phosphorus additions (Schindler and others 1972; Schindler 1988).

Such misinterpretations of bottle-scale experiments were at least partly responsible for the controversy over which nutrients should be controlled to reduce the eutrophication problem, delaying nutrient management in some jurisdictions. Bottle and small mesocosm experiments indicated that many culturally eutrophied lakes were carbon limited (Kerr and others 1970; Kuenzel 1970; Lange 1970), leading to the erroneous conclusion by some that eutrophication could not be controlled without controlling carbon [see Legge and Dingeldein (1970); reviewed by Edmondson (1991)].

However, early whole-lake experiments (Schindler and others 1971, 1972, 1973) clearly showed that even the most severely carbon-limited lakes developed intensive algal blooms when fertilized with phosphorus and nitrogen. The invasion of CO_2 from the atmosphere allowed carbon to be taken up in proportion to nitrogen and phosphorus. The results of smaller-scale experiments were an artifact of restricted invasion of carbon dioxide from the atmosphere to lakes (Schindler 1971, 1988; Schindler and others 1972; Schindler and Fee 1975). But easy,

precise methods die hard. Even today, a quarter-century after publication of our studies, bottle experiments are very common.

There appear to be problems with bottle-scale experiments with zooplankton as well. Marshall and Mellinger (1980) showed that although large bottle experiments with zooplankton replicated precisely, communities in bottles were less diverse than those in Lake Michigan and in ELA Lake 223.

There are cases where such very small scales appear to give useful results. Rudd and colleagues (1988) were able to assess the potential for sulfate reduction and denitrification in lakes from small sediment cores, demonstrating their validity by comparisons with results in reference lakes and those experimentally acidified with sulfuric and nitric acid. They were then able to demonstrate the widespread importance of these processes in internal alkalinity generation, enabling a general model to be developed (Kelly and others 1987).

Intermediate Scales: Mesocosms

Large mesocosms, constructed of clear or translucent polyethylene, have been used for over 30 years (Goldman 1962). They were assumed to add more realism than bottles, simply because they were larger and deeper, allowing phenomena such as vertical migration of zooplankton, and in the case of mesocosms bottomed in sediments, exchange of chemicals between mud and water. Mesocosms can be replicated, allowing rigorous statistical designs. However, my experience has been that even mesocosms 10 m in diameter, containing several hundred cubic meters of water, cannot be extrapolated with confidence to whole lakes unless carefully designed to duplicate key features of ecosystems. In brief, simply making an experiment larger does not make it ecosystem scale, for as I shall illustrate, key biogeochemical processes, habitats, and community components may still not be included.

Physical Shortcomings

One of our earliest applications of large mesocosms was to use them to try to predict physical phenomena such as mixing and gas exchange in ELA lakes. We determined early on that we were unable to use heat-flux methods used for mixing in larger lakes, for vertical transport of chemical substances in the thermocline of ELA lakes was less than the molecular diffusion of heat (Hesslein and Quay 1973; Quay 1977; Quay and others 1980). Instead, we added small amounts of radioactive tracers to estimate mixing. To determine the reliability of mesocosms, we deployed them in Lakes 224 and 227, where whole-lake isotope (tritiated water, radon) additions were being used to trace water movement. After observing that the surfaces of mesocosms were often calm when the lake had waves, we expected that mesocosms might have weaker physical mixing than lakes. Tracers showed that the opposite was true (Quay 1977). The difference was attributed to transfer of wave energy in the lake to turbulent energy in the mesocosm, and to bouncing of the mesocosm flotation collars on the lake surface. In addition, thermoclines were inexplicably shifted slightly downward in mesocosms, possibly as the result of precipitation or leakage through seams (Quay 1977). In later experiments, tritium was used as an epilimnion tracer to track water loss from mesocosms. The water loss was often substantial, even in mesocosms showing no physical evidence of collapse or leakage. These studies provided critical data for correcting nutrient addition rates to mesocosms (Levine and Schindler 1992, forthcoming). Mesocosms generally underestimated air–water gas exchange rates in lakes, presumably because of weaker surface wave energy in the enclosures (Schindler 1988).

Chemical Shortcomings

In the early years of ELA, we often performed mesocosm experiments as pilot studies for whole-lake experiments [Schindler and others (1971, 1980) and other articles in *Can. J. Fish. Aquat. Sci.* 37(3)]. From such studies, we correctly deduced that additions of trace elements and base cations were not necessary to produce algal blooms in even the ultradilute waters of Precambrian Shield lakes. This was not obvious from laboratory-scale experiments or observational studies of the day (Provasoli 1969; Goldman 1972). However, the short duration (less than one season) of the mesocosm experiments did not allow us to gauge properly the extent to which the lake would be able to compensate for carbon and nitrogen deficiencies. Development of a full steady-state nitrogen concentration required 17 years, due to the short period each year that nitrogen fixation was able to supplement nitrogen fertilization (Schindler and others 1987; Findlay and others 1994; Hendzel and others 1994). Without the latter result, we would have concluded from mesocosms that fertilization with nitrogen was required to keep bloom-forming cyanobacteria from dominating the phytoplankton (Schindler 1977).

It is noteworthy that standing crops of phytoplankton in reference mesocosms often declined relative to whole lakes, probably because mesocosms are cut off from catchment sources of nutrients (Schindler and others 1971; Lund 1972). Also, the relatively

high surface areas of the walls in even large mesocosms become sites where more and more nutrients are sequestered as periphyton (Levine and Schindler 1992). If the enclosures remain in place for long periods, the differences in nutrient concentrations and phytoplankton and zooplankton communities from those of whole lakes can be rather large (Lund 1972;. Smyly 1976; Levine and Schindler 1992).

A Bitter Lesson in Scaling Mesocosms

By the mid-1970s, we had performed a number of whole-lake experiments with different nitrogen–phosphorus (N:P) ratios. We were able to deduce that the division between nitrogen and phosphorus limitation occurred somewhere between ratios of added nutrients of 5:1 and 14:1 by weight (11:1 to 31:1 by moles). Whole lakes fertilized at the lower ratio produced massive blooms of nitrogen-fixing cyanobacteria, which had the advantage of being able to fix atmospheric nitrogen (Schindler 1977; Findlay and Kasian 1987). The cyanobacteria were seldom rare or absent in natural lakes of the area (Kling and Holmgren 1972). In lakes fertilized with higher N:P ratios, the green and chrysophycean community consisted largely of species commonly found in unfertilized lakes, but had simply increased in abundance, with perhaps some change in relative species composition (Kling and Holmgren 1972).

We believed that effective nutrient management hinged on pinpointing the precise N:P ratio where the switch to nitrogen-fixing cyanobacteria occurs, for these bacteria are often associated with aesthetically displeasing algal scums, taste and odor problems, and production of toxins (Kotak and others 1996). We decided to narrow down the nutrient ratio where the switch in species occurred, by using mesocosms that could be precisely replicated. We installed several 10-m-diameter mesocosms in Lake 303, which has a large uniform area 2 m in depth (Brunskill and Schindler 1971) and a uniform bottom composition of soft organic muds, into which we could seal the bottoms of the mesocosms. We installed the mesocosms and sealed the bottom edge of the plastic into the sediments by sewing lengths of steel bars into the hems and pushing them 0.5 m into the sediments. We then began fertilizing the tubes with different nutrient ratios, from N:P of 4:1 to 33:1 (moles).

We were surprised to find that we could not induce nitrogen deficits or blooms of cyanobacteria, even at N:P ratios of 4:1. Even at the lowest ratio of nutrient addition, the total N:P ratio remained high, near the natural values of more than 100:1 found in natural lakes of the area. The reason, we learned, was that the lake muds were retaining almost all of the sedimenting phosphorus in the form of algal remains, whereas there was considerable nitrogen return from the sediments. Subsequently, whole-lake fertilization showed the importance of nitrogen return from the sediments of such shallow lakes (Levine and Schindler 1989).

We deduced that in deeper lakes, epilimnions did not have such relatively large areas of sediment contact. We tried to correct the problem by installing a second set of mesocosms with sewn-in bottoms, so that the mud surface was not in contact with overlying water. Remarkably, this modification did not correct the problem. The plastic bottom surface was almost as efficient at retaining sedimented phosphorus as surface sediments. After a delay of a few weeks, it began returning nitrogen to the water column as the muds had done. Once again, we failed to produce nitrogen-fixing blooms at any added nutrient ratio.

We were finally able to make mesocosms simulate responses to fertilization of thermally stratified lakes by moving the mesocosm experiments to nearby Lake 302, which was deeper. We simply installed open-bottomed mesocosms long enough to reach through the thermocline. This design prevented the return of nutrients from the hypolimnion to the epilimnion while allowing the downward passage of nutrients in particulate form, as observed in pelagic regions of lakes. This enabled us to lower the N:P ratio enough to induce nitrogen-fixing blooms of cyanobacteria similar to those observed in lakes fertilized with low N:P ratios (Levine and Schindler 1992). However, another set of mesocosms in the same lake, placed in shallow water and bottomed with sediment, reacted similarly to the mesocosms in Lake 303. In this case, large mats of filamentous green algae attached to the plastic walls and littoral sediments, but no nitrogen fixers were observed in either attached or planktonic communities (Levine and Schindler 1992). Over 80% of the algal response in these enclosures was by periphyton rather than phytoplankton (Levine and Schindler forthcoming). Blumenshine and colleagues (1997) report similar results.

Tritium additions to the same mesocosms revealed still another problem. The tubes exchanged some water, received nutrients from precipitation, and, in the pelagic ones, received nutrients from metalimnetic entrainment. When corrected for these factors, the actual range of N:P supplied ranged from 8:1 to 50:1, substantially different from the aforementioned values, which considered fertilizer alone (Levine and Schindler forthcoming). While the mass balance budgets of whole lakes are corrected

for all inputs and outputs, these are typically disregarded in mesocosms.

In summary, after three attempts and some rather complicated corrections, we were able to get mesocosm experiments to duplicate the responses of whole lakes. If we had not had the perspective provided by whole-lake responses to fertilization, we would probably have accepted the results of the first set of mesocosm experiments at face value, concluding that low N:P loading ratios had no effect on blue-green dominance. Any resulting management decision would have been seriously flawed.

Even in answering rather simple questions, mesocosms required complicated correction for the magnitudes of several processes in order to simulate events in whole lakes properly. Hesslein and colleagues (1980) and Schindler and coworkers (1980) compared the results of radiotracer additions to whole lakes and mesocosms. Results were rather dissimilar, but the reasons could not be explained. In a subsequent mesocosm experiment, Santschi and colleagues (1986) developed a measurement and modeling program to separate the effects of particle settling and resuspension, adsorption/desorption to suspended particles, stagnant film thickness at the sediment–water interface, and benthic mixing rates to explain removal rates. When the different magnitudes of these processes in lakes were accounted for, their models reconciled whole-lake and mesocosm results.

In summary, even for rather simple physical and chemical questions, considerations of complex differences in several physical and chemical processes were required in order to design mesocosm experiments that could be extrapolated to whole lakes. If we are to rely on mesocosm experiments to make accurate predictions about changes to lakes, it is clear that we must first use lake experiments to understand, and possibly correct for, the shortcomings of mesocosms. As I shall discuss, incorporation of biology further complicates matters.

Biological Shortcomings

Problems with incorporating whole communities in mesocosms. The problem of incorporating higher trophic levels in mesocosm experiments has been noted by many (Carpenter and Kitchell 1988; Schindler 1988; O'Brien and others 1992; Pace 1998). In oligotrophic lakes such as those at ELA, lake trout or pike are present at densities of from 0.01 to 2 fish per 1000 m^3, so incorporating their effects into mesocosm experiments is all but impossible. Thus, mesocosms experiments involving more than three trophic levels cannot be done. Even when the effects of predators on planktivores were experimentally simulated, mesocosms did not predict well the long-term effects of predator manipulations on lower trophic levels (Vanni and Findlay 1990; Findlay and others 1994).

There are other components of aquatic communities that are difficult to incorporate in mesocosms. Recent studies have shown the importance of pelagic–benthic coupling to nutrient cycling or plankton predation in a wide variety of small lakes (Schindler and others 1996a; F. Wilhelm and D. W. Schindler unpublished). Only a small proportion of studies on lakes are done at night, so the activities of nocturnally active organisms are often underappreciated. Organisms that are benthic by day and pelagic at night are unlikely to be properly represented in pelagic mesocosms. Even if they were included, it is difficult to envision how to simulate their movements properly between littoral and pelagic zones, or between epilimnion and hypolimnion.

An example is useful to illustrate this point. Alpine lakes in the Cascade Valley of Banff National Park, Alberta have been sampled since the mid-1960s. *Gammarus lacustris* is known to be an important predator in these normally fishless lakes. Records based on daytime sampling show it to be largely benthic, with occasional large specimens caught in pelagic samples taken in profundal depths of the lakes. As a result, we did not incorporate *Gammarus* in the large sets of mesocosm experiments that we performed as pilot studies for whole-lake predator restoration (Paul and Schindler 1994; Paul and others 1995).

Nocturnal sampling was done for the first time in 1995 (a 14-mile hike through some of the best grizzly habitat in the park, frequent snow, strong wind, and subfreezing temperatures even in July are effective deterrents to nighttime work). It was discovered that in fishless lakes, high densities of *Gammarus* occupy near-surface waters of the pelagic zone at night. Sizes indicate that they originate largely in the littoral zone (that is, their migration is largely horizontal rather than vertical). They feed voraciously on *Hesperodiaptomus* and other pelagic crustaceans, but also transfer benthic nutrients to the pelagic during the night by excretion. As a result, phytoplankton biomass in Snowflake Lake is much higher than in nearby lakes which have no large *Gammarus* populations (F. Wilhelm and D. W. Schindler unpublished data).

Temporal problems. In my experience, temporal constraints are a severe handicap when extrapolating most mesocosm experiments (and, for that matter, many whole-lake experiments that are carried out only for a few years) to lake management.

A wide variety of management models, including those for nutrients, alkalinity generation, contaminant flushing, and conservative elements, are based on assumptions of first-order kinetics between well-mixed lake waters and sediments [for example, see Vollenweider (1969, 1976), Dillon and Rigler (1974), Ahlgren (1977), Schindler and others (1978), Baker and others (1986), and Kelly and others (1987)]. When either water-flow rates or chemical influx rates to such a system are changed, chemical concentrations approach new steady-state asymptotes exponentially. As a rule of thumb, the system requires at least three water renewal times to approach a new steady state (Riggs 1963).

For most management purposes, the long-term condition is of primary interest. Most lakes have water renewal times ranging from several months to over a decade. It would be difficult to use mesocosms to predict steady-state chemical conditions, unless complex models are used to design chemical input regimes to simulate steady-state conditions in lakes [for example, see Holoka and Hunt (1996)].

Even if chemical steady state can be well simulated, many organisms cannot respond to a treatment in the few months that are usually the limit for reliable mesocosm experiments. In northern waters, most invertebrates have life cycles requiring 1–3 years, so even experiments encompassing most of the ice-free season have low predictive power. As an example, following introduction of predatory *Hesperodiaptomus arcticus* to an alpine lake, the zooplankton community has continued to change for 5 years. There is still no evidence that *Hesperodiaptomus* has reached steady state (A. S. McNaught and others unpublished; D. W. Schindler unpublished).

There are even greater problems with larger organisms. As Carpenter and Kitchell (1988) noted, predator populations respond slowly to most perturbations, making it impossible to gauge accurately their effects on other components of communities in experiments that last only a few months, regardless of spatial scales. For example, fishes at the top of the food chains in ELA lakes required at least 8 years to respond fully to nutrient addition and acidification, as well as to the removal of these stresses (Mills and Chalanchuk 1987; Mills and others 1987; Schindler and others 1993). Whole-ecosystem experiments of short duration would have the same deficiency.

Biodiversity can also be a problem in mesocosms, for they may contain only a part of the total species assemblage in a lake. Many whole-lake responses occur either because of the surprise appearance of organisms that are too rare to detect prior to treatment or invade the lake from elsewhere following treatment. For example, after Lake 223 had been acidified to pH 5, chironomid emergence was undiminished. However, there was a dramatic change in species. Over 95% of emergence was by three species of the genus *Cladotanytarsus*, none of which had been recorded in the lake in several years of sampling at higher pH values. One of the species, *Cladotanytarsus aeiparthanus*, had never been recorded before (Schindler and others 1985; Bilyj and Davies 1989)! Similarly, following elimination of dominant crustaceans from Snowflake Lake by introduced nonnative salmonids, a succession of crustacean and rotifer species either rare or unrecorded in the lake occurred over the next several years (A. S. McNaught and others unpublished). In short, isolating small parts of the ecosystem from the whole may limit the range of responses possible in mesocosms.

On the other hand, mesocosms may attract unwanted "biodiversity." Elsewhere, I have recounted the mischief that otters, muskrats, and water birds can wreak on mesocosms, which offer nice perching sites and containers where prey cannot easily escape (Schindler 1988). Crayfish burrow under the walls of mesocosms, entering and leaving them at will.

The above is not a complete list of problems with mesocosms. Studies in other areas have revealed many others (Gachter 1979; Marshall and Mellinger 1980; Carpenter 1996).

Practical Constraints to Replicating Whole Ecosystems

We often considered replicating whole-ecosystem nutrient experiments at ELA, for the costs of fertilizer and acid are not formidable, ranging from a few hundred to ten thousand dollars per year for chemicals to treat a single lake. However, even with 46 lakes set aside for experimental purposes, it is difficult to find near-replicates. Lakes differ in fauna (Hamilton 1971; Patalas 1971; Beamish and others 1976); water renewal times, which determine the rate of response to chemical changes (Schindler and others 1978); and chemical concentrations (Armstrong and Schindler 1971). In the case of eutrophication experiments, we chose to use a covariance approach, where phosphorus loadings and water renewal times were different for every lake treated, to say nothing of interannual differences in water renewal (Schindler and others 1978). We treated each year of each treatment as a separate experiment, which is, of course, not true replication. However, phosphorus renewal times are only a few

months. Phytoplankton and zooplankton recovered completely in the first year after fertilization ceased (Shearer and others 1987). With respect to phosphorus–plankton systems, we believe that different years are essentially uncorrelated, as borne out by comparing the conclusions of using single years versus long-term average responses for the several lakes. Such fast-responding components are also amenable to treatment by time-series analysis, as long as periods of observation greatly exceed the response times of the variables in question. Despite the aforementioned long delays in responses of chemical and biological components, it is difficult to obtain funding for more than a few years, even for large-scale experiments. Many of the arguments to support long-term studies [for example, see Likens (1992) and Edmondson (1991)] apply to experimental as well as to nonexperimental ecosystems.

One advantage of ELA experiments is that permanent staff were hired to carry out the experiments. Equipment was used for several experiments, and accommodation was available at the field camp. As a result, individual experiments were not very costly to begin. Also, experiments could be maintained in the long term by reducing sampling scales. However, whole-ecosystem experiments can be more costly where overhead, personnel, and transportation and equipment must be purchased. Carpenter (personal communication) reports that lake manipulations in Wisconsin have required $350,000–$600,000 per year. The European CLIMEX project (climate change experiment), with its computer-controlled gas and temperature regimes was even more costly (R. F. Wright personal communication).

Whole-lake experiments with nutrients and strong acids have been carried out in several lakes and at different sites. The results and conclusions have differed only in minor details at lower trophic levels (Carpenter and others 1991; Schindler and others 1978, 1991), in line with the expectation described above. Also, the responses agreed well with those observed in nonexperimental, eutrophied and acidified lakes (Schindler and others 1978, 1991). Similarly, NITREX (nitrogen saturation experiments) at several sites across Europe fit one general model for nitrate release (Emmett and others 1998). These observations suggest that perhaps extensive replication at one site is not absolutely necessary. However, while lake-trout lakes responded similarly regardless of location, lakes with different fish assemblages exhibited very different responses, regardless of whether the lakes were in the same region (Schindler and others 1991). Presumably, this was due to the different sensitivity to acidification of different fish species. It suggests that if several whole-ecosystem experiments are possible, it may be more informative to do them in ecosystems with different species assemblages than to replicate them in nearly identical systems.

There are also institutional constraints to whole-ecosystem experiments in most areas. Few lakes or other ecosystems in the USA or Europe are free of conflicting interests, and it is difficult to have them set aside as the exclusive preserve of researchers. For example, permission for the Little Rock Lake experiment required a special act of the Wisconsin Legislature (T. M. Frost personal communication). Even when permission for an experiment is obtained, it is often impossible to control other uses of the ecosystem that can confound the interpretation of experiments. Many important perturbations are "off limits" even in dedicated whole-ecosystem research facilities. For example, whole-lake experiments with dioxins and nonnative species cannot be done at ELA and are unlikely to be permitted anywhere. Many case histories are available, however, for such "experiments" done accidentally or to "enhance" ecosystems. Carpenter (1998) discusses many other conflicts that are faced by those who would experiment at large scales. The bureaucracy of dealing with such problems can be a significant deterrent to young ecologists, anxious to demonstrate their research prowess by publishing research studies.

Experiments in previously perturbed ecosystems may not reveal the entire range of responses that are possible in unperturbed ones. In many cases, previous perturbations such as exploitation or introduction of nonnative species have already "peeled away" natural biodiversity that may, at least in theory, provide valuable protection for ecosystems, in terms of "functional redundancy" (Schindler 1988, 1990; Frost and others 1995). The presence or absence of natural species assemblages can affect the results obtained in experiments at any scale. I have written more extensively elsewhere on the pitfalls of not knowing the true "baseline state" of ecosystems (Schindler 1995).

Correction for Spatial Scales: An Underappreciated Problem

At least some of the problems in scaling of mesocosm results to whole ecosystems also apply when extrapolating from small lakes to large ones. Simple extrapolation is valid in some cases. For example, Schindler and colleagues (1978) showed that the same sort of simple models dependent on phosphorus loading and water renewal worked well for both large lakes and small. However, results from a study

deliberately designed to test the applicability of ELA results to larger systems show that, for some lake processes, scaling can be very important.

The Northern Ontario Lake Size Study (NOLSS) (Fee and Hecky 1992) examined changes in communities and in-lake processes in northwestern Ontario lakes over a size range of several orders of magnitude, ranging from ELA lakes of 4–55 ha to Lakes Nipigon and Superior. Up to 10 years of data were collected on some of the lakes. As lakes increase in size, advective mixing processes, most notably internal waves in the region of the thermocline, become increasingly important in determining the exchange of nutrients and other chemicals between epilimnion and hypolimnion. However, less obvious factors were also functions of size. Fish in smaller lakes tended to have higher mercury concentrations than in larger lakes, because the ratio of methylation to demethylation is a function of lake depth and temperature (Bodaly and others 1993; Ramlal and others 1993). Nutrient status and nutrient availability also depended on lake size (Fee and others 1994; Guildford and others 1994). Thermocline depth in ELA-size lakes is strongly affected by the attenuation of light by dissolved organic carbon (DOC) (Schindler and others 1996b), but in larger lakes DOC becomes less important as physical dynamics override the effect of light penetration on thermocline depth (Fee and others 1996).

SUMMARY

In summary, many microcosm and mesocosm experiments at ELA have yielded results that would have caused erroneous management decisions, because responses were different from those of whole lakes. In many cases, the problem was caused by inadequate or erroneous scaling of sediment–water interactions, physical phenomena, water renewal times, and temporal events, which can often be corrected. However, many of the faults are uncorrectable. In particular, the inclusion of rare but important top predators and highly motile species is impossible. I conclude that accurate ecosystem management decisions cannot be made with confidence unless ecosystem scales are studied. Even at ecosystem levels, attention to proper scaling enables more accurate conclusions to be made, as the NOLSS project has shown and Pace (forthcoming) has concluded by comparing other studies. Design of smaller-scale experiments to account properly for the different scales of physical, chemical, and biological processes is at least as important as replication. In many cases, proper scaling will be impossible, and experiments at less than ecosystem scales are inappropriate for making predictions about whole-lake responses.

ACKNOWLEDGMENTS

Steve Carpenter and two anonymous reviewers provided very helpful critiques of an earlier draft of the paper. Michael Pace and David Lodge kindly sent me prepublication copies of their manuscripts.

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