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Scale Effects and Extrapolation in Ecological Experiments

GÖRAN ENGLUND AND SCOTT D. COOPER

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I. SUMMARY

Most ecological experiments are performed on spatial and temporal scales that are much smaller and shorter than the systems and time frames of interest. Available data, however, suggest that experimental results often change with the size of the experimental arena and the duration of the experiment (i.e. are scale-dependent). As a consequence, the interpretation of experimental results often requires extrapolation from the limited spatial and temporal scales of experimental systems to the much larger and longer scales of natural systems. In this paper we discuss the

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implications of scale-dependence, particularly spatial scale-dependence, for the design and interpretation of experiments. We suggest that the problem of extrapolation across scales should be avoided when possible, either by matching the physical size of experimental units with the size of the system of interest or by designing small-scale experimental systems so that the processes of interest are given a realistic representation. When this is not possible it becomes necessary to translate experimental results to other scales, which requires that the mechanisms that generate scale-dependence are understood and that they can be incorporated into models that make predictions for other scales. We review and classify sources of scale-dependence in ecological responses to perturbations and describe attempts to incorporate these mechanisms into scaling models. Among the mechanisms we describe are exchange processes, nonlinear averaging in heterogeneous systems, and arena artifacts. At present, we do not know if available scaling models can make accurate quantitative extrapolations from experimental to natural scales. Thus, the primary, current value of scale models is the identification of scale ranges with particularly weak or strong scale-dependence.

We also note that well-known statistical methods for design, parameter estimation and inference can be used as a framework for extrapolation in field experiments, in the sense that observations from a small number of experimental units can be used to draw conclusions about whole systems. We discuss the value of different statistical designs as tools for extrapolation and note that the choice of scale of an experiment is a critical design decision. The scale of a design is determined by grain (size of experimental units or blocks) and the extent or range covered by the design. The scale range, delimited by grain and extent, determines the scale of the background heterogeneity that can influence the strength of treatment effects. Moreover, both grain and extent are related to the variance among experimental units, which means that the choice of scale influences the statistical power of a design as well as the magnitude of the aggregation error, a bias that can arise when the mean value of a set of measurements made in small experimental units are taken to represent a larger, more heterogeneous system.

II. INTRODUCTION

Much of our current understanding of the processes that control the dynamics of populations and communities stems from perturbation experiments. Typically some environmental factor, such as the density of competitors, predators, or resources, is manipulated in experimental units and unmanipulated units are used as controls. The approach has gained high status in ecology because it allows us to test mechanistic hypotheses

under realistic conditions (Diamond, 1986; Underwood, 1986, 1997; Hairston, 1989).

The fundamental assumption underlying the approach is that experimental results can be extrapolated to the natural systems of interest. In the last two decades there has been an intense debate over the validity of this assumption, particularly statistical issues such as the spatial arrangement of experimental units, choice of statistical model, and how to obtain adequate replication (e.g. Hurlbert, 1984; Underwood, 1986, 1990; Dutilleul, 1993, 1998a,b; Heffner *et al.*, 1996). Recently, more attention has focused on the realism of experiments, for example the spatial and temporal scales of manipulations, the assemblage of experimental communities, and the strength of treatments (e.g. Tilman, 1989; Englund, 1997; Peckarsky *et al.*, 1997; Schneider *et al.*, 1997; Thrush *et al.*, 1997; Bernardo, 1998; Cooper *et al.*, 1998; Gardner *et al.*, 2001).

Extrapolation across spatial scales has been singled out as a particularly important problem (Levin, 1992; Carpenter, 1996; Englund and Olsson, 1996; Schindler, 1998; Kemp *et al.*, 2001). Support for this view comes from the observation that most experiments are performed in experimental systems that are much smaller than the systems of interest (Kareiva and Andersen, 1988; Duarte *et al.*, 1997; Petersen *et al.*, 1999; Englund *et al.*, 2001), and that responses to experimental treatments often change with the size of the experimental system (e.g. Gieskes *et al.*, 1979; Hall *et al.*, 1991, 1993; Carignan and Planas, 1994; Barica *et al.*, 1980; Duffield and Aebischer, 1994; Sarnelle, 1997; Cooper *et al.*, 1998; Schindler, 1998; Pace, 2001). This view has been reinforced by the increasing awareness of the strong relationship between patterns and processes and the spatial and temporal scales of observation (Wiens, 1989; Levin, 1992).

The term scale has several different meanings in ecology (Meentemeyer and Box, 1987; Schneider, 2001a). Often ecologists use scale simply to mean the area or volume of an object and the time frame of observations (O'Neill and King, 1998). Another common definition relates to the finding that observed patterns in environmental heterogeneity change with the grain and extent of observations (Gardner, 1998; Wiens, 2001; Schneider, 2001b). The scale of a set of observations are defined as the grain, which usually refers to the area or time span covered by individual samples, and the extent, which refers to the total range in time or space over which samples are distributed. Both aspects of scale are relevant for extrapolation in ecological experiments.

The small size of experimental systems may cause them to respond differently to experimental treatments than their large-scale natural counterparts. The theory used to address this problem includes mechanistic scaling models that can be used to translate results from small to large systems (Frost *et al.*, 1988; Englund *et al.*, 2001), and dimensional analysis,

which can be used to construct small experimental systems that respond to manipulations in the same way as their natural counterparts (Uhlmann, 1985; Petersen and Hastings, 2001). In the first part of this paper we review this body of theory. Because dimensional analysis and scaling models require that the mechanisms generating scale-dependence are understood, we also review many of these mechanisms.

In addition to extrapolation from small to large units, experimentation also involves extrapolation by using observations from many small units to form a mean or a sum that is used to describe a large population or a large system. Statistical theory for experimental design, parameter estimation, and inference is a framework that often is used for this type of extrapolation in field experiments. We review statistical models, in particular, mixed model designs, which may be useful for this form of extrapolation. This type of extrapolation often involves the problem of aggregation error (Rastetter *et al.*, 1992). The response of a small subsystem is not equal to the response of the large system if responses to manipulations are nonlinear and if there is heterogeneity among subsystems. Thus, we will also review techniques for dealing with this source of error; however, we first review the evidence that experimental outcomes vary with arena size.

III. HOW OFTEN DO EXPERIMENTAL RESULTS DEPEND ON ARENA SIZE?

The evidence that experimental results change with the size of experimental units comes from studies where the same treatments have been applied at more than one spatial scale. Such multiscale experiments are scarce and most have been performed in aquatic systems, i.e. freshwater and marine pelagic systems (Gerhart and Likens, 1975; Gieskes *et al.*, 1979; Mazumder *et al.*, 1990; Sarnelle, 1997), stream benthic systems (Cooper *et al.*, 1998; Kohler and Wiley, 1997), and marine hard and soft bottom systems (Sousa, 1984; Hall *et al.*, 1993; Quinn and Keough, 1993; Fernandes *et al.*, 1999). Terrestrial examples of multiscale experiments are fewer and mainly limited to soil and agricultural systems (Duffield and Aebischer, 1994; Brown and Lightner, 1997). The questions most often addressed in multiscale experiments are related to the effects of trophic interactions (Lafontaine and Leggett, 1987; Cooper *et al.*, 1998; Bertolo *et al.*, 1999), disturbance and colonization (Sousa, 1984; Smith and Brumsickle, 1989; Ruth *et al.*, 1994; Thrush *et al.*, 1996; Anderson, 1998), fragmentation (Banks, 1998, 1999; Bowers and Dooley, 1999), and toxicants on natural communities (Perez *et al.*, 1991; Morris *et al.*, 1994; Flemer *et al.*, 1995, 1997; Cairns *et al.*, 1996).

To rigorously examine the frequency with which experimental results change with arena size, we examined experiments addressing trophic relationships in marine and freshwater pelagic systems. We chose these systems and studies because they are reasonably homogenous in methodologies, habitat structure, and organisms. We searched for papers in biological abstracts, as well as reference lists in published papers, and found 10 papers that examined the effects of nutrients or predators on planktonic organisms using realistic communities (Table 1). When a paper included more than one response, we included a maximum of four responses from a paper and, thus, ended up with a total of 22 responses for analysis.

We first examined the frequency with which the authors of these papers concluded that their results changed with experimental scale. The authors presented a conclusion for 15 of these responses and inferred that large- and small-scale responses differed in eight cases. In many cases, conclusions were based on tests with low statistical power and some of the largest effects, as determined by differences or ratios between control and treatment responses, were deemed nonsignificant (e.g. Bertolo *et al.*, 1999). As a consequence, we also quantified the slope of observed relationships between ecological responses and arena sizes. As a standardized measure of the size of responses or effects, we used the log response ratio, LRR, given by $\ln(R_c/R_t)$ where R_c and R_t are the responses in control and treatment units (Osenberg *et al.*, 1997; Hedges *et al.*, 1999). In most experiments cylindrical containers were used. In these multiscale experiments, we measured the linear dimension of experimental units as depth for experiments where the area was held constant, as radius where depth was kept constant, and as the cubic root of the volume when both area and depth were altered. The strength of scale-dependence was quantified as the slope of the log–log relationship between LRR and LENGTH, i.e.

$$\text{Slope} = \ln(\text{LRR}_2/\text{LRR}_1)/\ln(\text{LENGTH}_2/\text{LENGTH}_1).$$

This index of the strength of scale-dependence was chosen because it is dimensionless and thus lends itself to comparisons between different systems. A second reason for the choice of this index is that some scale models predict power relationships between ecological responses and arena size and such relationships, of course, are linear on a log–log plot (see Section IV.E). A disadvantage of this index is that it cannot be used if the sign of the response changes with arena size. This was the case for six of the responses examined in our analysis and some of these were quite strongly affected by the size of the experimental units (Barica *et al.*, 1980; Proulx *et al.*, 1996).

Table 1 shows that positive and negative slopes for relationships between ecological responses and arena size were equally common. As benchmarks,

Table 1 Results of multiscale experiments, where the same treatment was applied to experimental units of different size. The log response ratio is given by $\ln(R_c/R_t)$ where R_c and R_t are the responses in control and treatment units. The strength of the scale-dependence was calculated as $\ln(LRR_2/LRR_1)/\ln(LENGTH_2/LENGTH_1)$ where LRR is the log response ratio and LENGTH is the linear dimension of the arena

Study	Treatment	Response	Log Response Ratio, Small Unit	Log Response Ratio, Large Unit	Size Range (m)	Scale-Dependence (slope)	Conclusion	Scaling	Possible Confounding
Gieskes *et al.* 1979	–	Prim. prod.	0.55	8.97	0.031–0.16	1.73	Differ	≈Constant shape	–
Barica *et al.* 1980	Nutrients	Chlorophyll a	0.41	−1.01	2–10	–	No concl.	≈Constant depth	Year, treatment strength
Mazumder *et al.* 1990	Fish	Size distrib. of zoopl. (slope parameter)	−0.27	−0.15	8–205	−0.17	Not different	Constant depth	Duration, habitat
		Clorophyll a	−0.56	−1.70		0.34	Not different		diversity
Marrasé *et al.* 1992	–	Grazing rate	1.35	2.20	0.046–0.27	0.28	Differ	≈Constant shape	–
Carignan & Planas 1994	Nutrients	Chlorophyll a[3]	2.09	0.20[1]	0.1–48	−0.38	Differ	≈Constant shape	Habitat diversity
		Chlorophyll a[4]	1.58	0.12		−0.42	Differ		
Perin *et al.* 1996	Fish	Chlorophyll a	−1.23	−2.03	3–12	0.36	No concl.	Constant area	Habitat diversity
	Nutrients	Chlorophyll a	−0.13	0.07		–	No concl.		
Proulx *et al.* 1996	Fish	Tot. zoopl.	0.67	1.06	3–12	0.33	No concl.	Constant area	Habitat diversity
	Nutrients	Tot. zoopl.	−0.32	−0.56		0.41	No concl.		
	Fish	Daphnia	−0.92	2.74		–	No concl.		–
	Nutrients	Daphnia	0	−0.06		–	No concl.		–
Petersen *et al.* 1997	Nutrients	Gross prim. prod.[1]	−0.96	−0.21	0.5–2.2	−0.98	Differ	Constant shape	–
		Gross prim. prod.[2]	−1.20	−0.63		−0.43	Differ		–
Sarnelle 1997	Daphnia	Rotifers	−0.02	0.13	0.2–2.3	–	NS	≈Constant shape	Duration, treatment strength
		Ciliates	0.16	0.22		0.15	$p=0.001$		
		Nanoflagellates	0.32	0.22		−0.17	NS		
		Edible phytoplankton	0.30	0.22		−0.14	$p=0.0001$		
Bertolo *et al.* 1999	Fish	Chlorophyll a	−0.90	−1.39	2.5–4.5	0.73	NS	Constant area	–
		Tot. zoopl.	−0.53	0.20		–	NS		–
		Cladocerans	1.87	1.57		−0.29	NS		–

[1]Summer experiment.
[2]Fall experiment.
[3]Lake San Nicholas North.
[4]Lake San Nicholas South.

we suggest that a slope of ±1 should be regarded as showing strong scale-dependence and a slope of ±0.33 as moderate scale-dependence. A slope of one (or minus one) means that increasing the container radius or depth one order of magnitude produces commensurate increases (or decreases) in ecological response, whereas a slope of ±0.3 means that the response is doubled or halved. Using these benchmarks we conclude that a majority of the responses (10 out of 16) showed moderate to strong scale-dependence (Table 1).

In some studies, the effects of arena size on ecological responses may have been confounded by other factors such as habitat diversity and the duration or timing of experiments (Table 1). Some of these multiscale experiments, however, appeared to be unconfounded by other factors and still showed strong scale-dependence in ecological responses (e.g. Gieskes *et al.*, 1979; Petersen *et al.*, 1997). The scale-dependence of experimental results also has been demonstrated in various benthic (Linton and Davies, 1988; Hall *et al.*, 1991, 1993; Thrush *et al.*, 1996; Kohler and Wiley, 1997; Cooper *et al.*, 1998; Bergström and Englund, 2002), littoral (Sousa, 1984; Quinn and Keough, 1993), and terrestrial habitats (Duffield and Aebischer, 1994; Schoener and Spiller 1995).

IV. EXTRAPOLATION FROM SMALL TO LARGE SYSTEMS

A. Defining the Scale of Interest

A first crucial step when designing an experiment is to define the spatial scale of the focal question, which depends on the processes, organisms, constraints, or responses of interest (Wiens, 1989; Perrson and Diehl, 1990; Levin, 1992; Cooper and Barmuta, 1993; Poff, 1997; Cooper *et al.*, 1998; Gardner *et al.*, 2001). In general, the scale of the question should be the main determinant of the design of the experiment.

A useful distinction can be made between conceptual experiments and system-specific experiments (Pace, 2001). System-specific experiments are meant to mimic a particular natural system. Both processes and environmental conditions should be realistic and it is hoped that experimental results can be extrapolated to a specific field situation. To this category belong many experiments where the density of a key predator or competitor is manipulated in the field with the objective of estimating the effects of this species on population and community parameters. For system-specific experiments, it is often possible to define the scale of interest both in terms of grain and extent. For example, an experiment examining

nutrient limitation in lakes could define the grain as individual lakes of a certain size, and extent as all lakes of this size within a certain geographic area.

In contrast, conceptual experiments are focused on scientific generality and the testing of general models. The important point is to reproduce the processes of interest rather than to mimic a particular system. Experimental tests of food chain models using laboratory cultures of microorganisms (Luckinbill, 1974; Kaunzinger and Morin, 1998) and experiments conducted in facilities such as the Ecotron (Lawton, 1996) serve as examples of conceptual experiments. In short, conceptual experiments are conducted in model systems, which capture a key feature or process of interest and test general models focused on this feature or process. For conceptual experiments, it is often not possible to specify the scale of interest as the size of a system. Instead relevant scales may be defined relative to some scale-dependent property of the system, such as the edge to area ratio of the system or habitat, the relative mobility of interacting organisms, or the relative magnitudes of migration and vital rates (Uhlmann, 1985; Schneider *et al.*, 1997; Englund, 1997).

B. Matching Experiments with the Scale of Interest – Dimensional Analysis

Once the scale of interest is defined then an experiment can be designed so that the results are applicable to that scale. The most straightforward strategy is to match the scale of the experiment to the scale of interest. In system-specific experiments, matching requires that experimental units be of the same size and heterogeneity as the system of interest. This is feasible in some systems. For example, in streams composed of semi-isolated pools it is common that fish have a patchy distribution at the pool-to-pool scale. For many hypotheses related to the patchy distribution of fish on this scale, it is clear that pools are the relevant experimental units and, fortunately, fish densities in pools are easy to manipulate (Cooper *et al.*, 1990; Wiseman *et al.*, 1993; Sih *et al.*, 1992; Englund, 1999).

In many cases, however, the system of interest is much larger than feasible experimental units, particularly when testing hypotheses about factors controlling population processes. "Whole-system" manipulations, which encompass the scales appropriate for examining the population or community dynamics of most organisms, are only feasible in a limited number of systems, such as lakes, ponds, and islands, and for a limited number of factors. For example, in lakes it is relatively easy to manipulate nutrient concentrations but very difficult to manipulate densities of predatory insects. Thus, in many situations, the only alternative is to

perform small-scale experiments and attempt to translate the results to larger scales.

For conceptual experiments the objective is to obtain a realistic representation of critical processes, rather than matching the physical dimensions of natural and experimental systems. As scale effects often can be attributed to changes in the relative importance of two or more critical processes or variables, this often requires that realistic ratios between critical variables be preserved. For example, experiments examining the effects of the spatial structure of a population on its dynamics should incorporate realistic relative magnitudes of within-patch processes (birth and mortality) and between-patch processes (emigration and immigration) (e.g. Hanski, 1997; Tilman *et al.*, 1997). If critical ratios can be reproduced in small-scale experiments, this may allow the direct application of results from model systems to natural systems (Petersen and Hastings, 2001). Several authors have suggested that dimensional analysis can be used as a tool for matching experimental and natural scales in ecology (Uhlmann, 1985; Schneider *et al.*, 1997; Petersen and Hastings, 2001).

1. Matching Scales Using Dimensional Analysis

Dimensional analysis is an established method in engineering for constructing small-scale models of bridges, boats, buildings, etc. that behave similarly to their real world counterparts. The method requires the formulation of a mathematical model that describes the dynamical behavior of both the prototype and the physical model. The mathematical model is then used to derive critical nondimensional variables that govern the behavior of the prototype and the physical model. A nondimensional variable is simply one that has been constructed by combining original model parameters or variables so that their units cancel out. To ensure dynamical similarity between physical model and prototype, the model is designed so that the values of the critical nondimensional variables are the same as for the prototype (Legendre and Legendre, 1998). A reduction in the size of a model system usually means that important components are distorted and the general principle for model design is to counteract these distortions through compensatory distortions in other components. The formal mathematical apparatus for performing dimensional analysis is well developed and useful introductions are found in Platt (1981) and Legendre and Legendre (1998). A simple example that illustrates the general principles is the application of the Reynolds number to create model systems for bodies moving through water. The Reynolds number is a dimensionless number that describes the balance between the inertial and viscous forces acting on an object moving in a fluid. It is useful

because it characterizes the degree of turbulence. The Reynolds number is given by

$$Re = UL/v, \tag{1}$$

where the U is the velocity of the object (unit = m s^{-1}), L is the length of the object (unit = m), and v is the kinematic viscosity of the medium (unit = m^2 s^{-1}). Re is dimensionless because the units of U, L and v cancel out. If we are planning to use a small-scale model (small L) to study the behavior of a larger prototype (large L) and want to preserve the Reynolds number we can see from Eq. (1) that there are two options, i.e. the velocity can be increased or the viscosity decreased.

Applying dimensional approaches to the design of ecological experiments involves consideration of a range of conceptual and practical matters (reviewed in Petersen and Hastings, 2001). Ecological systems are more complex than physical systems and often the effects of system size on their dynamics are not well understood. Thus a difficulty when applying the method is to identify the critical variables to be conserved. Attributes of ecological systems that often are distorted in small-scale experiments include space and time scales, environmental heterogeneity, environmental gradients, and interactions between adjacent habitats (Petersen and Hastings, 2001). Which, and how many, of the identified variables to conserve in order to preserve the match between model and real counterpart behavior depends on the nature of the research question, e.g. the processes of interest and the desired level of realism. System-specific experiments demand a greater degree of realism than conceptual experiments and thus require a higher degree of similarity.

In practice, the design approach prescribed by dimensional thinking involves matching the scale attributes of organisms, processes, and the abiotic environment. Often this amounts to preserving the "effective scale," which describes the scale of the system as experienced by the organisms. Effective scales are dimensionless ratios that are calculated by standardizing attributes of the experimental system by attributes of the organisms. As an example, consider an experiment that examines the effect of spatial structure on the dynamics of a patchily distributed population. In this experiment an important effective scale may be the distance between patches divided by the dispersal or movement distance of the organisms. Effective scales can be manipulated by changing the absolute dimensions of the experimental system or by altering the scale attributes of the organisms (movement distance, reproductive rate, perceptive grain and extent, etc.). A common strategy to preserve the effective scale in small experimental arenas is to use small experimental organisms (Wiens *et al.*, 1993; Gonzales *et al.*, 1998). The study by Ims *et al.* (1993) illustrates the principle. Ims *et al.* found that the

habitat use responses of organisms of different size (root voles and capercaillie grouse) were similar as long as the ratios between home range size and fragment size were comparable. Many tests of ecological theory using artificial communities of small organisms, such as mites and protozoans, could also serve as examples of the principle (Huffaker, 1958; Luckinbill, 1974; Kaunzinger and Morin, 1998; Lawler, 1998; Gonzales *et al.*, 1998).

In other situations, the objective may be to conserve effective heterogeneity or effective gradients. Huisman *et al.* (1999) used a reaction–diffusion model of phytoplankton species dynamics to determine if the phytoplankton dynamics of a deep lake could be reproduced in a shallow mesocosm. A formal dimensional analysis of the model showed that a tenfold reduction in depth should be accompanied by an increase in turbidity of the same magnitude, which would lead to a compression of the light gradient. Preserving the effective gradient required that the transport of algae along the compressed gradient was similar to that in the lake. This could be obtained by decreasing the diffusion coefficient 100 times. This scaling would lead to increased densities of all organisms but leave the outcome of competition unaltered.

An important limitation to the application of dimensional approaches to ecological experiments is our inability to manipulate many scaling attributes, in particular organismal attributes such as mobility, reproductive rate, home range size, acclimation to changing conditions, etc. Often, the only option is to choose different species that makes the method less useful for system-specific experiments, where the biotic community is fixed. Physical scaling attributes may also be difficult to manipulate. A common problem in aquatic mesocosm experiments is that the ratio of wall area to volume is much higher than in natural systems, but it is impossible to build a small mesocosm with a very low wall to volume ratio. At present, the use of dimensional analysis is also limited by our ignorance about the scaling relationships that governs the dynamics of many natural systems. Finally, many ecological variables respond to multiple environmental factors, either sequentially or simultaneously, and their net responses cannot be distilled to a dimensional model using a few key factors.

C. Extrapolation when Responses Vary with Arena Size

Often it is not possible to match the scale of an experiment with the scale of interest, so it becomes necessary to extrapolate experimental results to other spatial scales. In some cases it is possible to extrapolate across scales by using scaling models that describe relationships between responses and, for example arena size or experiment duration. Such models allow investigators

to translate small-scale results to larger scales, and can identify situations when responses are scale-independent. Scaling models can be developed from empirical relationships or mechanistic models; however, the latter requires that the mechanisms causing scale-dependence have been identified and their effects are well known. Knowledge of the mechanisms causing scale-dependent responses also is essential when delimiting the spatial and temporal domains where empirical and mechanistic models are valid. In the following sections we will first describe and classify mechanisms causing scale-dependence, then delineate some scaling models, and, finally, demonstrate the use of scaling rules in identifying scale-domains with strong or weak scale-dependence.

D. Mechanisms Causing Scale-Dependence

When discussing mechanisms for responses varying with arena size, it is important to distinguish between exclosure experiments and enclosure–exclosure experiments. In the first type of experiment some organisms, usually predators or competitors, are excluded from an area with a fence or cage, and the surrounding, unmanipulated habitat functions as a control. In essence, a very large unit, the natural system, is compared with a very small unit, the cage or arena. This means that treatment effects are likely to be confounded with the effects of any scale-dependent processes that influence the response variable. For example, if the densities of a species are enhanced in cages because the organisms aggregate along walls, this will cause estimates of treatment effects to be biased, and the magnitude of the bias will be scale-dependent given that the strength of the wall effect on the density of organisms varies with arena size (e.g. Doherty and Sale, 1985). In enclosure–exclosure experiments confounding is not expected to be a problem because treatments are assigned to identical and replicated experimental units. Instead, scale-dependent responses can occur because the effects of treatment factors are modified by scale-dependent processes (Peterson and Black, 1994). In ANOVA terminology, this corresponds to a "scale–treatment interaction." For example, if, in a predation experiment, predation rate is density dependent (predation rate per prey varies with prey density) and prey density varies with arena size, then scale-dependent predation rates per prey will be observed.

When reviewing empirical and theoretical literature, we encountered a large number of mechanisms that can cause experimental responses to change with the size of experimental units. We have chosen to parse this diverse collection of mechanisms into six partly overlapping categories. Our first category includes mechanisms related to exchange processes and the following two classes are related to observations that environmental

heterogeneity and organizational complexity usually increase with the scale of the experimental system. Our fourth category is termed "number effects" and deals with scale effects that occur because large systems include a larger number of organisms than small systems and the fifth class of mechanisms producing scale-dependent results deals with interactions between the response time of an experimental system and its size. These are all mechanisms that cause ecological responses to change with system size, unrelated to the use of enclosures (called fundamental scaling relationships in Petersen *et al.*, 1997). In contrast, our last category includes scale effects that are caused by the use of enclosures. Enclosure artifacts are usually related to the use of fences, walls, etc. and we refer to this class of mechanisms as "wall effects."

1. Exchange Processes

The arenas used in ecological experiments vary in their degree of openness, i.e. their permeability to the exchange of organisms and matter between their interiors and exteriors. The influence of many exchange processes on within-system dynamics is a function of perimeter-to-area ratios (or area/volume). Because this ratio is a function of arena size, it is expected that the influence of exchange often is scale-dependent. A well-studied empirical example is the negative relationship between per capita emigration rate and patch or arena size for many terrestrial insects (Kareiva, 1985; Matter, 1997; Sutcliffe *et al.*, 1997; Thomas and Kunin, 1999; Hanski *et al.*, 2000; Petit *et al.*, 2001).

The effects of organismal exchange (immigration, emigration) on experimental responses have been studied primarily in predation experiments in stream systems. Cooper *et al.* (1990) performed a meta-analysis of stream experiments and found a negative relationship between predator impacts on prey populations and various indices of prey mobility. Experiments where prey migration across cage boundaries is manipulated by varying the size of the mesh used to enclose predators show that prey migration rates often affect the impact of predators on prey populations; however, the direction of this effect is variable and depends on prey behavioral responses to predators (Cooper *et al.*, 1990; Lancaster *et al.*, 1991; Dahl and Greenberg, 1999; Sih and Wooster, 1994). A negative relationship between predator impact and prey migration is expected if prey decrease their dispersal rates in the presence of predators and actually accumulate and become denser in predator versus control cages, or if prey movements are independent of predator densities. The opposite pattern is expected if prey have a strong avoidance response, i.e. increase their dispersal rates in the presence of predators, contributing to an observed

predator reduction of prey densities beyond that expected from predator consumption rates alone.

Thus, we should expect predator impacts to change with scale in experiments where prey migration depends on arena size. Theory suggests that this should be the case when arenas are large compared to the movement scale of the organisms (i.e. each movement step does not result in emigration from the arena (see *scaling models; movement rates*, Englund and Hambäck ms). Available data on stream invertebrates suggest that indeed per capita emigration and colonization rates are scale-dependent on the scales typically used in stream experiments (Lancaster, 2000; Englund *et al.*, 2001; Englund and Hambäck, unpublished data). The interactive effects of prey exchange and arena size on predator impacts on prey populations were examined in a series of models by Englund (1997, presented in detail in Section IV.E.5). Cooper *et al.* (1998) examined the effects of predatory stoneflies on *Baetis* mayfly nymphs in stream channels ranging from 0.4 to 25 m in length. The effect of predators on prey densities decreased with increasing channel length. This was an expected result as *Baetis* nymphs usually increase their emigration rates in response to stonefly predators. In short, the model predicted that stonefly effects on mayfly prey would be enhanced by mayfly fleeing behavior at small scales, but that large scale impacts would be due entirely to stonefly consumption of mayflies. Similar results, however, were observed in channels where the prey exchange was prevented suggesting that some mechanism other than prey exchange (e.g. changes in environmental heterogeneity) was involved.

Exchanges of matter and energy between the inside and outside of experimental arenas have not been studied to the same extent as organismal movements; however, we expect the influence of these exchanges to be governed also by perimeter:area ratios. Petersen *et al.* (1997) presented data on primary productivity in mesocosms that were of identical shape and that ranged in size from 0.1 to 10 m^3. Under light-limited conditions it was found that primary productivity per unit volume decreased with increasing mesocosm size. Petersen and colleagues argued that total primary productivity should be proportional to the surface area that receives light under light-limited conditions. Thus, a low productivity per volume in large (and deep) mesocosms reflected the low ratio of surface area to volume.

2. Spatial Heterogeneity

Heterogeneity is a scale-dependent quantity in the sense that its description is determined by the grain (or resolution) and extent (or range) of observations. A general result is that the spatial heterogeneity of biotic and abiotic conditions within an arena increases with increasing arena area.

This scale-dependence of spatial heterogeneity can modify experimental responses in several different ways.

When the environment is heterogeneous on a scale that is large compared to the size of experimental arenas, it is likely that increasing arena size leads to a change in the mean levels of driving variables. For example, increasing the size of the experimental unit can alter the proportion of the area that functions as a prey refuge, affecting, in turn, the rate of predation (Englund and Olsson, 1996; Sarnelle, 1997). Although there are situations where the proportion of refuge space may increase or decrease with arena size, we suspect that large arenas usually contain a higher proportion of prey refuge habitat than small arenas, simply because it does not make sense to perform a small-scale predation experiment in a habitat where predators cannot capture prey.

Even if the mean level of a driving variable is scale-independent, it is likely that its spatial variance within experimental arenas increases with increasing arena size (see Section IV.E.6, Figure 7b, Wiens, 1989; Levin, 1992; Gardner, 1998). This scale-dependence of the within-arena variance for the driving variable can render the studied mean response scale-dependent if the level of the response variable is a nonlinear function of the driving variable (Rastetter *et al.*, 1992; Chesson, 1998). To see that variation in a driving variable, Z, can alter the observed response, $F(Z)$, consider the simple case when the driving variable only takes two values, Z_1 and Z_2, and the function relating Z and $F(Z)$ is nonlinear as shown in Figure 1a. The expected response for this case is indicated by A in Figure 1a. If, instead, the driving variable takes only one value, equal to $\bar{Z}$, the response indicated by B is expected. The effect of increased variability in the independent variable on the response is the difference between A and B in Figure 1a. In this figure, we can also see that the difference between A and B can be increased by increasing the depth of the curvature of the function and by increasing the variance in Z (i.e. increasing the distance between Z_1 and Z_2).

The potential importance of spatial heterogeneity is well-documented in mathematical population and community ecology. Spatially explicit models, such as reaction–diffusion models, lattice simulations, and individual based models, show that spatial heterogeneity in the densities of organisms often arise as a result of limited movements and local interactions between individuals (Tilman *et al.*, 1997), or arise from local stochastic variation in vital rates (Donalson and Nisbet, 1999). Heterogeneity alters global process rates if local processes are nonlinear as described above (e.g. Chesson, 1998). Often the processes generating heterogeneity also produce positive or negative correlations between the local densities of interacting populations. Such spatial correlations affect contact rates, e.g. encounter rates, between predators and prey, and thus have effects on global process rates (Law and Dieckmann, 2000). The influences of heterogeneity on the dynamics of

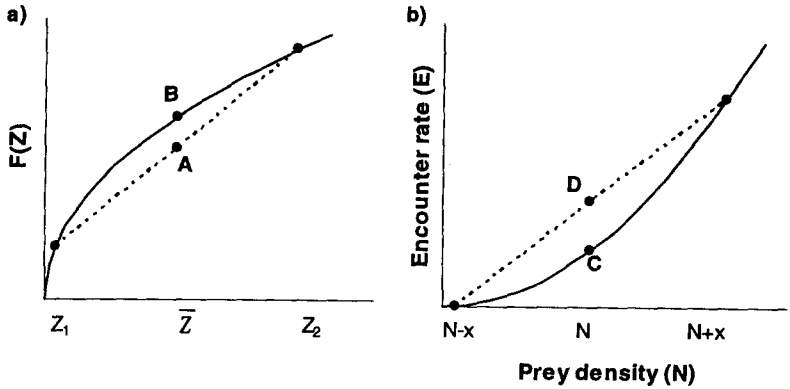

Figure 1 a) The figure illustrates that variation in a driving variable Z can alter the response $F(Z)$. If the driving variable takes two values, Z_1 and Z_2 the response indicated by A is expected and if the driving variable takes one value $\bar{Z}$ the response indicated by B is expected. b) Encounter rate as a function of prey density in a system with perfect coaggregation of predators and prey. The plotted function is of the form $E \propto N^2$. The encounter rate for a homogeneous system with density N is denoted C, whereas D denotes the encounter rate in heterogeneous system consisting of two habitats with densities $N-x$ and $N+x$.

interacting populations have been studied by comparing spatially explicit models and so-called mean-field models, which deal with the dynamics of mean densities averaged over space. Such comparisons show that spatial heterogeneity has a range of important effects on the outcome of species interactions, altering the qualitative outcome of competition (Levin and Pacala, 1997), promoting coexistence between competitors (Lehman and Tilman, 1997), stabilizing consumer–resource dynamics (deRoos *et al.*, 1991; Nisbet *et al.*, 1997; Pascual and Levin, 1999; Gurney and Veitch, 2000; but see Donalson and Nisbet, 1999) and influencing such food web characteristics as connectance and interaction strength (Keith, 1997). There is also empirical support for many of these predictions (e.g. Huffaker, 1958; Maly, 1978; Holyoak and Lawler, 1996; Holyoak, 2000a,b).

An empirical example where scale-dependent variation in driving variables caused the outcome of experimental manipulations to be scale-dependent was given in Bergström and Englund (2002). The interactions between a predatory isopod and its amphipod prey were studied in short-term experiments with no prey reproduction and constant average prey and predator densities across containers of different volume. It was found that the per capita mortality rate of prey increased with container size. Both predators and prey aggregated along container walls and their local densities along the walls were highest in large containers. Bergström and Englund argued that the scale-dependent per capita mortality rate of prey was caused

by the scale-dependent coaggregation of predators and prey. A simple model, shown in Figure 1b, can be used to illustrate this argument. Assume that predators track prey density perfectly, so that the predator density (P) is a fixed proportion of prey density (N), and assume that the encounter rate (E) is proportional to the product of prey and predator density. Thus we have $E \propto N^2$ (Figure 1b). A uniform prey density (N) produces the encounter rate response indicated by C in Figure 1b, whereas a higher average encounter rate (D) will result if there are two equally sized habitats with prey densities $N-x$ and $N+x$. Increasing the spatial variation (x) increases the difference between C and D. This means that an increase in arena size that results in more pronounced predator–prey coaggregation, and thus higher spatial covariation in predator and prey densities, is expected to increase encounter rate.

The two conditions required for this kind of scale effect to occur, nonlinear relationships between independent and response variables and increasing spatial variance with increasing size of the focal system, are widespread in ecological systems, suggesting that this scale-dependent mechanism is ubiquitous. General techniques that correct for scale effects caused by this mechanism are given in Section IV.E.6.

3. *Organizational Complexity*

Small-scale experimental systems often have a simpler structure than their natural counterparts, which can alter responses to experimental manipulations. When an experimental community is assembled by sampling a small fraction of the natural system, it is likely that the experimental community contains a reduced number of species and, consequently, that food chains are shorter and less complex than in larger natural systems (e.g. Schoener, 1989; Have, 1993; Spencer and Warren, 1996). Species most likely to be excluded unintentionally from experimental arenas are those occurring in low numbers, e.g. large species at high trophic levels and species strongly reduced by predation or competition. The low diversity of small systems limits the range of possible responses, which is particularly problematic in experiments where strong predators or competitors are removed. Obviously, a species that is excluded by a dominant competitor cannot respond to the removal of that competitor if it is not present and unable to colonize from some other system.

An empirical example of this mechanism was provided by Kohler and Wiley (1997) who studied the effects of *Glossosoma*, a grazing caddisfly that is a competitive dominant in small Michigan streams, on the rest of the stream community. Reductions in *Glossosoma* density in whole streams, caused by an invading parasite, resulted in the appearance of several species

of grazing caddisflies, which were presumably reduced to undetectable densities by *Glossosoma* in the unaltered situation. In contrast, *Glossosoma*'s effects on these caddisflies could not be demonstrated in small-scale removal experiments, probably because experimental units were too small to include very rare taxa or because these units were too small to attract or accommodate taxa colonizing from other areas.

Experimental systems may also have a simplified structure because some components are too large to be included. Trees, elephants, whales, salmon, and other large or wide ranging species must often be excluded. This is also true for many abiotic processes such as large-scale turbulence and stratification/destratification events in aquatic mesocosms (Scheurer *et al.*, 2001). Feedback mechanisms that involve the transport of organisms or matter may also require very large areas to be expressed. For example, Kohler and Wiley (1997) reported an increase in the densities of filter-feeding insect taxa when the dominant caddisfly grazer *Glossosma* was reduced in whole streams, presumably because declines in the dominant grazer caused large increases in algal biomass over large areas of the stream bottom resulting in higher levels of drifting algal food for filter-feeders. Such impacts were not observed in small, short-term field experiments, presumably because the spatial and temporal scales of grazer reductions were not sufficient to produce these large-scale, long-term indirect effects.

4. Number-Dependent Processes

If we increase the size of experimental units while keeping densities of organisms constant, there will be more individuals in large units. This can cause scale-dependence if the effects of an experimental treatment depend on the number of individuals present in each unit. For example, interference between predators can reduce predation rates, but requires more than one predator in the system. Similarly, aggregating, flocking, or schooling behaviors, which often affect predation rates, require a certain number of individuals to be expressed. Extinction thresholds are another form of number-dependence. In a classic laboratory study, Luckinbill (1974) studied cyclic population dynamics in a simple model protozoan community with one prey species and one predator species. One or both species quickly went extinct in small arenas but persisted much longer in large arenas. Crowley (1979) analyzed the system mathematically and suggested a hypothesis accounting for this pattern. He assumed that populations go extinct when the number of individuals, rather than the density of individuals, falls below a threshold. Increasing the total area of an arena, and thus the total number of individuals, decreases the probability that the total number will fall below

this threshold; consequently, expected persistence times increase with increasing arena size.

The number of habitat patches available to a population also can influence the risk of extinction. Populations whose long-term persistence depends on the movement of organisms between patches show increasing probabilities of extinction as the number of patches or subpopulations decrease (e.g. Holyoak and Lawler, 1996; Hanski, 1997; Hassel and Wilson, 1997).

5. *Effects of Experiment Duration; Interactions Between Response Time and System Size*

Theoretical and empirical investigations show that there are often delays in the responses of populations and communities to manipulations or perturbations. As a consequence, the temporal scale of experiments is very important in determining if transient dynamics or equilibrium responses are being observed. Interactions between response times and system size can cause responses to be scale-dependent if (a) the time to steady state after an experimental perturbation depends on arena size and (b) the experiment is sampled before steady state is reached. There is a range of mechanisms that potentially could cause response times to increase with spatial scale.

For open predation experiments, where prey movements affect local prey densities, Englund's (1997) model predicts that the time to reach steady state is particularly fast in small experiments where very high per capita migration rates are expected (see Section IV.E.5 and Figure 6). Similarly, it has been suggested that the time to reach chemical steady state in a lake after a perturbation is a function of hydrological turnover rate and, thus, of inflow rates and lake volume (Schindler, 1998). In these examples, it is the magnitudes of exchange rates in prey or water that determine the response time. Another illustration of this principle is that the time required for recolonization after a disturbance usually increases with patch size (e.g. Smith and Brumsickle, 1989; Duffield and Aebischer, 1994; Lancaster, 2000).

Sampling effects may affect response times. Large (and rare) taxa are often excluded from small units due to sampling effects. Because large taxa tend to have low vital rates (Peters, 1983; Schmidt-Nielsen, 1984; Dickie and Boudreau, 1987), we expect their presence to prolong response times. Also, small units tend to have shorter and simpler food chains (Schoener, 1989; Have, 1993; Spencer and Warren, 1996), and some mathematical models suggest that more complex food webs have longer recovery times after a perturbation (Pimm and Lawton, 1977).

Finally, as stated above, theoretical and empirical evidence suggests that the time to extinction increases with arena size (Luckinbill, 1974;

Crowley, 1979; Dickerson and Robinson, 1986; Bengtsson, 1993; Schoener and Spiller, 1995; Donalson and Nisbet, 1999). Species extinctions can have dramatic effects on the dynamics of natural systems (see review by Pimm, 1991) and we expect that extinctions, when they occur in experimental systems, will alter the effects of experimental treatments on ecological responses.

Although direct empirical evidence is scarce, it seems reasonable to assume that slower responses in large systems can cause treatment effects to be scale-dependent. This may make experiments conducted at different scales hard to interpret or compare, because manipulations conducted in arenas of different size will, at any given time, be at different points in their response trajectories. As a consequence, the appropriate temporal scale of an experiment will often depend on arena size. Indeed, it seems that many ecologists have adopted this view. Several recent meta-analyses reported positive correlations between the duration of experiments and the size of experimental arenas (Duarte *et al.*, 1997; Petersen *et al.*, 1997; Lodge *et al.*, 1998; Rafaelli and Moller, 2000).

6. Wall Effects

Walls and fences can have large effects on ecological patterns and processes and we expect their influences to be most important in small arenas, because small arenas have a large ratio of wall or edge to interior habitat. Walls, fences, or cage sides affect experimental systems and influence experimental outcomes because they are used as substrates by sessile organisms, because they alter the behavior of the enclosed organisms, because they alter environmental conditions (e.g. current velocity, sedimentation, air flow) inside cages, or because they hinder the exchange of organisms, matter, or energy.

The most intensively studied wall effect is the growth of periphyton on the sides of aquatic mesocosms. Although periphyton also grow on hard substrata in natural systems, it is clear that mesocosms, owing to their small size, have unrealistically high wall area to volume ratios. Wall periphyton often dominate primary production in mesocosms within 2–4 weeks (Rees, 1979; Chen *et al.*, 1997) and can influence important processes such as the uptake and regeneration of nutrients and the partitioning and degradation of toxic substances (Eppley *et al.*, 1978; Perez *et al.*, 1991; Chen *et al.*, 1997). Wall growth is particularly problematic when phytoplankton assemblages are the focus of an investigation because there can be intense competition for nutrients between periphyton and phytoplankton in small mesocosms (Chen *et al.*, 1997). Various mechanisms seem to influence the contribution of the wall periphyton to the total primary production in

experimental containers (Dudzik *et al.*, 1979; Chen *et al.*, 1997; see Section IV.E.2).

Walls can affect the behavior of organisms in various ways. Above we described the aggregation of organisms along walls, which can affect the strength of predatory and competitive interactions (see Section IV.D.2). Walls may provide cover for prey from predators, food for grazers, (Kennelly, 1983) and a favorable light environment for organisms preferring low light levels (Steele, 1996). Several authors have suggested that walls decrease predation rates because predators are stressed, or do not exhibit normal foraging behaviors, in small containers (Virnstein, 1977; Theliacker, 1980; Choat, 1982; Schofield *et al.*, 1988; Øiestad, 1990; Wilson, 1991; Paradis *et al.*, 1996; Heath and Houde, 2001). Others have suggested that the presence of walls increase predation rates (Peckarsky, 1991), possibly because predators trap prey in corners or because predators and prey aggregate along walls (Bergström and Englund, 2002).

Finally, it has often been demonstrated that walls and fences alter environmental conditions and exchange processes. Opaque walls cause a reduction in the amount of light available for primary production and this effect is most pronounced in small experimental units (Kennelly, 1991; Chen *et al.*, 1997). Walls also can alter the transmission of wave or wind energy. Usually walls impede the transfer of wave energy to the enclosed water body, which results in lower turbulence levels in mesocosms compared to the surrounding habitat (Verduin, 1969; Steele *et al.*, 1977; Bloesch *et al.*, 1988; Petersen *et al.*, 1998); however, the opposite pattern also has been reported (Quay, 1977; cited in Schindler, 1998). The level of mixing can affect a range of critical processes in pelagic systems, including nutrient dynamics, primary productivity, competitive interactions among phytoplankton species, and the growth and feeding rates of zooplankton (Perez *et al.*, 1977; Saiz and Alcaraz, 1991; Saiz *et al.*, 1992; Petersen *et al.*, 1998; Huisman *et al.*, 1999).

Cages often alter flow patterns and sediment deposition inside and around experimental units (Snelgrove *et al.*, 1995). For example, Kennelly (1991), who used cages to exclude fish in a kelp community, found greater reductions in water flow and higher sedimentation rates in small than in large cages. Often cages act like "sediment traps" causing increased internal densities of both organisms and sediments (Peckarsky and Penton, 1990). For example, Lancaster *et al.* (1990) found that the density of stream invertebrates in cages open to organismal exchange was four times higher than in the surrounding stream habitat during a period with high flow.

Solid walls can affect ecological processes by blocking the movements of organisms. A common situation is that prey migrate daily to avoid habitats or areas where predators are dense or particularly efficient (e.g. Jacobsen and Perrow, 1990; Ohman, 1990; Sih, 1992). Preventing such prey movements can substantially increase predation rates. Melville and Maly (1981)

presented data on the vertical distribution of predatory *Chaoborus* larvae and their zooplankton prey suggesting that zooplankton avoid *Chaoborus* by diel patterns in vertical migration. In a subsequent experiment they showed that preventing prey vertical migration increased predation rates 3–5 times compared to situations where zooplankton were allowed to vertically migrate. This situation is less likely to occur in large arenas because large (or deep) arenas more likely include habitats where prey can take refuge. Models incorporating this mechanism are given in Sih *et al.* (1988) and Englund and Olsson (1996).

E. Scaling Models

Several researchers have suggested that we should develop scaling models that describe how experimental results change with arena size and which, thus, can be used to extrapolate small-scale results to larger scales (Frost *et al.*, 1988; Wiens, 1989; Perez *et al.*, 1991; Schneider *et al.*, 1997). Such models also can be used to identify situations where experimental outcomes are scale-independent and, therefore, where extrapolations to other scales are relatively uncomplicated. Scaling models can be mechanistic or empirically derived and we present some examples of such models below. Most of the models deal with scale-dependent mechanisms related to arena edges and are based on simple geometric relationships, such as those between arena perimeter and area (or surface area and volume).

1. Movement Rates

Englund and Hambäck (ms) used diffusion models and random walk simulations to demonstrate that the scale-dependence of migration rates depends on the relationship between movement scale and patch size (Figure 2). The scale of movements is, in most situations, determined by the length of steps, which in an empirical context can be interpreted as the lengths of directed movements. When patches are large compared to the scale of movements, the relationship between migration rate (m) and patch size ($SIZE$) is described by a power function $m = k \times SIZE^{-\beta}$ where k is a constant and β describes the strength of the scale-dependence (domain III in Figure 2). The scale coefficient β depends on the dimensionality of the patch and is 1 for linear habitats and $1-d/2$ for two-dimensional patches (d is the fractal dimension of the perimeter). Thus, for two-dimensional arenas with smooth perimeters (e.g. circles or quadrates) the dimension is $d=1$ and the scale coefficient is $\beta=0.5$. The dimensionality of the perimeter of natural "two-dimensional" patches is typically somewhat higher than 1

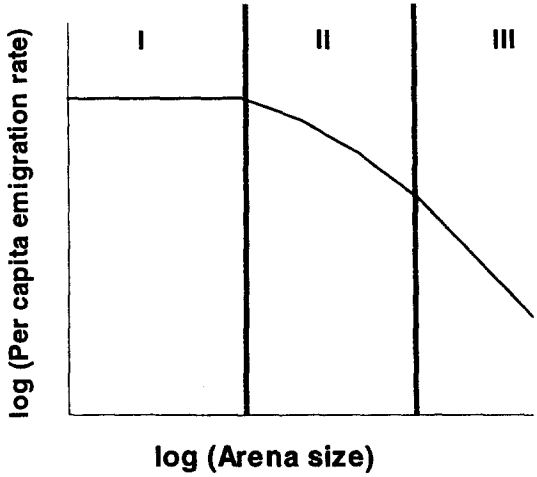

Figure 2 General scale-dependence of log per capita emigration rate versus patch size based on analyses of theoretical models. Roman numerals indicate scale domains that differ in the degree of predicted scale-dependence. In domain I there is scale independence and in domain III a power function relationship, whereas domain II represents an intermediate zone (modified after Englund and Hambäck ms).

($d = 1.1-1.5$) (e.g. Rex and Malanson, 1990), and, thus, such patches are expected to show weaker scale-dependence ($\beta = 0.25-0.45$).

For patches small compared to the scale of movements (domain I in Figure 2), per capita emigration rates are predicted to be independent of patch geometry and size. This result occurs because steps taken by organisms in the patch are so large that every movement results in emigration. As a consequence, small changes in patch size have no effect on the per capita emigration rate.

Empirical observations support these theoretical results. Englund (unpublished data) found that the scale coefficient (β) for emigration by aquatic invertebrates decreased with increasing step size, and the scaling coefficients for migration in terrestrial insects in natural two-dimensional patches tend to be in the expected range, i.e. $\beta = 0.2-0.5$ (e.g. Karevia, 1985; Kuussaari *et al.*, 1996; Matter, 1997; Sutcliffe *et al.*, 1997; Thomas and Kunin, 1999; Hanski *et al.*, 2000; Petit *et al.*, 2001).

2. *Growth of Wall Periphyton in Aquatic Mesocosms*

Several authors have suggested that the biomass of periphyton per unit volume in cylindrical mesocosms should be inversely proportional to the radius (r) of the container. This relationship is based on the fact that the

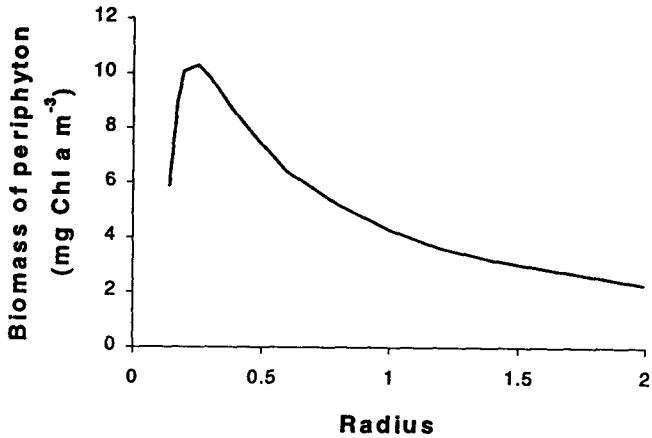

Figure 3 A model of the scale-dependence of periphyton biomass in a mesocosm experiment. The biomass of periphyton per volume (B_V) is given by Eq. (1) in the text and radius refers to the radius of mesocosms. Parameter values are taken from the autumn experiment in Chen *et al.* (1997).

ratio between wall area (A) and volume (V) for a cylinder is equal to $2/r$, and the assumption that periphyton biomass per unit wall area is independent of container size.

In an experimental study, Chen *et al.* (1997) found that the biomass per unit wall area (B_A), rather than being independent of container size, decreased linearly with the wall area to volume ratio (A/V), i.e. $B_A = a - b(A/V)$ where a and b are constants. Multiplying this expression by A/V gives the scaling relationship for biomass per volume $B_V = a(A/V) - b(A/V)^2$. Substituting A/V with $2/r$ gives

$$B_V = 2a/r - 4b/r^2. \tag{2}$$

This equation produces a hump-shaped relationship between biomass per volume and container size (Figure 3). At large scales B_V decreases in proportion to $1/r$ which indicates that periphyton biomass is determined by surface area-to-volume ratios. However, in small containers some other process, represented by the negative term ($-4b/r^2$), influences the scale-dependence of B_V.

3. Predation Along Edges

Predation rates can be affected by edges because predators are more effective at encountering or catching prey in edges or corners. For example,

if predators and prey have a random distribution and predators catch most of their prey near container walls, we can expect the number of prey eaten by predators to be approximately proportional to the wall area. Thus, the number of prey eaten per predator (E) in a cylindrical container should be approximately proportional to the ratio between wall area and container volume i.e. $E \propto r^{-1}$, where r is the radius. The scaling relations found in empirical studies often deviate from this expectation. A common result in studies of pelagic predator–prey systems is that feeding rates increase with arena size (Cooper and Goldman, 1982; Fulton, 1982; LaFontaine and Leggett, 1987; Marrasé *et al.*, 1992; Gorokhova and Hansson, 1997; Bergström and Englund, 2002). As discussed in Section IV.D.2, a possible explanation for this pattern is scale-dependent aggregation along edges by both predators and prey (Bergström and Englund, 2002).

A simulation model incorporating this mechanism for scale-dependent effects was developed by Bergström and Englund (2002). Predators and prey were assumed to perform a random walk in a circular arena that was divided into an interior habitat and a narrow wall habitat. When an individual encountered the wall, the direction of the next step was determined by the organism's affinity for the wall, a variable specifying the probability that the next step would be taken along or away from the wall. Encounter rates were assumed to be proportional to the product of predator and prey density in each habitat. The model predicted a positive relationship between predator–prey encounter rates and arena radius in small arenas, but a negative relationship in larger arenas (Figure 4). The initial increase of encounter rate occurred because densities of predators and prey in the wall habitat increased with increasing arena size. This raised the encounter rate in the wall habitat and, thus, the predator–prey encounter rates in the whole arena. Several mechanisms accounted for the declining phase of the curve, the most important being that individuals in large containers spent a larger proportion of their time in the interior habitat before encountering the wall.

4. Competition Between Littoral Grazers

MacNally (1997, 2000) used spatially explicit simulation models to examine how foraging behavior and arena size affected the consumption rates and exploitation competition among intertidal grazers, such as gastropods. Consumers were placed in model habitats consisting of cells arranged in a grid. Within cells, algal growth was density-dependent and algal mortality due to consumption was described by a satiating functional response. Consumers moved between cells but did not grow, die, or reproduce. Experiments with enclosures of different size were simulated by restricting movements to a smaller number of cells.

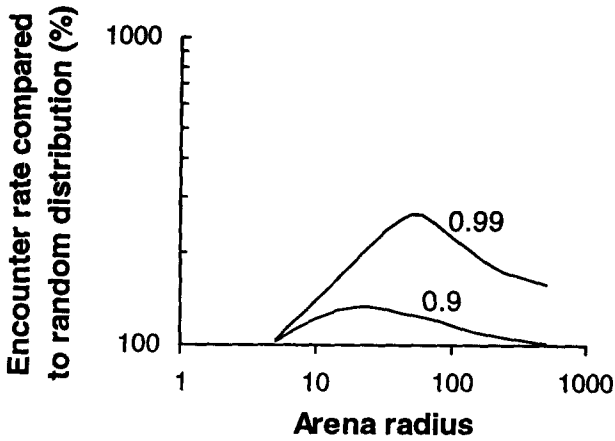

Figure 4 The graph shows how encounter rates change with arena radius when predators and prey coaggregate in a narrow edge habitat. Predictions were generated by the simulation model presented in Bergström and Englund (2002). The two curves represent different values of wall affinity, which is the probability that an individual that has encountered a wall will take the next step along the wall or into the interior. Encounter rate values are standardized by dividing by the encounter rate expected if predators and prey have a random distribution.

In general, the model predicted increasing grazer consumption rates with increasing enclosure area; however, this pattern was modified by the grazers' foraging strategies and movement rates. For optimal foragers that selected the most profitable food patches, a different pattern was observed. At low and intermediate grazer movement rates, the effects of enclosure size on grazer consumption rates were notably nonlinear with the lowest consumption rates observed in enclosures of intermediate size (MacNally, 2000). As a consequence, the outcome of exploitative competitive interactions between grazers using different foraging strategies changed with arena size in a rather complex manner. Competition coefficients observed in simulated enclosures differed from those of free-ranging individuals by as much as 30–40%, and for some foraging strategies it was found that small scale experiments would produce erroneous conclusions about the relative strengths of intra versus interspecific competition at large scales.

5. Predation and Prey Movements

Englund (1997) analyzed scale-dependence in the effects of predators on local prey populations using models of open predation experiments where prey could move into and out of experimental units. The fundamental

assumptions of these models were that the influence of prey migration on prey density decreased with increasing scale whereas predation rate was scale-independent. A consequence of these assumptions is that prey densities are controlled by prey migration in small arenas and by direct predation in large arenas. One of the models was intended to mimic short-term cage experiments performed in a system without predators in the surrounding, natural habitat. It was assumed that prey densities were determined by migration in control units and by both migration and consumption in predator units, i.e.

$$dn_c/dt = m_o n_o - m_c n_c \tag{3}$$

$$dn_p/dt = m_o n_o - (m_p + q)n_p \tag{4}$$

where the subscripts c, p, and o denote control units, predator units, and the area outside the experimental units, n is prey density, q is predation rate per prey, and m is a constant that relates the number of individuals that cross the perimeter (i.e. cage walls) per unit time to the density in the source area. Scale-dependence is introduced by assuming that the constant, m, decreases with arena size, i.e. $m = k \times SIZE^{-\beta}$, where k is a constant and β describes the strength of the scale-dependence.

This model predicts that predator impacts on prey densities ($PI = \ln(n_c/n_p)$) vary in a sigmoidal fashion with increasing arena size as long as the migration rate is scale-dependent ($\beta > 0$)(Figure 5). The relationship between PI and arena size can be positive or negative depending on the behavioral response of the prey to predators. Increasing PI with increasing arena size is expected if prey migration is independent of predator presence ($m_p = m_c$ in Figure 5) or if prey "freeze" in response to predators, i.e. decrease their dispersal out of predator units ($m_p < m_c$). The opposite relationship, i.e. decreasing PI with increasing arena size, is expected if prey increase their dispersal out of predator versus control units (e.g. $m_p > m_c$ in Figure 5). Arena size also affects the response time of prey populations to predators (Figure 6). In small arenas, the PI value quickly reaches an asymptote set by $\ln(m_p/m_c)$ whereas PI in very large arenas is predicted to increase linearly from small to moderate amounts of time (t), i.e. $PI = qt$ (Englund *et al.*, 2001).

6. Scale-Dependent Heterogeneity and Nonlinear Responses – Aggregation Error

If small-scale experiments show a nonlinear relationship between a response (e.g. consumer consumption rate) and independent variable (e.g. resource density), then these results cannot be extrapolated directly to larger scales if

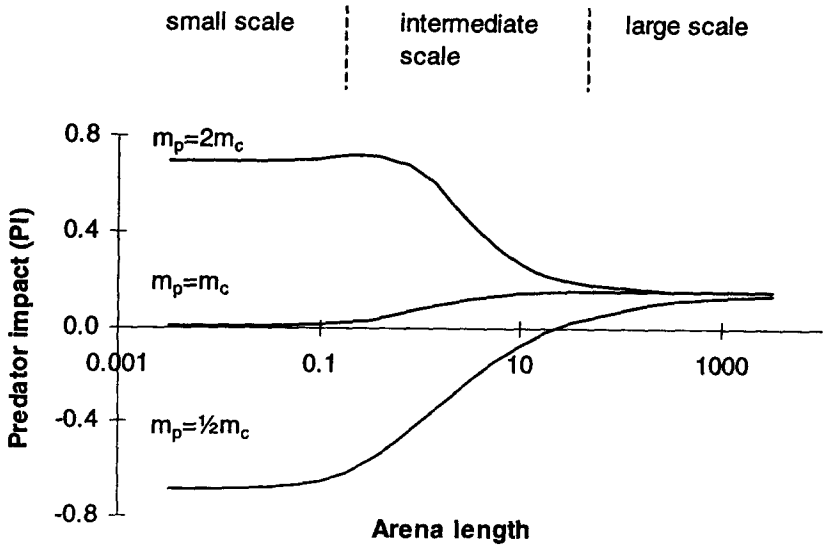

Figure 5 Predicted relationships between predator impact and spatial scale for experiments performed in a habitat without predators in the background. The predator impact index is given by $PI = \ln(n_c/n_p)$, where n_c and n_p are prey densities in control and predator treatment units. $m_p = 2m_c$ refers to a situation where area-specific migration rates are higher in predator than control cages (avoidance), $m_p = m_c$ means that emigration rates are equal in the two types of cages, and $m_p = 0.5\ m_c$ refers to a situation where prey decrease emigration rates in the presence of predators ("freezing"). Predictions were generated by solving Eqs (3) and (4) with respect to time (see Englund *et al.*, 2001) and assuming that migration rates $m \propto Area^{-1/2}$. Consumption rate (q) is 0.01 per unit time, area-specific emigration rate in control cages (m_c) is 0.05 per unit time, and the model is run for 20 time units. At the top we have indicated the approximate boundaries between the three scale domains described in the text.

levels of the independent variable in the larger system are more spatially heterogeneous than in the experimental system. The underlying mechanism is illustrated in Figure 1. The bias caused by this mechanism is often called aggregation error and there are several general methods that can be used to modify a function estimated from small-scale units so that it applies to larger and more heterogeneous systems (O'Neill and Rust, 1979; O'Neill, 1979; King, 1992; Rastetter *et al.*, 1992).

When the small-scale function is simple and the variation between small-scale units can be quantified, it is often possible to derive a corrected function that gives an unbiased description of the behavior of the large-scale system. One such method is extrapolation by expected value (Rastetter *et al.*, 1992). Extrapolation by expected value requires that the small-scale function $f(z)$ is known and that the variation among small-scale units in the driving

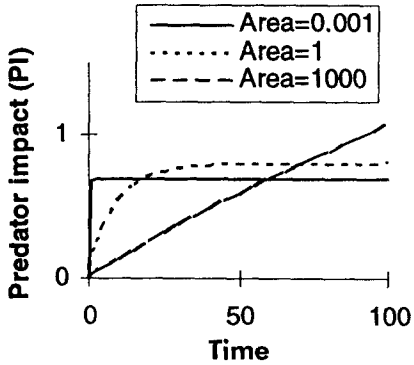

Figure 6 Predicted changes in predator impact on prey density (*PI*) through time for experiments conducted at three different spatial scales. Predictions were generated by solving Eqs (3) and (4) with respect to time (see Englund *et al.* 2001) and assuming that migration rates $m \propto Area^{-1/2}$. Area-specific emigration rates were 0.05 per time unit in control cages and 0.1 per time unit in predator cages. Other parameter values are given in Figure 5.

variable (z) is quantified by a probability density function $\rho(z)$. The resulting large-scale function F is found by solving the integral

$$F = \int_{-\infty}^{+\infty} f(z)\rho(z)\,\mathrm{d}z \tag{5}$$

The resulting equation has a different structure than its small-scale counterpart as the original driving variable (z) is replaced by the parameters of the probability density function $\rho(z)$. Alternatively, spatial variation among small-scale units can be described by specifying the driving variable (z) as a function of the spatial coordinates, $z = g(x,y)$ (for details and relevant models see King 1992).

When the small-scale function is complex, it may become impossible to solve the integrals, or the complexity of the solution may reduce its usefulness. A Taylor series expansion can be used to find simpler approximate functions. Expanding the small-scale function $f(z)$ around the mean ($\bar{z}$) yields the following series

$$F = f(\bar{z}) + \frac{f^{(2)}(\bar{z})}{2!}m_2 + \frac{f^{(3)}(\bar{z})}{3!}m_3 + \frac{f^{(4)}(\bar{z})}{4!}m_4 \tag{6}$$

where $f^{(i)}(\bar{z})$ is the ith derivative of $f(z)$ evaluated at $\bar{z}$ and m_i is the ith statistical moment of $f(z)$ about $\bar{z}$, i.e. m_2 is the variance, m_3 is the skew, and m_4 is kurtosis (Chesson, 1998). The first term in this series is the small-scale function, $f(z)$, evaluated at the mean value of the heterogeneous driving

variable (z). The following terms represent corrections to this first estimate. If the small-scale function can be approximated by a quadratic equation, a good approximation to the large-scale function F is obtained by retaining the first two terms. The resulting large-scale function is given by

$$F = f(\bar{z}) + c\sigma^2, \tag{7}$$

where σ^2 is the variance in z among small-scale units and $c = 0.5f''(\bar{z})$ (Chesson, 1998). The following example illustrates how this result can be used. The densities (N) of an organism in a number of small patches are recorded and it is found that the change in densities from one year to the next in a patch is described by the equation:

$$N_{t+1} = N_t + rN_t(1 - N_t/K). \tag{8}$$

If we want to find an equation that describes the dynamics of the collection of patches using the mean density across all patches ($\bar{N}_t$) as the argument we can apply Eq. (7). The second derivative of Eq. (8), $(\mathrm{d}^2N_{t+1}/\mathrm{d}N_t^2)$, is $-2r/K$. Thus the correction factor is $c = -r/K$ and the corrected equation is

$$\bar{N}_{t+1} = \bar{N}_t + r\bar{N}_t(1 - \bar{N}_t/K) - \sigma^2 r/K, \tag{9}$$

where σ^2 is the variance in density among the patches. Equation (9) is exact because Eq. (7) is a quadratic function and the higher order terms in the moment expansion are zero. For functions not well approximated by a quadratic, it may be necessary to retain more terms which requires the estimation of higher statistical moments (skew, kurtosis etc.).

So far we have shown how corrections can be made for a single variable. Although the methods can be extended readily to include corrections for several variables (see Rastetter *et al.*, 1992), the complexity of the resulting functions will often prevent their application. Extrapolation by calibration is another approximate method that can be used when large-scale data are available (Rastetter *et al.*, 1992). In this case, the small-scale function is fitted to the large-scale data and new parameter values are estimated. The most important strength of this method is that it allows all sources of aggregation errors to be corrected, even unknown sources, without increasing the complexity of the model. An obvious disadvantage is that it requires large-scale data, when it is precisely the lack of such data which motivates the need for extrapolations from small to large scales.

A related problem is an active area of research in mathematical population ecology. The output of spatially explicit simulation models often deviates substantially from corresponding mean-field models that ignore spatial variation in the levels of driving variables. Due to the complexity of spatial simulation models, it is often difficult to elucidate the

essential processes that determine spatial and temporal dynamics; however, understanding can be obtained by formulating analytically tractable models that reproduce the output of spatial simulation models. One method to simplify stochastic spatial models is to use moment equations. The mean abundances of each species are described as functions of mean densities, variances, and covariances. As variances and covariances are dynamic state variables that are influenced by local interactions, it is necessary to formulate equations that govern variances and covariances as well. These equations contain third-order moments, which also are dynamic entities. It is thus necessary to find methods to truncate the series of equations. Important results are given in, for example, Matzuda (1992), Pacala and Levin (1997), Pascual and Levin (1999), Ellner (2001), and Filipe and Gibson (2001).

Because the error caused by nonlinear averaging is approximately proportional to the variance among small-scale units (σ^2), it is important to know how this variance depends on the grain and extent of our observations. A general pattern is that an increase in the grain (with extent kept constant) reduces the variance among units at a decelerating rate (Figure 7a) (Wiens, 1989; Gardner, 1998). For a randomly distributed variable (no spatial autocorrelation), the variance is expected to be inversely proportional to grain size, i.e. the relationship is described by a power function of the form $VARIANCE = k \times AREA^{\beta}$, with β being equal to -1 (Wiens, 1989; Gardner, 1998). Note that this result assumes that the random variable is a concentration variable, such as the density of organisms. If the variable is spatially autocorrelated, which is the case for the tree density data shown in Figure 7a, the slope parameter (β) will generally be between 0 and -1 (Wiens, 1989; He *et al.*, 1994; Gardner, 1998). In contrast, an increase in the

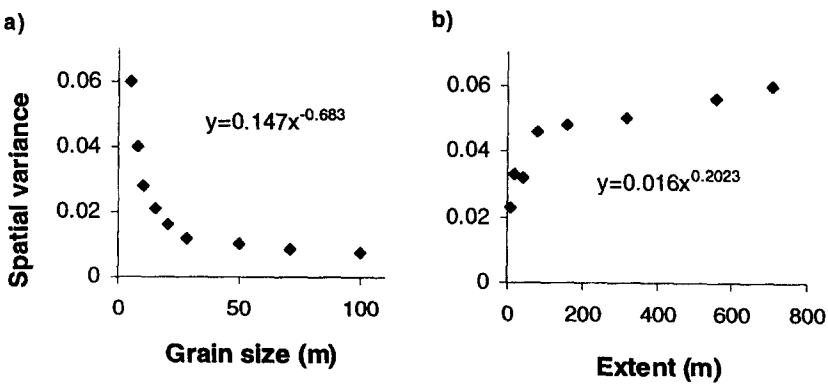

Figure 7 Relationships between (a) grain and variance and (b) extent and variance for data on tree density in a Malaysian rainforest (data from He *et al.*, 1994).

extent of an experiment (with grain kept constant) causes the variance among units to increase at a decelerating rate (Figure 7b), because new types of patches will be encountered at a decelerating rate as the range of observations increases. From these relationships it follows that the magnitude of the aggregation error is a function of the scope, or the ratio of extent/grain (Schneider *et al.*, 1997). In general the magnitude of the aggregation error is expected to increase with increasing scope. However, for more complex functions involving several variables with opposing effects on the aggregation error, the opposite pattern can be observed (Melbourne, 2000).

F. Using Scaling Models to Identify Critical Scales and Scale Domains

Scaling models used for quantitative extrapolation must be validated by comparing predictions with empirical data, and the empirical domain for which the model has validity must be carefully defined. Because experimental results typically are influenced by more than one scale-dependent process, we also expect that useful scaling models often will include several different processes. Obviously, few, if any, of the scaling models presented above meet these criteria.

At this stage we believe that the value of scaling models primarily lies in their ability to make broad, qualitative predictions. Perhaps most importantly, they can be used to identify scale domains with little or no scale-dependence, making extrapolations across scales straightforward. This use of scaling models is exemplified by a study of grazing on bacteria (Marrasé *et al.*, 1992). Marrasé *et al.* (1992) found that container size had little effect on grazing rates when containers were one liter in volume or larger, resulting in their subsequent use of 1-liter containers in experiments.

Many of the models based on perimeter/area relationships suggest that scale-dependence in ecological responses to manipulations or perturbations tend to disappear at large scales. The contribution and effects of wall periphyton on total primary production approach zero at large scales (Chen *et al.*, 1997) and the effect of predators on prey densities approaches an asymptote set by the product of time and predation rate in the model examined by Englund (1997). Likewise, in the model of predation along edges it was found that encounter rate was unaffected by predator–prey coaggregation above a certain arena size (Bergström and Englund, 2002). Other factors and processes that cause scale-dependent responses also have an asymptotic or logistic relationship with arena size. This is true for species richness (He and Legendre, 1996), for number effects due to interference and grouping behaviors, and for the effects of demographic stochasticity and the

number of subpopulations on extinction risk (Bengtsson, 1989; Hassel and Wilson, 1997). It, thus, may be possible to identify a threshold size above which scale-dependence is negligible. Experiments in this scale domain should provide accurate estimates of whole-system responses. A relevant question, then, is how small arenas can be and still provide accurate estimates of large-scale results. Sarnelle (1997) examined this question in the context of *Daphnia*'s effects on micro-zooplankton and concluded that experiments in large plastic bags (diameter 1.5 m, depth 7 m), but not in small bags (15 l), provided reasonably accurate estimates of whole-lake responses to *Daphnia* removals. Englund (1997) used models of predation in an open system to answer a similar question, namely, how much migration could be allowed given that predator impacts on prey populations should be within ±5% of the impact seen at the whole (i.e. closed) system scale (i.e. the population level response). He found that a migration rate representing 1–4% of the prey population inside arenas per day would produce similar results to those at the largest scales, given experimental durations and predation rates typical for stream predation experiments. Much lower relative migration rates were required if prey altered their movement behaviors in response to the presence of predators.

Scaling models of this type also can be used to identify scale domains where scale-dependent responses are very strong or complex. Extrapolation of experimental results obtained in such domains to other scales is likely to be especially difficult. Scale domains with particularly strong scale-dependence can be identified in the model of wall periphyton (radius 0.2–0.4 m, Figure 3) and in the model of predator impacts on prey in open predation experiments (arenas of intermediate size, Figure 5).

Often the strongest scale-dependencies are observed at the "critical scale," where two antagonistic rates are of equal magnitude. In the model shown in Figure 5 the strongest scale-dependence occurred when both migration and predation mortality influenced prey densities. Critical scales can be plotted in a rate diagram such as Figure 8. In this plot the solid lines indicate the spatial and temporal scales where movement and mortality rates are equal for large Atlantic cod (Schneider *et al.*, 1999). In such a graph it is easy to determine what processes dominate responses or patterns at the scale covered by an experiment or a sampling program. It also has been proposed that results should not be extrapolated across critical scales (Schneider, 2001b).

We used a related approach to study scale domains for published stream predation experiments using the model in Englund (1997). Figure 5 shows that the model can be used to identify three scale domains: a small-scale domain where prey movements (including movement responses to predators) control prey densities, a large-scale domain where prey densities are controlled by predation, and an intermediate domain where both

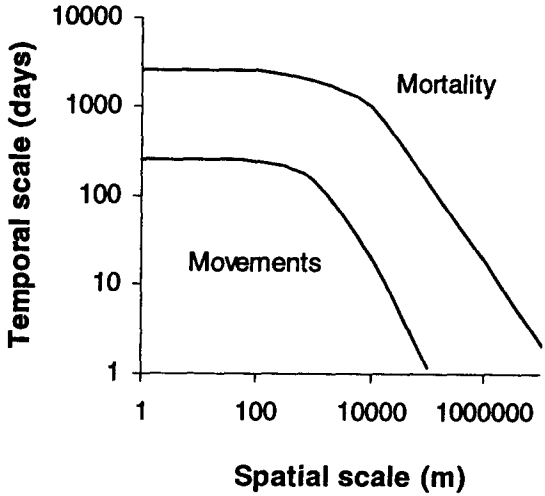

Figure 8 Rate plot comparing mortality rate (M) and movement rate (F) as a ratio ($R = M/F$) in large Atlantic cod (length > 100 cm). Estimates of rates are based on literature data. Because published estimates of rates varied between studies, two lines were drawn that represent critical scales ($R = 1$). The lines were calculated using either a high estimate of mortality rate and a low estimate of movement rate or a low mortality rate and a high movement rate, respectively. Thus the area between the two lines represents scales where data are not precise enough to determine which of the two rates is higher. Lines were computed with Monte Carlo methods (redrawn from Schneider *et al.*, 1999).

processes are important. Response times also differ among domains, with the longest times to equilibrium being predicted for experiments conducted in the large-scale domain (Figure 6). To determine the scale domain of published experiments, we used estimates of prey migration rates and predator consumption rates reported in the literature, as well as Englund's (1997) model, to simulate scale-dependence in the results of experiments examining the effects of stream predators on benthic prey (Englund *et al.*, 2001). Figure 9 shows the predicted scale-dependence of predator impacts on prey for a small experiment, where 1.5 m long channels were used as experimental units (Dahl, 1998), and a much larger experiment, where 35-m long sections of a stream were used (Forrester, 1994). For two highly mobile prey taxa, *Baetis* and Simuliidae, Dahl's experiment was conducted in the small-scale domain with weak scale-dependence and predator impacts controlled by prey movements (Figure 9a), whereas the predicted predator impact on mayfly taxa was close to the asymptotic value predicted for very large arenas in Forrester's experiment (Figure 9b). Thus Forrester's experiment belongs to the large-scale domain where predator consumption of prey controls predator impacts on prey populations. This exercise

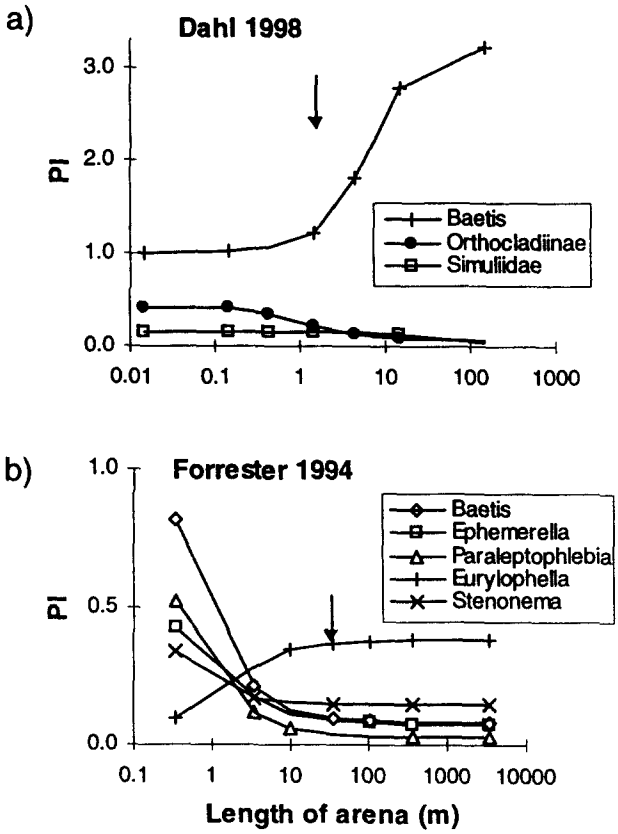

Figure 9 Predicted relationships between predator impacts on prey taxa (*PI*) and spatial scale in two experiments. Predictions were calculated using a model assuming that there are predators in the background habitat. The model was parameterized using predation and prey migration rates given in Forrester (1994) for the treatment with intermediate char density, and Dahl (1998) for the trout treatment. *PI* is defined in Figure 5. Arrows denote the length of experimental units used in each experiment (from Englund *et al.*, 2001).

suggests that some results of Dahl's experiment should be interpreted in the light of habitat selection models rather than traditional models of population dynamics, whereas the results of Forrester's experiment may indicate predator impacts on prey populations.

An analysis of a data set that included most stream predation experiments published before 1997 showed that most studies used arenas that were much smaller than those of Dahl and Forrester. Seventy-three percent of the experiments were performed in arenas ranging from 0.1 to 1 m in length, indicating that many of these experiments estimated the effects of prey

movements and habitat selection rather than the effects of direct predation on local prey populations (Englund *et al.*, 1999a,b).

V. EXTRAPOLATION BY COMBINING MANY SMALL-SCALE MEASUREMENTS

A. Statistics as a Framework for Extrapolation in Field Experiments

Statistical theory relevant to experimental design, parameter estimation, and inference is used frequently as a framework for extrapolation in the sense that observations of a limited number of individual units are used to draw conclusions about whole populations or systems. General statistical theory and methods are available in standard textbooks (Winer *et al.*, 1991; Manly, 1992). The use of mixed model designs and random block or site factors is a particularly powerful framework for extrapolation in field experiments (Dutilleul, 1993, 1998a,b; Beck, 1997). As an example of a mixed model design, consider an experiment where a treatment with two levels is applied to pairs of ponds, which are near each other. The pairs, henceforth called blocks, are randomly chosen from a larger population of ponds. A design of this type is called "mixed" because it contains both a random factor (block) and a fixed factor (treatment). The strength of this design is that it allows conclusions about treatment effects to be generalized to the population of ponds (Beck, 1997). It is crucial, however, that the units specified by the block factor are selected at random. Ecologists commonly repeat experimental manipulations at different sites that are selected because they represent different levels of some environmental factor, e.g. sheltered/exposed or dry/moist conditions (Menge *et al.*, 1994; Englund and Krupa, 2000). In these cases the site factor must be treated as a fixed factor and, strictly, treatment responses cannot be extrapolated beyond the examined sites (Winer *et al.*, 1991; Beck, 1997). An alternative to mixed model designs is completely randomized designs where treatments are applied to randomly selected experimental units (Winer *et al.*, 1991). This design allows extrapolation to a larger population of units but, because it does not account for spatial heterogeneity on scales larger than experimental units, it will often have lower statistical power than block designs (Dutilleul, 1993, 1998a,b). Finally, if environmental factors potentially affecting treatments are selected a priori, then investigators often use ANCOVA designs which allow the influence of environmental factors on treatment effects to be inferred. However, results cannot be extrapolated outside the range of values of environmental factors encountered.

The treatment effect in a mixed model ANOVA design, i.e. the differences in response between treated and control units within blocks, is analogous to individual observations in a sampling program. This suggests that we can apply general theory about how the scale of a sampling program affects its sensitivity to spatial heterogeneity at different scales (Allen and Hoeckstra, 1991). According to this theory we expect that an increase in the sampling grain and/or extent makes the sampling program more sensitive to large-scale heterogeneity. Because different processes create heterogeneity at different scales, it is, to some extent, possible to control the processes that are studied by selecting the scales of observation (Allen and Hoeckstra, 1991). Thus, this theory suggests that the grain and extent of experiments determines the scale of heterogeneity and, thus, the underlying processes that can possibly modify treatment effects. Conversely, this reasoning implies that experiments conducted at different scales test somewhat different hypotheses even though identical treatments are applied. As a consequence, the grain and extent of an experiment should be a deliberate choice, motivated by the hypothesis tested and based on knowledge about how heterogeneity of the system under study changes with the scale of observation.

Other practical and statistical considerations typically influence the design and scale of experiments, perhaps most importantly the trade-off between scale (grain and extent) and statistical power. Increasing the extent, by covering a larger area or by covering a wider range in some environmental variable, tends to increase the variation among experimental units (Figure 7b) and thus reduces statistical power. Conversely, restricting the experiment to a small area, or a narrow range of environmental conditions, increases statistical power but reduces the generality of the results. The grain of an experiment also may influence its statistical power. If the size of experimental units are increased, this leads to reduced variation among experimental units and blocks (Figure 7a), and thus to increased statistical power. Another important aspect of the scale of an experimental design is the lag or the distance between neighboring units. As the lag influences the degree of spatial autocorrelation in the observed responses, it can affect the accuracy of estimated parameter values and confidence intervals (e.g. Carrol and Perrson, 1998; Bonham and Reich, 1999).

B. Sample Experiments, System-Unit Experiments, and Aggregation Error

When discussing extrapolation in field experiments it is useful to distinguish between "system-unit experiments," where each experimental unit is a system that we want to make inferences about, and "sample experiments,"

where the experimental units are samples from a larger system and the objective is to use observations from the experimental units to estimate parameters that characterize the large-scale system. An example of a system-unit experiment could be the manipulation of fish densities in a number of small isolated lakes. The objective, then, could be estimating parameters that describe the effects of fish manipulations on prey densities in this population of lakes. The parameters can be used to predict predator effects on prey densities in a typical lake with similar characteristics. An example of a sample experiment would be to subdivide a small lake into sectors and manipulate fish densities in the sectors (e.g. Tonn *et al.*, 1992), with the objective of using observations in sectors to estimate parameters that describe the effects of fish density on prey populations in the entire lake. Other examples are many field experiments in agricultural research. A field, which often corresponds to the scale of interest, is subdivided into plots that receive different treatments.

The nature of extrapolation is different in the two types of experiments because the experimental units are different (parts or the whole). One consequence is that aggregation error is a potential problem in sample experiments but not in system experiments. This, in turn, has implications for how measurements made in experimental units should be aggregated in sample experiments. Aggregation errors can arise when measurements made on small-scale units are applied to larger and more heterogeneous units (Rastetter *et al.*, 1992; Chesson, 1998). In particular, such errors occur when a) the studied response is a nonlinear function of variables or parameters, and b) there is variation among small-scale units in these variables or parameters (see Section IV.D.2. and Figure 1a for an explanation of this mechanism). To illustrate this problem, consider a sample experiment with a mixed model design. Predator densities are manipulated so that units within blocks either have natural predator densities, P, or no predators, and the densities of prey, N_p and N_c, in predator and control cages are recorded after some time t. A biological interaction coefficient such as $a = \ln(N_c/N_p)/Pt$ (Laska and Wootton, 1998; Osenberg *et al.*, 1997) is estimated with the ultimate objective of incorporating it into a population model that can predict the dynamics of the predator and prey populations (Berlow *et al.*, 1999; see also a critique in Abrams 2001). Note that the interaction coefficient, a, corresponds to the attack coefficient in a model of the form $N_t = N_0 e^{-at}$, and thus that its relation to prey density (N_t) is nonlinear.

If we first calculate a for each block and then the mean a value for all the blocks (which would be the natural choice for a system-unit experiment), i.e. $a = (1/n)\sum_{i=1}^{n} \ln(N_{ci}/N_{pi})/tP$, and include this estimate of a in a population model, then the predicted dynamics will not accurately reflect the dynamics of the entire system, given that there is variation in a among blocks. If, instead, a is calculated from the mean density for all predator units and the

mean for all control units, i.e. $a = \ln(\bar{N}_c/\bar{N}_p)/Pt$, the resulting estimate can be used to characterize changes in prey densities owing to predation in the whole system.

In this simplified example, the objective was to estimate a single response value for an entire system and it was possible to calculate an unbiased estimate of the large-scale response. However, often we want to estimate how response values vary across some heterogeneous property of the system, such as the functional response that describes how the interaction coefficient varies with prey density (e.g. Melbourne, 2000). In this case, it may be possible to estimate a small-scale function from experimental data if there is sufficient variation among units in the driving variable, and a large-scale function, that describes the ecological responses of the larger and more heterogeneous system, can be estimated using the methods proposed in Section IV.E.6.

C. How to Quantify Heterogeneity

From the discussion in the two previous sections it is clear that knowledge about how the heterogeneity of the study system changes with scale can improve the design and interpretation of field experiments. Many statistical techniques have been developed to examine relationships between scale and heterogeneity (Legendre and Fortin, 1989; Rossi *et al.*, 1992; Cressie, 1993; Legendre, 1993; Cooper *et al.*, 1997). Different techniques can deal with categorical (presence/absence, patch type) or quantitative (density, biomass, concentration) data and include methods based on fractal geometry and information theory, pattern analysis, nested hierarchical ANOVAs, spatial autocorrelation and semivariogram analysis, relationships between symmetrical matrices (e.g. Mantel test), and, when examining dominant scales of periodic patterns, spectral analysis (Legendre and Fortin, 1989; Diggle, 1990; Hastings and Sugihara, 1993; Legendre, 1993; Cooper *et al.*, 1997). These and similar techniques can provide metrics for quantifying aspects of spatial heterogeneity or patchiness in measured variables, including the size, shape, magnitude, spatial arrangement, and connectedness of patches or continuous variation in measured variables over space.

Autocorrelation and semivariogram analyses can be used to delineate ranges of spatial dependence, where values at one spot are correlated with those at a distant spot, versus spatial independence, allowing the experimentalist to space experimental units so that they are independent. On the other hand, these techniques can allow the modeling of spatial dependence directly to permit valid parameter estimation and hypothesis testing (Cressie, 1993; Legendre, 1993; Carrol and Pearson, 1998; Bonham and Reich, 1999). Hierarchichal ANOVAs are particularly useful for

predicting the magnitude of aggregation error for different combinations of grain and extent (e.g. Melbourne, 2000). Often, quantitative studies of the scales of patchiness and correlations between densities of interacting species are used to formulate hypotheses about the mechanisms that generate spatial structure (Underwood *et al.*, 2000). Such studies provide valuable information about the scale of experimentation that should be used when testing these hypotheses. Maps or functions describing spatial patterns in driving variables can be used to distribute experimental arenas so that they encompass the range of environmental conditions of interest, allow the clear designation of blocks for block designs, and weight overall responses by the relative area encompassed by each set of environmental conditions (Legendre, 1993; Thrush *et al.*, 1997). Finally, analyses of time series data, for example via spectral analysis, can be used to determine the duration of experiments so that experiments encompass the temporal patterns, cycles, and processes of interest (Platt and Denman, 1975).

VI. CONCLUDING REMARKS

Ecologists will continue to perform experiments in systems that are much smaller and shorter lived than the natural systems of interest. This is because small-scale experiments often are the only practical alternative but also because small-scale experiments offer advantages over large experiments in terms of control and interpretability. Thus, we need a theory that allows us to use results of small-scale experiments to make predictions about the behavior of natural systems. Ideally, such a theory should allow us to make unbiased predictions with known precision. Although this may be an unachievable objective at present, such theory could usefully indicate the direction of future research.

Our review shows that important advances have been made in the development of such a scaling theory. To develop this theory further, it is important to widen its empirical base. Meta-analyses of experiments performed at different scales may help us to identify environmental conditions, types of systems or organisms, and other conditions where scale-dependent processes dominate (e.g. Petersen *et al.*, 1999; Englund *et al.*, 2001); however, it is important to remember that such analyses are correlative and that the observed effects of arena size often are confounded with other experimental conditions, such as treatment strength and experiment duration that vary with arena size. Multiscale experiments, where the same treatment is applied to systems of different size, are particularly valuable (Cooper *et al.*, 1998). Such experiments produce less ambiguous results than meta-analysis and can be used to construct empirical scaling functions (e.g. Chen *et al.*, 1997).

In addition, multiscale experiments often engender hypotheses about the mechanisms that produce scale-dependent responses. A detailed understanding of such mechanisms is necessary when constructing mechanistic scaling models. We expect that small-scale laboratory experiments in combination with simple mathematical models will be a useful approach (e.g. Bergström and Englund, 2002). Detailed behavioral analyses of organisms constrained to small arenas can help us to understand and model many scale artifacts (Heath and Houde, 2001). Further development of scaling models requires tests in multiscale experiments and comparisons between experimental and whole natural systems. Such tests validate model predictions and promote the modification and refinement of model assumptions. However, few, if any, rigorous tests of scaling models have been published to date.

Dimensional analysis, both in its formal mathematical form and as the more intuitive dimensional approach proposed by Petersen and Hastings (2001), is a powerful tool and we expect that its systematic application will greatly improve the designs of conceptual experiments. A particularly useful concept when applying dimensional thinking is "effective scale," which relates the dimensions of the physical environment to scaling attributes of organisms (e.g. size and movement). However, its application requires detailed knowledge about organismal scaling attributes such as perceptive grain and extent for different environmental variables, and movement parameters, such as step length, step frequency, and turning rates (Morris, 1987, 1992; Turchin, 1998). Dimensional analysis also can be a useful tool when standardizing measurements used in different studies (Paloheimo and Dickie 1965). For example, when comparing the outcomes of experiments conducted at different scales in a meta-analyses, it may often be more meaningful to use the effective scale (e.g. arena size relative to organism body size or duration in generation units) rather than the absolute scale of the arena as an explanatory variable (Englund *et al.*, 2001).

The fact that experimental responses often are scale-dependent no doubt renders the study of ecology more difficult. The dilemma faced by the experimental ecologist has been formulated as "whether one does experiments and ignores scale, or whether one respects scale and abandons experiments" (Wiens, 2001). We hope that this review has demonstrated that there is a growing theory that allows us to consider scale problems when designing, and interpreting the results of, experiments.

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