CHAPTER 11

Issues of Scale in Land-Margin Ecosystems

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If we study a system at an inappropriate scale, we may not detect
its actual dynamics and patterns but may instead identify pat-
terns that are artifacts of scale. Because we are clever at devising
explanations of what we see, we may think we understand the
system when we have not even observed it correctly.

—J. A. Wiens, *Spatial Scaling in Ecology* (1989)

It always seemed a fine idea to me to build a showboat with just
one big flat open deck on it, and to keep a play going continu-
ously. The boat wouldn't be moored, but would drift up and
down the river on the tide, and the audience would sit along
both banks. They could catch whatever part of the plot hap-
pened to unfold as the boat floated past, and then they'd have to
wait until the tide ran back again to catch another snatch of it, if
they still happened to be sitting there. To fill in the gaps they'd
have to use their imaginations, or ask more attentive neighbors,
or hear the word passed along from upriver or downriver. Most
times they wouldn't understand what was going on at all, or
they'd think they knew, when actually they didn't. Lots of times
they'd be able to see the actors, but not hear them. I needn't
explain that that's how much of life works.

—John Barth, *The Floating Opera* (1967)

WE DECIDED TO BEGIN THIS CHAPTER WITH THE ABOVE QUOTES, which come from very different perspectives, to entice the reader into reading on and to remind ourselves that scale is so very central to our understanding of most things, be they arts or ecology. This chapter discusses issues of scale primarily in those ecosystems that form the interface between the terrestrial and marine realms, the estuaries, coastal embayments, lagoons, and salt marshes we refer to as land-margin ecosystems.

On a global basis, land-margin ecosystems constitute a small percentage (~0.5%) of the world's oceanic areas. However, the high fisheries production, proximity to major urban areas and associated transportation networks, and the use of these areas for recreational purposes makes them far more important than indicated by spatial extent alone (Houde and Rutherford 1993). Because of the location of these systems at the margin between land and ocean, serious degradation has become widespread during the last few decades. Current demographic projections indicate that human activities in the coastal zone will continue to intensify. For example, the average population density in coastal counties in the northeast region of the United States (Maine to Virginia) was about 340 people per square mile in 1988 and is expected to increase by an additional 30 percent by 2010 (Culliton et al. 1990). Of the 140 land-margin ecosystems recently reviewed by NOAA (1998), about 80 percent were classified as moderately to seriously impacted by excessive nutrient inputs and other materials.

Sediments, nutrients, and an array of toxic materials will continue to find their way into these aquatic systems, leading to further declines in water quality, habitat conditions, and living resources, especially if these areas do not have effective management programs. In addition, increased human activities will intensify pressures on the habitats and living resources characteristic of these systems (Matson et al. 1997; Vitousek et al. 1997). In many such systems, seagrass communities and other habitats have already been lost or degraded, tidal wetlands filled, and fish and shellfish stocks overfished or contaminated (e.g., Duarte 1995; Rabalais et al. 1996). Rapid and poorly designed development and other activities within adjacent drainage basins have destroyed or negatively impacted the very resources that were the prime reasons stimulating development in the first place.

In the last few decades the rapid growth in human activities in watersheds surrounding land-margin ecosystems has resulted in numerous resource use conflicts. One of the pressing needs in many of

these areas concerns establishment of cause-effect linkages. Basic questions and debate often focus on cause(s) of some ecosystem change. For example, what was the factor or factors causing the great decline in seagrass communities in many land-margin systems? On the other hand, questions are asked about the consequences of increasing or decreasing some input (e.g., nitrogen) or extraction (e.g., fish catch) from land-margin ecosystems. Answers to these types of questions are often developed through some form of controlled experimental study, and mesocosms of some shape and size are often used as primary tools. The appeal of mesocosms is based on several characteristics, including the facts that (1) experiments are often impossible, too costly, or too risky to perform on natural land-margin systems, (2) experiments testing a variety of cause-effect linkages can be done relatively quickly in mesocosms compared to waiting for a time-series of measurements to be collected from natural land-margin systems, (3) mesocosm approaches often, but not always, allow for some replication and hence added confidence in results, and (4) there is a reasonable amount of control inherent in this approach that is generally lacking in natural land-margin systems. In short, mesocosm approaches offer an experimental tool to answer pressing management questions of what is causing what and will this happen if we do such and such (Crossland and La Point 1992). The problem is that mesocosm approaches, almost without exception, operate at small spatial and short temporal scales but basic questions about how ecosystems operate and more applied questions about which of many management options will provide desired results mainly occur at larger and longer scales (Hoekstra et al. 1991). So, how do we scale-up when using mesocosm approaches in land-margin systems and how do we conduct better comparative ecological analyses of these systems in search of general principles?

This chapter resulted from discussions, presentations, and literature reviews during and following a workshop on scaling relations in experimental ecology sponsored by the Multiscale Experimental Ecosystem Research Center (MEERC). Its focus is on scaling issues in land-margin systems. Specifically, we considered the following: (1) definitions of scaling and scale–dependent behavior; (2) characteristics of land-margin systems as these relate both to the need for scaling mesocosm-based studies of these systems and the possibilities of using the systems in a comparative mode to develop better understanding of scale-dependent behavior in these systems; (3) examples of scaling in land-margin systems

and mesocosms to assess the current state of the art and the degree to which scaling is an explicit part of land-margin science; and (4) recommendations about what might be done in the short- and long-term to improve our understanding of scale-dependent behavior in these systems and use of mesocosms in land-margin studies.

DEFINITIONS OF SCALE, SCALING, AND SCALE-DEPENDENT BEHAVIOR

Although it might seem unnecessary to provide definitions of the central topic of this workshop, we found within our working group a diversity of opinion concerning what was meant by scale, scaling, scale–dependent behavior, and other associated terms. To clarify this, and to make the topic more accessible to those who have not had dealings with ecological scaling, we have assembled some definitions from the recent literature.

Definitions of Scale

- A change in pattern as determined by the spatial and/or temporal extent of measurements necessary to detect significant differences in the variability of the quantity of interest (Gardner 1998).

- Scale refers to resolution (spatial grain, time step, or degree of complication) and to extent (in time, space, and number of components included) (Costanza et al. 1993).

- Scale denotes the resolution within the range of a measured quantity (Schneider 1994).

- Scale refers to the resolution (grain) and to the range (extent) of research activities and ecological rates (Schneider et al. 1997).

- Scale is defined by the temporal and spatial characteristics of energy and matter within and among ecological systems. The scale of a study is determined by the size and extent of the observations in time and space, as well as by the resolving power of the individual measurements (Hoekstra et al. 1991).

Definitions of Scaling

- Scaling refers to the application of information or models developed at one scale to problems at other scales (Costanza et al. 1993).

- Scaling is that which is needed when the "ballgame rules" change; when relationships break down; when size (for example) changes and some other feature does not change in a linear fashion (from workshop notes).

- Scaling pertains to the use of rules to explain the manner in which processes change when extrapolating from short to long and small to large time and space scales; all measurements are related to scale (from workshop notes).

Definitions of Scale-Dependence

- Scale-dependent pattern can be defined as a change in some measure of pattern with a change in either the resolution or range of measurement (Schneider 1994).

- Scale-dependent pattern refers to the way in which a statistical summarization of a quantity changes with spatial or temporal scale.

- Scale-dependent processes are those where the ratio of one rate to another varies with either resolution or range of measurement (Schneider 1994).

Other Definitions

- *Extent* is the overall area encompassed by a study.

- *Grain* is the size of the individual units of observation. Extent and grain define the upper and lower limits of resolution of a study (O'Neill et al. 1986).

- *Allometric* relationships are those wherein a part of an organism or a process is related to or scaled to another and the scaling is not a direct proportion (i.e., the scaling factor is not unity); *isometric* relationships are those related by direct proportion (i.e., the scaling exponent is unity) (Calder 1983).

- *Normalization* is scaling that is done with simple direct proportions; identical with isometric scaling.

- The scope of a natural phenomenon is defined as the ratio of the upper to lower limit. Scope is thus the ratio of the extent to the grain or the ratio of the largest to the smallest size scale of measurement. Scope also provides an indication of the degree of extrapolation that is needed or used (Schneider 1998).

• Multiscale analysis is simply the recognition that there is no single "right" scale for analysis at levels of organization above an individual organism (Schneider 1994).

The workgroup distinguished between scaling to properly understand scale-dependent features in land-margin ecosystems from scaling so as to avoid including experimental artifacts, particularly those associated with mesocosm studies, in results and interpretations. Initially, the issue seemed clear; the type of scaling we are talking about involves primarily the former and the latter is simply to be avoided. However, if as suggested at the beginning of this chapter, all measurements are matters of scale, both need to be considered although the exact methodological approaches for dealing with these problems are not clear.

The workgroup also identified several categories of scaling issues, including (1) isometric scaling or normalization (e.g., converting total nutrient loads to an estuary to load m^{-2} based simply on the size of the estuary); (2) homogeneous spatial scaling (i.e., the scaling exponent is not unity, as in normalization, but the systems to be scaled one to the other are considered to be relatively homogeneous); (3) heterogeneous system scaling (i.e., deals with nonuniform processes in time and space in the systems being scaled; scaling with measures of variance are included here); and (4) scaling for sharp gradients or discontinuous properties (i.e., new organisms are added to an experiment, water transparency changes so sediments have the potential to have autotrophic components, water flow characteristics change from laminar to turbulent).

CHARACTERISTICS OF LAND-MARGIN ECOSYSTEMS

A complete list of all characteristics of land-margin ecosystems is not the goal here. Rather, a subset of those systems that occur at the boundary of land and water were considered and these mainly included estuaries, coastal embayments, and lagoons. We recognize that there are other land-margin systems, including tidal and nontidal marshes and forested wetlands and bogs, but have chosen to not explicitly consider those systems in order to limit the task at hand.

The following characteristics are particularly relevant descriptors of land-margin systems, although they are not necessarily unique to such systems; however, all have some bearing on the issue of scaling and mesocosm design.

- Land-margin systems tend to be small. For example, the median size of coastal lagoons was found to be about 7,800 ha with a range of size from 3 to 800,000 ha (Nixon 1982). On a global basis, such systems comprise less than 0.5 percent of the world's oceanic areas.

- These systems tend to exhibit relatively high rates of primary and secondary production and contribute about 20 percent of the world fisheries catch (Houde and Rutherford 1993). At broad temporal and spatial scales (annual or multiyear and whole system), there is a strong correlation between primary production and fishery yields despite generally poor understanding of food web structure and dynamics. Fishery yields per unit primary production also appear to be considerably higher than for lakes, but the exact reasons are not clear (Nixon et al. 1986).

- The suite of organic matter sources in land-margin systems is often diverse, including phytoplankton, seagrasses, macroalgae, benthic microalgae, and inputs from terrestrial sources. Typically, not all sources are important at the same time of the year or in all years.

- Many land-margin systems exhibit strong physical, chemical, and biological gradients. The relatively small size of the systems coupled with the enclosed nature of estuaries contributes to the formation of gradients. In stratified systems, such as the Chesapeake Bay, some of the strongest gradients occur in the vertical direction over spatial scales of meters.

- In part because of close association with the land, these systems are often exposed to high temporal variability in inputs, particularly from rivers. Costanza et al. (1995) have argued that this variability limits the development of complexity in land-margin systems but favors high net production. Input variability is not limited to land linkages; ocean inputs of water, salt, nutrients, and biological populations also exhibit considerable variability in land-margin systems (Smith et al. 1991).

- Land-margin systems often have complex and variable rates of physical transport and mixing, including those associated with seasonal scale weather, local and nonlocal storm effects, and short scale tidal and local wind forcing.

- Benthic-pelagic coupling is characteristic of most land-margin systems and the strength of the coupling appears to be directly related to water depth (Kemp and Boynton 1992). The generally shallow nature of the systems makes depth a particularly important feature. The sediment-water interface is one of several physical interfaces characteristic of these systems and not so characteristic of many others.

- These systems are often characterized by seasonally migrating subsystems of organisms. Larval and juvenile stages of many fish species move from the coastal ocean to estuaries for at least part of their life cycle (blue crab [*Callinectes sapidus*], Atlantic croaker [*Micropogonias undulatus*], menhaden [*Brevoortia tyrannus*]) and anadromous fish spawn in estuarine systems and then participate in seasonal coastal migrations (American shad [*Alosa sapidissima*], striped bass [*Morone saxatili*]).

Steele (1985, 1991) and Steele et al. (1993) have compared and contrasted characteristics of terrestrial and aquatic systems and physical forcing on these systems with the goal of better understanding the utility of theory and measurement across system types. Marine and terrestrial systems both exhibit a variety of temporal patterns, but in marine systems large-scale factors (e.g., El Niño) have been typically invoked as prime factors causing variability and dramatic change whereas predator-prey and other community-level explanations are invoked for terrestrial systems. Steele and Henderson (1994) indicate that these different explanations are based on the overlap of time and space scales of physics and biology in the ocean and the wider separation of these in atmospheric and terrestrial systems.

The above authors and others (e.g., Stommel 1963; Haury et al. 1978; Denman 1992; Hildrew and Giller 1992) have developed versions of time-space diagrams to examine characteristics of terrestrial and marine system physics and biology and to look for overlaps of time and space scales that may suggest patterns of control. However, we are not aware of such a synthesis for land-margin systems and have included a preliminary version of such a diagram which includes time-space characteristics of physics, weather, biology, and commonly used research approaches in these systems (figure 11.1). As expected, there are some similarities with previously developed diagrams, including weather events (thunderstorms and hurricanes) and large time and space scale atmospheric perturbations (droughts). Some important ocean physics (ocean basin gyres and deep ocean circulation) do not register on the spatial scales of land-margin systems. However, several physical processes are unique and prominent features of many of these systems, including turbidity maxima, river floods, and sediment resuspension events. Most representations of marine communities show a progression from autotrophs at short and small time and space scales to large and long-lived heterotrophs at large time and space scales.
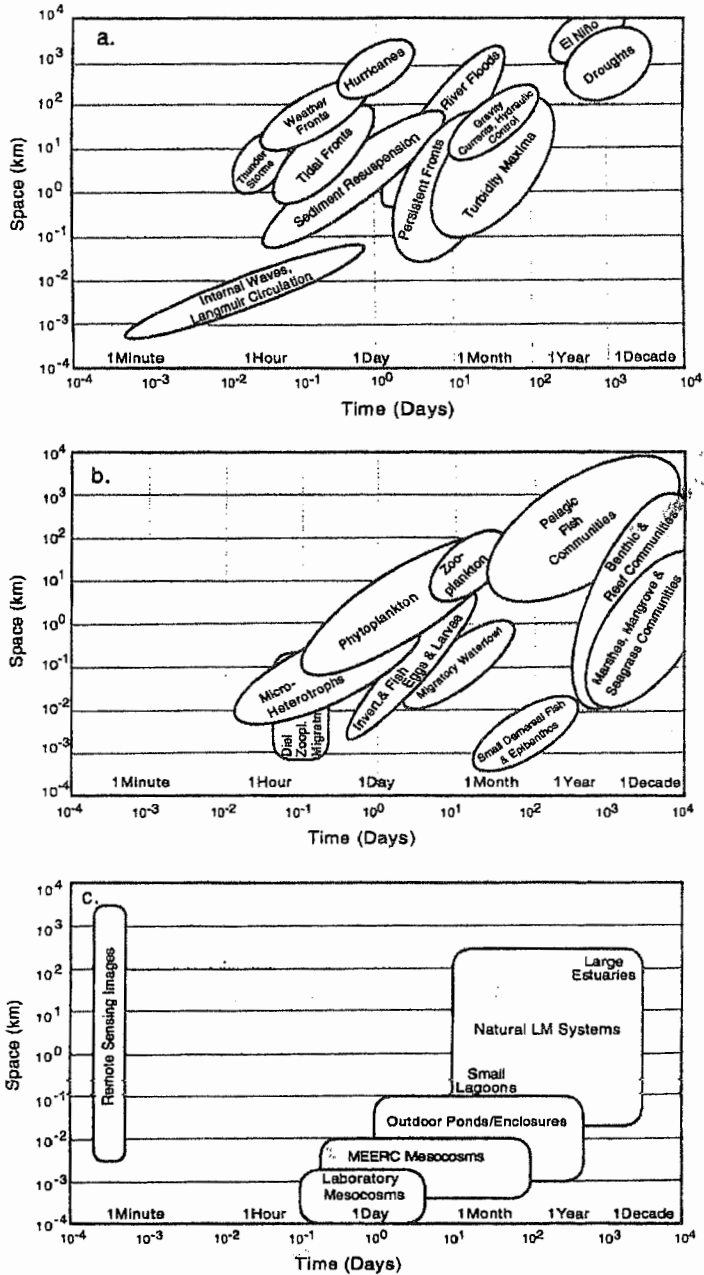
FIGURE 11•1 *Time Versus Space Scales*

Approximate time and space scales relevant to land margin (LM) ecosystems for (a) physical circulation, weather, and climate, (b) biotic components, and (c) commonly applied research approaches.

This simple continuum from small and short-lived to large and long-lived is certainly not the case for land-margin systems; autotrophs can occur at extremes of time and space scales as do some heterotrophic components; land-margin system representations look like a partial combination of terrestrial and marine diagrams, which is intuitively pleasing because these systems are located at the transition of the land and sea. There is considerable overlap in the time and space scales of physical processes and biological components, which is probably involved in creating the qualitative idea that land-margin systems are complex, messy places of substantial variability both because of changing physics and interacting biological communities. Because only a portion of the time-space domain of land-margin processes can directly be examined with even the largest of mesocosms, and because there is the potential for interaction among the rich milieu of land-margin processes, questions of scale and problems of scaling-up or scaling-down are of real importance.

SCALED RELATIONSHIPS IN LAND-MARGIN ECOSYSTEMS AND MESOCOSMS

Several authors have developed literature reviews that indicate a strong increase in interest and activity related to scaling issues in environmental research since the mid-1980s (e.g., Schneider 1994; Kemp et al., this volume). Schneider (1992) suggested a number of reasons for this, including great improvements in computing power and software capability, instrumentation of all sorts that has allowed investigators to measure environmental features not previously measured, and growing recognition that biological-physical coupling, environmental variability, and propagation of physical and biological effects through food webs are all scale-related and central to improving understanding of how natural systems operate. Although we have not conducted another comprehensive literature review, our distinct impression is that scaling issues have received considerably more attention in terrestrial ecology (landscape ecology), ecophysiology, and oceanography than in studies of land-margin systems, despite the fact that there have been pressing practical needs for such activities for quite some time. We examined results from several electronic searches (*Aquatic Sciences and Fisheries Abstracts, 1978–1998; Ecology Abstracts, 1981–1998*) and found one to two

papers per year concerned primarily with issues of scale in land-margin systems. We also reviewed publications in several journals that emphasize studies of these systems (*Estuaries, Estuarine Coastal and Shelf Science,* and *Marine Ecology Progress Series*) and found relatively few citations (1 to 3 papers per year).

However, some examples of scaling of land-margin organisms, ecosystem processes, and mesocosms are available, although not in the numbers that would indicate scaling to be a prominent component of land-margin research thinking. We have assembled representative results from some studies in Table 11.1. Our goal is to provide a flavor of some scaling activities in land-margin (and closely related) systems rather than organize a comprehensive synthesis, although this needs to be done. Several of the ecosystem-level examples can be thought of as comparative ecology studies where the scaling turned out to be isometric, or at least was treated as isometric. The relationships observed by Monbet (1992) between nutrient concentrations and algal stocks were weak among estuarine study sites until observations were categorized into micro- and macro-tidal range sites, a nice example where issues of scale explain variability in the fashion suggested by Carpenter and Kitchell (1987). We did not find many examples of scaled relationships involving data collected from both small-scale (e.g., mesocosm) and natural ecosystems, but of those we did, system depth was an important scaling variable. We found several examples of artifacts in mesocosm systems and the effect these have on relating results to larger systems at lower (e.g., Chen et al. 1997; Petersen et al. 1997) and higher (de Lafontaine and Leggett 1987a) trophic levels. The research area with perhaps the most information is that of ecophysiology of land-margin (and related) organisms. We readily found allometric relationships relating a variety of processes to functions of phytoplankton cell size (e.g., Chisholm 1992), zooplankton size (e.g., Kiorboe and Sabatini 1995), and seagrass morphology (e.g., Duarte 1991). These latter results are not surprising because ecophysiology has used allometric scaling as a tool for some time and this class of measurement is relatively easy to make.

We conclude this section with several examples that emphasize the use of scale concepts in design and analysis of environmental data sets. These studies did not produce general scaled relationships (e.g., allometric relationships of phytoplankton cell size to growth rate) but issues of scale and scale-dependent pattern were central to design and analysis.

TABLE 11·1 *Examples of Scaled Relationships Based on Data Collected from Land Margin (LM), Marine, and Lake Ecosystems and Land Margin (LM) Mesocosms; and Some Allometric Relationships for Various Organism Groups*

Scaled Feature	System Size or Type	Scaling Variable	Comments	Reference
Nutrient-loading rates	LM ecosystems	Size (area or volume)	Simple, linear normalization	Boynton et al. (1982, 1995)
Phytoplankton production and biomass	LM ecosystems	Nitrogen load (areal or volumetric)	Log-log relationship of load vs pri prod rate or biomass	Nixon (1992)
Phytoplankton biomass	LM ecosystems	Nitrogen concentration and tidal range	Log-log relationships	Monbet (1992)
Plankton C:N ratios	LM mesocosms and Narragansett Bay	Phytoplk production rate	Phytoplk C:N Ratio=23.8 + 6.0 Log (pri prod rate)	Nixon (1992)
Autotroph/heterotroph ratios	LM, marine and lake ecosystems	Autotrophic biomass	Negative log-normal relationships for ocean, LMs, and lakes	Gasol et al. (1997)
Nitrogen export	LM, marine and lake ecosystems	Water residence time	%TN exported= 64.8 - 27.0*log (water residence time)	Nixon et al. (1996)
Fisheries yield	LM, marine and lake ecosystems	Phytoplk production rate	Log-log relationship between pri production and fisheries yield	Nixon et al. (1986)
Sediment-water	LM mesocosms	Depth	Sediment NH4 Flux/TN Load = $0.85 \cdot Depth^{-2.00}$	Kemp and Boynton
Nutrient exchanges	Chesapeake Bay subestuaries	Depth	Sediment NH4 Flux/TN Load = $26.9 \cdot Depth^{-1.71}$	(MEERC data)
Water column DIN loss rate	LM mesocosms and Chesapeake Bay	Depth	DIN loss rate(uM day^{-1}) = $0.084 + 0.99 \cdot Depth^{-1}$	Kemp (MEERC data)
Spring zooplk abundance	LM mesocosms and Chesapeake Bay	Depth	Zooplk abundance (g C m^{-3}) = $0.0005 + 1.07 \cdot Depth^{-1}$	Kemp (MEERC data)
Phytoplankton prod rates	LM mesocosms (0.1-10 m^3)			
Spring, light-limited		Depth	Volumetric prod (P_v) = $P_a \cdot z^{-1}$; P_a = production per area	Peterson et al. (1997)
Summer, nutrient-limited		Depth	Areal prod (P_a) = $P_v \cdot z$	
Periphyton biomass	LM mesocosms (0.1-10 m^3)	Size (mesocosm volume and wall area)	Quadratic relationship between periphyton biomass and wall area (Aw) to water volume (V) ratio (Aw:V)	Chen et al. (1997)
Larval fish predation/mortality	Mesocosms (0.3 - 6.4 m^3)	Mesocosm volume	lnY = 4.3 - 0.76 ln x : Y = mortality rate; x = mesocosm volume	de Lafontaine and Leggett (1987a)
Marine phytoplankton	Individual size classes and species	Size	Multiple relationships in the form of Y = aX^b	Chisholm (1992)
Marine phytoplankton	Individual size classes and species	Cell carbon	Cell growth = a(cell carbon)^b; b~ 0.75	Banse (1976)
Phytoplankton nutrient uptake	Different species	Body size	Multiple relationships in the form of Y = aX^b	Moloney and Field (1989)
Marine copepods	Female zooplankton	Body weight and egg number	Multiple relationships in the form of Y = aX^b	Kiorboe and Sabatini (1995)
Seagrass form and productivity	Different seagrass species	Rhizome diameter and shoot weight	Multiple relationships in the form of Y = aX^b	Duarte (1991)

Notes: phytoplk = phytoplankton; pri prod = primary production; TN = total nitrogen; 300plk = 300 plankton

The first is a well-known and instructive analysis of scale-dependent pattern involving sea bird distributions (common murres [*Uria aalge*] and Atlantic puffins [*Fratercula arctica*]) relative to prey (capelin [*Mallotus villosus*]) in the northwest Atlantic (Schneider and Piatt 1986). In this study, counts of birds and fish were made along a 15 km transect with a minimum resolution of 0.25 km. Counts were grouped into mean counts at a variety of spatial scales (0.25, 1.5, 2.5, and 3.0 km). Spatial association between birds and prey was strongest at the larger spatial scales, which are the scales at which birds were adjacent to the fish schools between feeding periods. The multiple scales of observation used were critical in understanding these predator-prey interactions.

A number of coordinated studies were conducted on an intertidal sandflat in Manukau Harbour, New Zealand, by Thrush and his colleagues. The theme of these studies was to investigate issues of scale using field measurements and experiments. Specific elements of these studies considered factors controlling spatial distributions of dominant bivalves and adult-juvenile interactions (Legendre et al. 1997), factors controlling macrofaunal recolonization rates (Thrush et al. 1995, 1996), evaluations of methods for scaling up small-scale manipulation experiments to large-scale areas (Thrush, Schneider et al. 1997), scale-dependent patterns of sediment reworking and transport (Grant et al. 1997), and others (Thrush, Cummings et al. 1997; Thrush, Pridmore et al. 1997). An important aspect of the study design was that routine sampling and experiments were conducted at several spatial and temporal scales and a variety of modeling and statistical techniques were used for analysis. Investigators found negative correlations between juvenile and adult bivalves at spatial lags of 1 m but positive correlations at spatial lags of 5 m; sediment reworking and transport were variable over spatial scales of 10 to 100 m and temporal scales of several days; at larger spatial scales, physical factors (elevation, wave disturbance) were important in determining bivalve densities but at smaller spatial scales intrinsic factors were more important. The authors observed that had these studies been conducted at but one scale, much of the interesting information concerning factors apparently controlling biology and physics of the sandflat would have not emerged or would have appeared to be contradictory. They also observed that despite increasing interest in issues of ecological scale, practical advice for field ecologists relative to study design and analysis is limited.

A final example is from Rose and Leggett (1990), who used simulation models and acoustic data to examine signs and strengths of spatial correlations between Atlantic cod (*Gadus morhua*) and its prey, capelin. They found that when the prey species was not in a thermal refuge, capelin and cod densities were coherent across spatial scales of 2 to 30 km. At spatial scales > 4 to 10 km, densities of both species were positively correlated; at scales less than school sizes (3 to 5 km), densities were negatively correlated; and at the smallest scales (2 to 3 km) negative correlations were strongest. When capelin were in thermal refuges, predator-prey relations were in phase only at scales larger than the thermal refuges.

It comes as no surprise, indeed it is intuitively satisfying, that there are scale-dependent patterns that emerged in all of these studies. However, as Rose and Leggett (1990) note "the spatial dynamics of predator-prey interactions are clearly complex, and quantification is particularly difficult in the wild." Tools are more available now than in the recent past for making similar measurements in land-margin systems at scales of grain and extent that are appropriate for a variety of organisms. It is probable that some of the conflicting or uncertain interpretations of cause and effect in these systems will be resolved when issues of scale are considered more explicitly.

ISSUES OF SPECIAL CONCERN IN DESIGN AND USE OF LAND-MARGIN MESOCOSMS

There are many publications on mesocosms, including experimental ecosystem design (Kemp et al. 1980; Ives 1996; Lawton 1996; Petersen et al. 1999; Kemp et al., this volume), turbulence and mixing in experimental systems (Oviatt 1981; Sanford 1990), fish and other predators (Gamble 1985; Houde 1985), benthic studies (Bakke 1990), benthic-pelagic interactions and land-margin system responses to nutrient additions (Pilson 1990), toxic contaminant effects (Morgan et al. 1990), and others. It is not the intent of this chapter to review all or even most of these. Rather, we summarize some of the pressing issues of scale in the design of mesocosm research concerned with land-margin ecosystems; the above sources have been indicated as a point of departure for those interested in specific design issues.

As Petersen et al. (1999) have pointed out, mesocosms are smaller than natural systems, have reduced spatial and biological complexity, are surrounded by walls for organisms to grow on, have modified physics compared to natural systems, and are often operated for relatively short periods of time. Encapsulated in this summary statement are many of the design issues of interest to those working in land-margin ecosystems.

Distinguishing fundamental effects of scale from artifacts of the mesocosm itself is clearly a prominent and difficult problem. In experiments reported by Chen et al. (1997), periphyton biomass and metabolism increased as a quadratic function of increasing mesocosm wall-area-to-volume ratio. In addition, in these experiments there were significant negative correlations between periphyton biomass and measures of phytoplankton and zooplankton abundance. In mesocosms of this size (0.1 to 10 m^3), periphyton exerted major artifactual effects on important components in only several weeks. In similar studies focusing on plankton dynamics, Petersen et al. (1997) found fundamental relationships of production to scaling factors as well as artifactual effects on plankton metabolism associated with wall effects of periphyton and light availability.

To examine the artifactual effect of walls and periphyton at a larger scale, we combined several comparative analyses based on field data and included similar data collected from MEERC mesocosms (figure 11.2). In the top panel, when areal nutrient loading rates for a variety of land-margin systems are compared to rates in MEERC mesocosms, there is little disparity, as expected in these well-controlled systems. However, the percentage of total nitrogen exported (middle panel) as a function of water-residence time for a variety of land-margin systems is similar to that estimated in MEERC mesocosms in spring (period of low periphyton growth) but very different in summer when wall growth is actively sequestering added nitrogen. In the lower panel, annual average water column chlorophyll a biomass in plankton in the mesocosms had a strong relationship relative to scaled nutrient loads for a number of sites in the Chesapeake Bay. However, chlorophyll a associated with periphyton on the mesocosm walls departed strongly from other observations, probably because periphyton were not subject to export from the mesocosms as were phytoplankton. Clearly, wall effects can be important artifacts in mesocosms. The degree of interference can be minimized by using large-diameter systems of mesocosms and by keeping experimental periods relatively short.
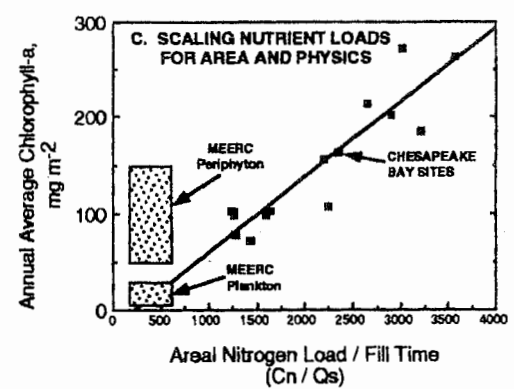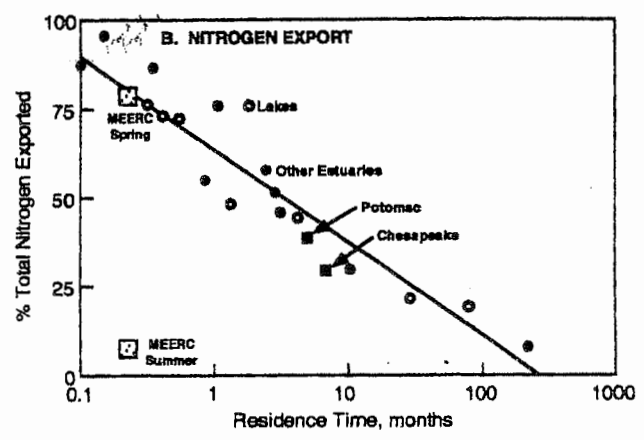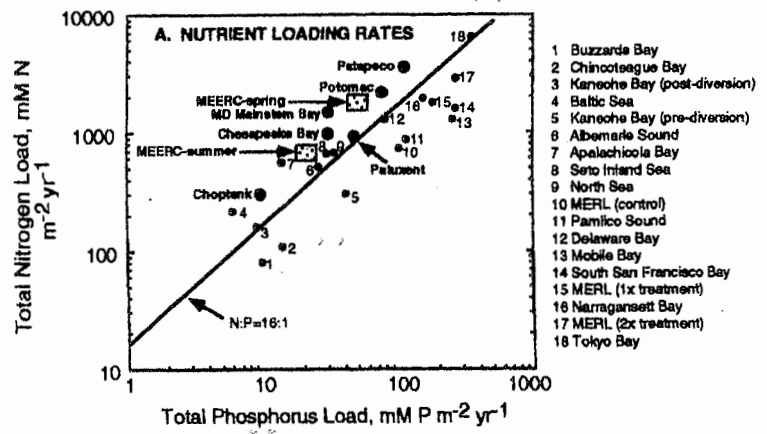
FIGURE 11•2 *Scaling Patterns*

Examples of preliminary scaling exercises using data from coastal systems, Chesapeake Bay subsystems and MEERC mesocosms. (A) adapted from Boynton et al. (1995); (B) from Nixon et al. (1996); (C) from Boynton (unpublished data). Cn and Qs in the lower panel refer to areal total nitrogen loading rate (g N m^{-2} y^{-1}) and freshwater fill time (years).

Often land-margin research and management questions involve higher trophic level components. Questions such as why shad are not reproducing well, what controls bay anchovy (*Anchoa mitchilli*) growth rate, how important is jellyfish predation on larval fish survival, and others are common. Inclusion of upper trophic levels in mesocosm design has been, and probably will continue to be, a difficult issue for several reasons. The more obvious concern is the larger size of higher trophic level organisms relative to mesocosm space and the behavioral patterns of these organisms. Petersen et al. (1999) reported that in a large sampling of mesocosm experiments there was a significant increase in volume between mesocosms that contain only one as opposed to two or three trophic levels. As mesocosm size is decreased it is clear that artifacts come into play; survival of fish larvae, for example, increases sharply as mesocosm size increases (Theilacker 1980; de Lafontaine and Leggett 1987a). It seems that there is emerging consensus that larval fish studies need mesocosms on the order of 3 m^3 or larger and that depth characteristics of the mesocosms also come into play (de Lafontaine and Leggett 1987b). Also, the use of "pulse" experiments (fish are added, then removed) with larger fish may be useful (Frost et al. 1988) and smaller fish predators can be used in a "press" mode (fish are added and remain in the mesocosms) for some types of experiments. The careful consideration of species-specific (and life-stage specific) neighborhood size evaluations may also be useful in designing mesocosm experiments with larger animals (Addicott et al. 1987).

One of the benefits of new technology in the last decade has been the much enhanced ability to measure variability on large and small spatial scales. For example, Harding et al. (1992) used a radiometer (ODAS) on a fixed-wing plane and conducted weekly or bi-weekly surveys of chlorophyll, temperature, and salinity throughout Chesapeake Bay (300 km × 20 km) in a few hours. Patches of high chlorophyll water were almost always evident, with patch size varying from fractions of a km^2 to hundreds of km^2. The point that spatial and temporal heterogeneity is important in structuring ecosystems has been made repeatedly in recent years (Wiens 1976; Barry and Dayton 1991; O'Neill et al. 1991; Levin 1992). However, creating and maintaining or realistically evolving heterogeneity in mesocosms is difficult at best, although at small enough scales it may persist even if not wanted (Lehman and Scavia 1982; Atkinson et al. 1987; Duarte and Vaqué 1992). Short of building very large mesocosms or using semi-enclosed natural systems (Davies and Gamble 1979; Oiestad 1990), some degree of variability can be achieved

by connecting mesocosms one to another and allowing different regimes to develop while still maintaining some degree of connectiveness. Alternatively, some experiments could be done in separate mesocosms (with different treatments) and the results used in spatially explicit simulation models as suggested by Denman (1992). We suggest careful consideration of what can be left out of mesocosm studies for the sake of tractability, but also recognize that suppression of variability in and among mesocosms may be a mistake if ecosystem depends on some feature of variance.

One of the approaches that has been successfully used elsewhere in dealing with ecological questions that appear too large to be studied directly in mesocosms has been called the "scale-down approach" (Vitousek 1993). In this approach some "whole system" measurements are made and then, where appropriate, mesocosm experiments are conducted to estimate rates and examine mechanisms. For example, in Hubbard Brook Experimental Forest, nutrient and other types of budgets were developed under undisturbed and perturbed circumstances (Vitousek 1993; Carpenter 1996). Smaller and more controlled experiments were then done to investigate rates; these experimentally developed rates could then be compared to whole system rates as a check for realism. In some land-margin systems similar "whole system" estimates of rates are also possible. For example, Hagy (1996) developed an estuarine box model to generate transport estimates and used these, in conjunction with nutrient and carbon concentration measurements, to compute net fluxes of nitrogen, phosphorus, and carbon in different sections of the estuary. These large-scale measurements were then compared to small-scale and short-term mesocosm rate estimates. In several cases mesocosm estimates appeared to be low, possibly because of variability in sediment properties that were not captured in the small-scale studies.

Finally, the time might be right for a manual of mesocosm design for land-margin systems. More specifically, this would be an engineering-like handbook that contains scaled relationships and could be used to develop issue-specific mesocosm systems. Our sense is that enough is now known to produce a first edition similar to the handbook developed by Jorgensen et al. (1991) for ecological and ecotoxicological parameters. This manual could also contain evaluations of various scaling variables such as depth, mixed layer depth, photic depth, important system component neighborhood sizes, surface area to volume effects, residence time and mixing schemes, and the like. The manual would be an effort to

move mesocosm design from the artful or intuitive stage it is now in to a more quantitative stage. It probably would go a long way toward limiting re-invention of mesocosm wheels and avoiding results that are dominated by experimental artifacts.

TOOLS FOR ANALYSIS OF SCALE AND EXTRAPOLATING AMONG SCALES IN LAND-MARGIN SYSTEMS

This section begins with a few examples of scope to help examine the adequacy of typical environmental measurements and the degree of extrapolation required in land-margin studies. In other words, how big is the problem of going from measurement scales to land-margin ecosystems or how big is the jump from mesocosm scales to natural land-margin systems?

In Table 11.2, we assembled size data (volume) for a range of land-margin ecosystems and compared these to the sizes of three mesocosm systems. The scopes range from large to huge and make the point that guidance for extrapolation is very important. Even if we take the point of view that just one mesocosm would not be used as representative of Chesapeake Bay, or even a small lagoon, we still could not possibly use enough mesocosms to reduce the scope to more comfortable levels. In Table 11.3 we made some assumptions about the volume of water swept (i.e., volume represented by a measurement) and compared these to volumes of water in several natural systems. These estimates involve approximations as to effective swept volume and reasonable effort levels and thus the focus should be on the order of magnitude obtained rather than the actual estimate of swept volume. Moreover, a comparison of swept volume does not encompass a complete comparison of the effectiveness of a technology for any particular purpose. For example, for chlorophyll-*a*, ODAS offers synopticity over a large area at the expense of very fine-scale resolution that can be obtained by SAIL or DATAFLOW. Metabolism is simply harder to measure than basic water quality variables. Nonetheless, for water quality variables, the significance of the orders of magnitude increase in swept volume per boat day with newer technologies should not be lost as scientists and environmental managers struggle to obtain better information at lower cost.

The above concerns aside, the results indicate that unless much more generous assumptions are made about the degree of spatial auto-

TABLE 11·2 *A Comparison of Several Size Classes of Land Margin Mesocosm and Land Margin Ecosystem Volumes*

Land Margin Ecosystem Examples	Ecosystem Volume (10^6 m^3)	Ecosystem: Mesocosm Ratio		
		MEERC "C" Tank (1 m^3)	URI MERL Tank (13 m^3)	EXP Ponds (400 m^3)
Chesapeake Bay, MD/VA	74,000	7.4E+10	5.7E+09	1.9E+08
Patuxent River, MD	650	6.5E+08	5.0E+07	1.6E+06
West River, MD	12	1.2E+07	9.2E+05	3.0E+04
Small Coastal Lagoon, MD	4	4.0E+06	3.1E+05	1.0E+04
Global lagoons				
Smallest	0.03	3.0E+04	2.3E+03	7.5E+01
Mode	35	3.5E+07	2.7E+06	8.8E+04
Median	78	7.8E+07	6.0E+06	2.0E+05
Largest	8,000	8.0E+09	6.2E+08	2.0E+07

NOTE The MEERC "C" mesocosms are a part of an experimental mesocosm facility at the University of Maryland, Center for Environmental Science (Petersen et al. 1999), the MERL mesocosms are a facility at the University of Rhode Island and the Experimental Ponds (EXP Ponds) are at the University of Maryland, Center for Environmental Science.

SOURCE Lagoon data are from Nixon (1982), and other site data are from Boynton et al. (1995).

correlation, all of these methods are inadequate to sample all of Chesapeake Bay with a high degree of synopticity. For smaller systems, the more advanced technologies approach the ability to obtain more complete information in a short period of time, even without more generous assumptions about spatial autocorrelation. Older technologies for water quality measurements and the more challenging measurements (e.g., metabolism, nutrient flux) face more severe limitations regarding undersampling. In large land-margin systems, sampling spatial and temporal variability is clearly difficult at the whole system level, even with the most advanced technologies. So, we are often left with difficult issues of scaling up from local measurements and experiments to the scale of natural systems.

A number of analytical and statistical approaches have been developed in recent years for issues relating to scale, particularly in terrestrial and marine systems, and several reviews of these methods and approaches have been published. For example, Turner (1989) and Garcia-Moliner et

TABLE 11·3 *A Summary of Volumes of Water Swept with a Variety of Sampling Techniques Often Used in Land Margin Ecosystems and Estimates of the Time Required to Completely Sample Land Margin Ecosystems of Several Classes Using These Techniques*

Sampling Method	Volume Swept[a] $(10^4 m^3 d^{-1})$	Time Required to Sample System Volume, d			
		Chesapeake Bay	Patuxent River, MD	West River, MD	Small Coastal Bay, MD
In situ nutrient concentrations	79	94,752	831	15.3	5.10
Plankton metabolism (bottle incubations)	39	189,262	1,659	30.5	10.18
Sediment nutrient fluxes (in situ incubations)	8	947,516	8,306	152.9	50.96
Traditional CTD casts	157	47,376	415	7.6	2.55
Continuous surface water sampling (large ship)	4,260	1,746	15	0.3	0.09
Continuous surface water sampling (fast small boat)	2,220	3,350	29	0.5	0.18
Undulating CTD (e.g., GMI-scanfish)	16,700	445	4	0.1	0.02
Aerial remote sensing (e.g., ODAS radiometer system)	22,224	2,010	18	0.3	0.11
Ichthyplankton tows (e.g., tucker trawl)	247	30,113	264	4.9	1.62
Fish tows (e.g., mid-water trawls)	370	20,103	176	3.2	1.08
Chesapeake Bay Monitoring Program (physical)	785	9,475	83	1.5	0.51
Chesapeake Bay Monitoring Program (chemical)	314	23,688	208	3.8	1.27
Fish acoustics (sensor deployed from large ship)	11,112	669	6	0.1	0.04

[a]Calculating reasonable estimates of these scaling comparisons requires some assumptions that qualify the value. For example, the interpretation of a scaling comparison for chlorophyll a measurements made in a laboratory from filters depends on the number of samples that is reasonable to run and any underlying model of spatial correlation that is assumed. At the extremes, it isn't reasonable to assume that a single measurement represents the whole system, nor is it reasonable to assume that the sample represents nothing more than the water that was actually filtered. The range of reasonable values may span a large range, but probably does not include these extremes. In these comparisons, we assume homogeneity over a horizontal distance of 100 m and a vertical distance of 1 m. Under this assumption, the volume "swept" by a sampling method allowed a minimum sampled volume of 7.85×10^3 m³ per sample. Sampling at high resolution was considered continuous sampling, where the unit of sampling was not the sample, but a tow or cast. These types of sampling techniques result in volumes swept which have either cylindrical or rectangular parallelepiped geometries. The amount of effort applied to the method is standardized to one team of scientists on one boat for one day. The volumes of Chesapeake Bay, Patuxent River, West River and a small coastal bay used to compute days needed for complete sampling were 7.44×10^{10} m³, 6.52×10^8 m³, 1.2×10^7 m³, 4×10^6 m³, respectively.

al. (1993) provided useful examples of techniques used for description and analysis of spatial patterns including autocorrelation, spectral density functions, wavelet analysis, and fractal geometry. More recently, Gardner (1998) has reviewed reasons for investigation of spatial scales and patterns and also suggested analytical approaches including dimensional analysis, allometric relationships, and use of variance estimates such as semivariograms and correlograms. Some interesting characteristics of normalized biomass and allometric relationships have been used to estimate trophic biomass and production in the Great Lakes (Sprules and Stockwell 1995), and Plotnick et al. (1993) applied a technique called lacunarity to determine characteristics of spatial dispersion. It is clear that an impressive array of techniques is available for investigation of issues related to scale. However, it also appears that these techniques have not been used to any large extent in land-margin systems. The reasons for this are not completely clear to us but the lack of time-series data and the relatively rare fine-scale spatial data sets needed for some of these analyses are certainly part of the reason. Application of newer technologies capable of making routine measurements at appropriate time and space scales is needed in land-margin system studies.

A number of authors have considered practical approaches to the issue of relating results obtained at one scale to issues at other scales in terrestrial and marine systems and some may have direct application to land-margin ecosystem scaling issues. At one end of the spectrum, Carpenter (1996) argued that mesocosm experiments (bottom-up approach) are not very useful and probably misleading when not done in conjunction with large-scale field studies. He urged extreme caution in scaling when using data obtained from such studies. The size and duration of mesocosm studies either exclude or distort important features and some relevant components or important/interesting processes simply will not fit in any mesocosm. Carpenter (1996) suggested that results of large-scale studies (e.g., whole lake experiments, forest manipulations) be used to guide the selection of mesocosm experiments and that these be conducted to estimate rates and to evaluate alternative hypotheses. Although there is certainly merit in this argument, this approach still begs the question of how to scale rate measurements conducted in mesocosms and, as Petersen et al. (1999) have noted, the results of whole ecosystem experiments (usually conducted in small whole ecosystems) often need to be scaled to even larger whole ecosystems (i.e., ponds to lakes). Given the large number of lagoonal systems in the United States and elsewhere, it might

be worth considering using some selection of these system types for whole system experiments analogous to the way the Experimental Lakes are used as a research tool. Earlier, Vitousek (1993) suggested that "interaction between the top-down (whole-system experiments) and bottom-up approaches can yield better results more rapidly than can bottom-up analyses alone; the interaction can yield an understanding (of mechanisms) that is wholly inaccessible to top-down analyses."

Schneider (1994) has suggested a series of practical strategies (strengths and weaknesses) for scaling up environmental data. These included (1) multiplication of small-scale measurement to the size of the natural system; (2) use of linear scaling only for those quantities that have limited scope values (ratio of largest to smallest expected values); (3) use of large extent, fine-grain data (e.g., ocean color images) coupled with small time and space scale measurements (e.g., direct algal biomass estimates) to obtain large-scale estimates via summation rather than multiplication; (4) use of statistical models to scale limited measurements to larger areas; (5) use of hierarchy theory to identify nested systems (with internal similarities) within larger systems; and (6) use of dimensionless ratios to compute large-scale estimates from small-scale measurements. With respect to this last strategy, Miller et al. (1984) and Horne and Schneider (1994) used dimensionless ratios to evaluate some aspects of benthic deposit feeding and temporal and spatial dynamics of a coastal fish stock, respectively.

Other investigators have recommended practical approaches for dealing with scale-up issues and these are also worth noting for possible use in land-margin system research. Root and Schneider (1995) summarized problems associated with projecting results of studies to the scale of the natural world. For example, they note that use of the "scale-up" paradigm (building the whole from detailed, mechanistic, small-scale results) suffers from the fact that conspicuous features at small scales may not reveal dominant processes that generate large-scale pattern. However, the "scale-down" paradigm suffers from an inability to reveal cause-effect relationships. Root and Schneider (1995) suggest use of "strategic cyclical scaling" wherein both scale-down and scale-up approaches are cyclically used and strategically applied to practical problems. In short, they recommend using the larger scale to guide studies at the smaller scale. In fact, this theme is repeated in the literature, often prefaced by some statement to the effect that this is the best that can be done at present because of a lack of solid and practical theory (e.g., Turner 1989).

Vitousek (1993) also argued for use of detailed satellite data to establish pattern coupled with plot-level measurements and experiments for examination of mechanisms and the like. Other authors have called for use of mathematical models in the extrapolation process. Rastetter et al. (1992) and Caldwell et al. (1993) reported on using both statistical tests and models to better use fine-scale data in models of regional-level dynamics. Reynolds et al. (1993) suggested identifying hierarchical levels of the system of interest and then developing nested sets of models.

RECOMMENDATIONS CONCERNING FUTURE WORK ON SCALING OF LAND-MARGIN SYSTEM PROPERTIES

During the past fifteen years or so, substantial progress has been made relative to scaling issues in terrestrial, freshwater, and marine ecosystems. Scaling activities have ranged from microscopic to global and from physiological to ecological. However, it appears to us that scaling has not yet entered the mainstream of thought in land-margin research, despite motivation that might have come from successful applications in other fields and despite some of the characteristics of land-margin systems and land-margin mesocosms that indicate that issues of scale are particularly important. There is a great deal of room for increased activity in this area. Toward this end we have assembled a series of suggestions as to what might be done to initiate and augment future work concerning scaling of land-margin system properties and mesocosms.

- Start regular graduate-level teaching of scaling concepts and methodologies as an important tool for ecologists and others involved in field and mesocosm studies. It appears to us that other disciplines (e.g., landscape ecology, elements of oceanography, physiological ecology) are more advanced in this area. Fisheries scientists have what amounts to a "methodological toolbox" from which to select appropriate methods for particular problems, some of which involve scaling. While land-margin scientists have a variety of methods at their disposal, an active appreciation of scale does not seem to be one of them. In the past few years, books have been published on various scaling issues (Ehleringer and Field 1993; Schneider 1994; Peterson and Parker 1998) that could serve as a basis for advanced courses. Scaling, both theory and practice, needs to find its way into the land-margin research toolbox.

- Syntheses of known scaling relationships are available in a few disciplines. Possibly the most diverse concerns allometric scaling relationships for mammals and birds (e.g., Calder 1981, 1983) but also for marine plankton and benthic invertebrates (e.g., Banse 1976; Chisholm 1992). Some particularly instructive examples of successful use of scaling ideas are available, particularly from terrestrial ecology (e.g., Wiens 1989). However, a synthesis of scaling relationships (allometric or otherwise) is not available for land-margin systems. Such a synthesis, possibly beginning with plant and animal allometric relationships, would be immediately useful for a number of investigations (bioenergetics, food web analyses) and would stimulate further interest in scaling applications.

- In a similar fashion, continued syntheses of land-margin mesocosm design is needed. In this area, MEERC has a good start in examining effects of size and shape and small-scale physics in experimental mesocosms. Petersen et al. (1999) reviewed design characteristics of 360 experimental mesocosm studies and, based on this review, urged mesocosm users to more explicitly assess the effects of scale with "scale-sensitive" experiments. For example, the depth, volume, and area of mesocosms need to be considered in light of ecological characteristics such as home range, organism size, and life history stage. Crossland and La Point (1992) also urged continued investigation of scale issues (e.g., scaling up mesocosm results to natural ecosystems) in mesocosms used for toxicological studies, particularly for pesticide registration.

- There is a pressing need for the use of new measurement technologies in land-margin research. The use of technologies that allow for greater temporal and spatial resolution will be of prime importance in determining what characteristic spatial and temporal scales are important for a variety of organisms and processes in these systems. In many cases, available data sets have increased in quality and size in the last several decades. However, the temporal and spatial sampling regimes have not been determined with scale in mind. Sampling regimes for dissolved nutrients, phytoplankton, zooplankton, benthos, or fish tend to be the same as each other. This being the case, examination of these data sets for scaling relations is of limited potential. We suggest use of high frequency moored and towed devises that use optical, electronic, and acoustic sensors. Aerial remote sensing in land-margin systems is also rapidly improving. Certainly, components such as zooplankton, fish larvae, and adult fish have been highly undersampled in the past; however, new technologies could go a long way toward providing data sets that would be rich in scaling issues and answers to pressing ecosystem questions.

- Likewise, there are a number of statistical tools that have been applied to landscape and some oceanographic issues. These need to

be tested for application in land-margin systems; such applications may be more attractive when more high resolution data are available.

• Uncertainties about system function span large scales of time, space, and organism/community characteristics. Commonly used mesocosms, as described by Petersen et al. (1999), can be used to good effect for some problems, have limited use for others, and cannot be used at all for still others. The scope calculations we presented earlier suggest the size of the problem. Use of spatial models and linked mesocosms are two ways to scale-up from smaller to larger sizes and from shorter to longer time periods, but there are obvious limits to this approach. Limnologists have had good success using whole lake ecosystem approaches (Schindler 1987; Carpenter et al. 1995), but these also have problems and limitations. It seems to us that land-margin scientists might consider establishing a whole ecosystem approach with lagoons as a primary focus. These systems are common, often somewhat protected from weather extremes, small enough to be readily sampled, and large enough to be relevant for experiments that can not be done in traditional mesocosms. An experimental lagoon facility would extend land-margin mesocosms by the same large-scope factor that experimental lakes extended limno-corrals and other lake mesocosms.

ACKNOWLEDGMENTS

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