Spatial and temporal scaling

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Spatial and temporal scales in mesocosms affect our ability to extrapolate from experiments to nature

The spatial and temporal scales of mesocosms and related experimental ecosystems regulate responses of system components to perturbations and other changes in external conditions. Therefore, a fundamental understanding of the scale-dependence of experimental ecosystem behavior is essential for quantitative extrapolation of mesocosm results to conditions in nature. The spatial and temporal scales of experimental coastal ecosystem studied in MEERC and other research are generally much smaller than the scales of the natural ecosystems to which one might wish to extrapolate research results.

Scaling theory predicts that certain patterns and processes only become evident as scale is increased beyond thresholds of extent.[17] Furthermore, our own hypotheses and data indicate that scaling patterns tend to be non-linear.[18] So it is possible, for instance, that patterns that were determined to be scale-dependent in MEERC mesocosm experiments become scale-independent at larger scales of natural systems (solid line in Fig. 49). Likewise, it is possible that relationships that one sees as scale-independent in mesocosms are functions of scale in larger natural ecosystems (dashed line in Fig. 49). Finally, it is possible that thresholds exist over which small changes in scale result in dramatic and possibly discontinuous changes in ecological dynamics. Given these possibilities, it is important that findings from multi-scale experiments be validated with data collected from a range of larger scale ecosystems in nature.[19]

In this section, results from MEERC and other research are used to develop scaling guidelines for designing experimental systems and conducting experimental research. This discussion considers scales (size, shape) and temporal scales (duration, frequency) of experimental ecosystem studies.

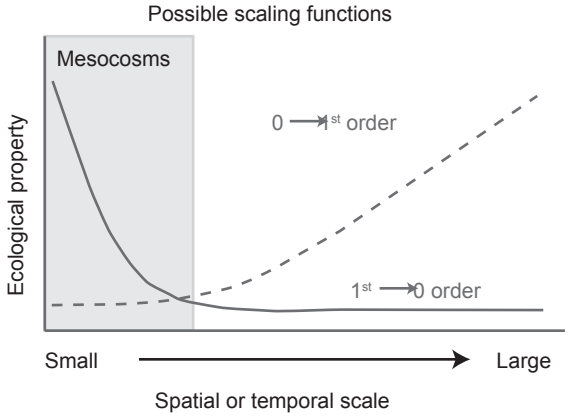

Figure 49: *Hypothetical responses of two distinct ecological properties to changes in the scales over which they are observed. Mesocosm scales (shaded region of graph) are inherently smaller than the scales of most natural systems. Trajectories shown indicate how different properties may be affected differently by changes in scale.[18,19]*

17. Wiens 2001, 18. Kemp et al. 2001, 19. Petersen et al. 2003

Spatial scaling: Container depth, width, and shape constrain ecological properties of mesocosms

Aquatic mesocosms are characterized by clearly defined boundaries, surfaces, and dimensions (Fig. 50). The size and shape of cylindrical mesocosms can be described by two linear dimensions (depth, z, and width or radius, r) and two volumes (water and sediment [if present], where h is the height of sediments). In addition, there are three surface areas (air-water surface, sediment-water surface, mesocosm wall surface) that define the mesocosm's boundaries (Fig. 50). Light enters the mesocosms primarily at the air-water interface, which is also the site across which important gases such as oxygen, carbon dioxide and nitrogen are exchanged between experimental water and the overlying atmosphere. At the sediment-water interface, key solutes (e.g., oxygen, inorganic nutrients) move between water and sediment as a result of benthic biogeochemical processes. Also across this interface, particulate materials sink from the water column to the sediments and may be resuspended back into the water. The walls of aquatic mesocosms constitute a unique surface representative of hard substrates that typically occur in nature at much lower ratios of surface area to water volume. Walls constrain lateral exchanges of water and organisms between the container volume and surrounding region, and they provide a physical substrate for growth of attached organisms.

We examined 360 reports for data on mesocosm dimensions to explore patterns of shape, with an initial hypothesis that researchers may have implicitly tended toward use of experimental systems (Fig. 51) characterized either by constant depth ($z = C_1$), constant radius ($r = C_2$), or constant shape ($r/z = C_3$). Meta-analysis of reported dimensions of experimental systems revealed that published research results have been generated from mesocosms having remarkably similar shape.[20]

This shape-bias shared among researchers using enclosed experimental ecosystems is somewhat disturbing. This is because the similarity in shape of aquatic mesososms implies that there is no consistency in other important geometric properties of experimental systems. Specifically, for containers with constant shape, the relative importance (per water volume) of both wall area and horizontal surface area will tend to decrease with the size of the experimental system. Hence, the relative importance of wall artifacts such as periphyton growth and benthic processes such as nutrient regeneration will differ among experimental containers in proportion to their size (Fig. 34).

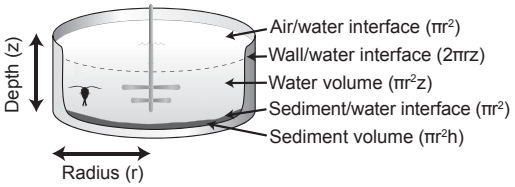

Figure 50: *Conceptual diagram showing key regions of biogeochemical activity associated with the spatial scales of a pelagic-benthic mesocosm. (*h*=sediment depth)*

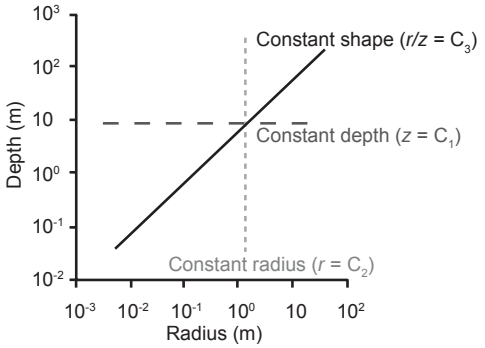

Figure 51: *Alternative simple relationships by which depth and radius of mesocosms might tend to be related. Constant radius: depth is varied but width (radius) is held constant. Constant depth: radius is varied but depth is held constant. Constant shape: depth and radius are varied in constant proportion to one another. Researchers tend to use containers with relatively constant shape.[20]*

20. Petersen et al. 1999

Spatial scaling: Ecological effects of water column depth depend on light and nutrient conditions

In the MEERC pelagic-benthic experimental studies, fifteen cylindrical mesocosms were constructed with 5 distinct dimensions, 3 volumes, and 3 replicates per dimension (Fig. 52). These mesocosms were organized into 3 series: one with a constant depth (A, C and E tanks; depth = 1.0 m), one with constant shape (B, C, and D tanks; radius/depth = 0.56), and one with constant volume (E and D tanks = 10 m^3; A and B tanks = 0.1 m^3; Fig. 52). These mesocosms with estuarine water and sediments were used to conduct a series of multi-scale studies examining how container size and shape influence ecosystem behavior.

Scientists in MEERC developed a set of simple scaling hypotheses related to variations in depth of the upper mixed water column. Depth-scaling hypotheses started with the understanding that primary productivity in temperate coastal ecosystems often experiences a seasonal shift from light limitation in the spring to nutrient limitation in the summer. An important dimensional difference between these two limiting factors is that light energy is received on an areal basis (e.g., units of µmol photons m^{-2} s^{-1}) and is then absorbed as it is travels down to deeper parts of the water column. In contrast, plankton experience nutrients on a volumetric basis (e.g., µmol m^{-3}), and concentration is relatively constant over depth in a well-mixed water column. These dimensional differences in nutrients and light suggest two simple depth-related scaling hypotheses that were tested in our mesocosm experiments.

Because aquatic ecosystems experience light on an areal basis, under purely light-limited conditions one might expect gross primary productivity (GPP) and related ecological variables to be constant among different depth systems when expressed on an areal basis: $GPP_{Area} = C_1$, (C_1 = a constant, units = g O_2 m^{-3} h^{-1}). In contrast, because biota contact nutrients on a volumetric basis, under purely nutrient-limited conditions primary productivity should be constant when expressed per unit volume: $GPP_{Vol} = C_2$. In this nutrient-limited case, by definition productivity expressed per unit area should be directly proportional to depth: $GPP_{Area} = C_2 * z$.

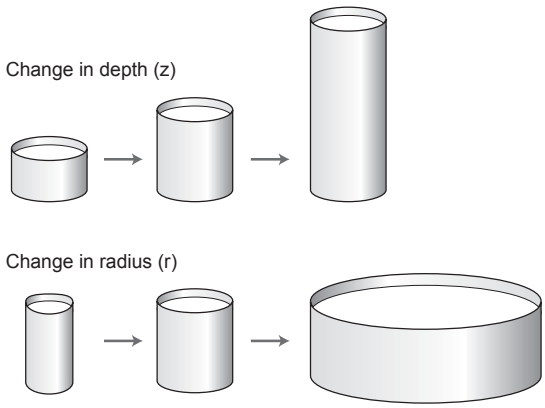

Figure 52: *Multi-scale studies in MEERC involved observing dynamics in a series of mesocosms that differed in container depth, radius, and shape.*

Spatial scaling: Water column depth regulates algal biomass and production

One set of MEERC multi-scale experiments illustrated how water column depth regulates gross primary production (GPP) of the integrated ecosystem by comparing the GPP (= daytime increases in O_2 minus nighttime decreases) for mesocosm systems of differing depth during spring (light-limited) and summer (nutrient-limited) conditions. Mean values for GPP normalized both per unit water volume and surface area generally followed the hypothesized relationships (p. 52) with spring GPP per area constant among systems but GPP per volume inversely related to depth (Fig. 53). For the nutrient-limited summer experiment, GPP per unit volume was relatively independent of water depth and, GPP per area increased with depth as predicted. These depth-scaling relationships

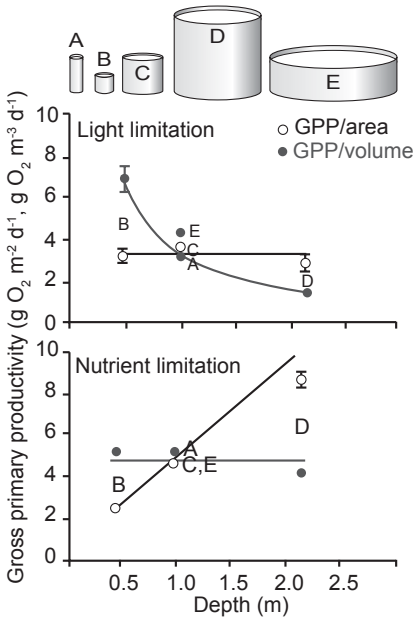

Figure 53: *Variations in gross primary productivity (GPP) in mesocosms of different depths. Mean GPP values (calculated both per water volume and per water surface area) and water column depth for (top panel) spring experiments under light-limited algal growth conditions and (bottom panel) summer experiments under nutrient-limited growth conditions.*

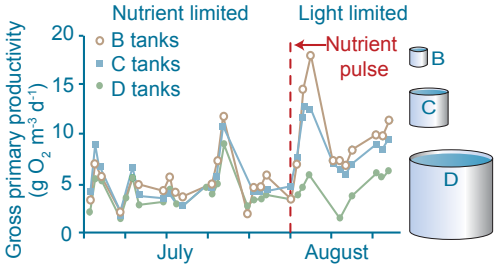

Figure 54: *Example time-series of GPP per water volume for three mesocosm types (B, C, D) of identical shape but different depth during nutrient limited summer before and after pulse addition of nutrients.*[21]

derive from the fundamental differences in the way nutrient and light availability change with overall water column depth.

Further demonstration of the scaling relationship for nutrient-limited conditions is evident in temporal variations in GPP per unit volume for the three systems with the same shape but different depth (B, C, D) during summer (Fig. 54). Under these nutrient-limited conditions, GPP per unit volume was constant among the three mesocosm types despite differences in depth. Gross primary production expressed per unit volume exhibited the same temporal patterns of weekly variations in the different mesocosms until early August when a nutrient pulse was added to all systems. With this addition and the associated temporary transformation from nutrient-limited to light-limited conditions, GPP per volume increased inversely with water depth as predicted.

These experimental findings indicate the value of multi-scale experimental ecosystem studies in revealing fundamental scaling relationships. They reinforce the conclusion that the design and interpretation of mesocosm experiments must consider the water depth, nutrient conditions, and water clarity of the experimental system in relationship to these properties in the natural environment that the mesocosm is designed to represent.

21.Petersen et al. 2003

Spatial scaling: Enclosure depth affects primary productivity and zooplankton abundance

In situations where ecosystem production tends to be light-limited (e.g., temperate estuaries in spring), the abundance of zooplankton (the major plankton grazers in many natural and experimental coastal ecosystems) tends to vary with water depth in a relationship similar to that for the gross primary production (GPP). For the spring MEERC experiments, concentrations of dissolved inorganic nutrients (N, P, Si) were well above levels that limit primary production, such that availability of light was relatively more important as a control on algal growth. When mean values for both GPP and zooplankton biomass (both expressed per m^3 water volume) in the mesocosms were combined with similar spring data for stations in the mesohaline regions of Chesapeake Bay and one of its major tributary systems (Patuxent River estuary), there were parallel trends with increasing depth (Fig. 55).

Initially, a statistically significant negative exponential equation was developed using only the mesocosm data (within the shaded area to the left). However, the regressions were unchanged when Bay data were included, suggesting that mesocosm scaling relationships could be extrapolated directly to conditions in nature. In this case, however, all of the significant changes in GPP and zooplankton occur within the mesocosm range of depths, such that changes in these variables become essentially independent of depth when depth exceeds 2 or 3 m. This threshold point for depth-dependence likely varies with water clarity, becoming deeper in clearer water columns.

These results also imply that, under resource-limited growth conditions, scaling relationships may propagate from lower to higher trophic levels. This is essentially a situation of *bottom-up control* (i.e., resource limitation) on organism growth and production. These depth-scaling relationships might be less evident under conditions of *top-down control* (i.e., limitation via consumption) on production resulting from externally induced changes in consumer abundance.

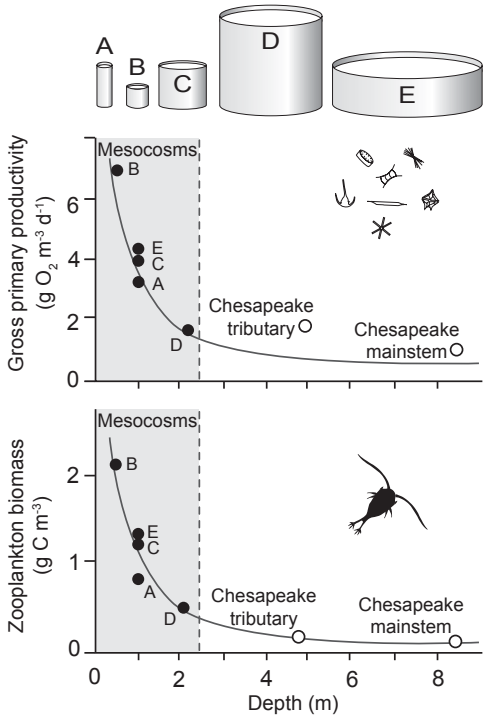

Figure 55: *Variations in primary production and zooplankton biomass with changes in water column depth for five experimental and two natural estuarine ecosystems with similar salinity. Experimental ecosystems have five different sizes or shapes and the estuarine sites are in the mainstem and a tributary of Chesapeake Bay. Data are mean values for gross primary productivity (GPP per unit water volume) measured from changes in dissolved oxygen concentration.*[22-24]

22. Kemp and Boynton 1984, 23. Kemp et al. 2001, 24. Roman unpublished

Spatial scaling: Enclosure depth affects nutrient recycling but does not simulate natural ecosystems well

For both gross primary productivity and zooplankton biomass, scaling coefficients derived from mesocosm data alone were almost identical to those derived by combining data from mesocosms and natural ecosystems (previous page). It is worth noting, however, that GPP data for the Patuxent estuary fall some distance from the fitted equation. Had data for other natural ecosystems been included, there would likely be considerable scatter around the regression because many factors other than depth vary among estuaries. Indeed, in many ways this is the point; a great strength of multi-scale mesocosm experiments is that these other factors, such as nutrient loading, can be held constant so that scaling effects can be isolated successfully. This comparison suggests that, at least for some variables and under some circumstances, scaling relationships revealed in mesocosms are robust and can be directly extrapolated to nature.

For other variables, however, the potential value of mesocosms for revealing fundamental scaling relationships and the potential for direct extrapolation may be more complicated. For instance, benthic recycling of dissolved inorganic nitrogen was expected to conform to the depth-scale hypothesis. In this case, although an inverse equation ($Y = N_1 (z)^{-1}$, where Y is the ratio of N recycling to N input and N_1 is a coefficient) neatly fitted data from the mesocosms (Fig. 56), the extrapolation of this equation (dashed line beyond mesocosm scales) did a poor job of predicting data gathered for larger natural ecosystems. The same inverse equation with a different coefficient did, however, fit the data from five field sites (dashed line).

There are a number of explanations for why scaling relationships may have altered relative regeneration of dissolved inorganic nitrogen might differ between mesocosms and nature. For example, although the horizontally rotated impellers in the experimental systems produced realistic mixing in the water column, the bottom shear velocity at the sediment-water interface was unrealistically low (≈0.1 cm s^{-1}). This enhances key benthic processes such as microphytobenthic production and nutrient uptake[28]; unrealistically low shear at the bottom interface would thus tend to inhibit nutrient regeneration rates. Moreover, in benthic-pelagic coupling experiments in MEERC a moderate bottom shear velocity of 0.6 cm s^{-1} resulted in microphytobenthos erosion and affected subsequent nutrient regeneration compared to experiments in tanks with the same water column mixing but low bottom shear.[28]

The important lesson is that although multi-scale experiments can be used to identify valid scaling relationships in some cases, unrealistic biological and physical conditions within mesocosm studies (i.e., an inadequate representation of physical complexity) can sometimes distort ecological dynamics and result in erroneous conclusions when extrapolating results from mesocosms to nature.

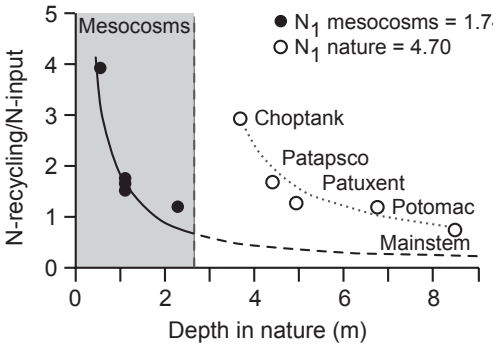

Figure 56: *Relationships between relative rates of benthic nitrogen recycling (as a fraction of N input) and depth in mesocosms and in large natural estuarine tributaries and the mainstem of Chesapeake Bay.*[25-27]

25. Mesocosm data from Cornwell unpublished; field data from Boynton et al. 1995, 26. Kemp et al. 2001, 27. Petersen et al. 2003, 28. Porter et al. 2004b

Spatial scaling: Water depth and light availability control benthic microalgal production

Benthic primary production by microalgae tends to vary with water column depth simply because of depth-dependent variations in light levels reaching the sediment surface. Figure 57 demonstrates how depth regulates benthic primary production (BPP) by comparing estimated BPP for three experimental mesocosms having different water column depths (B, C, and D, with depths of 0.5, 1.0, 2.2 m) with BPP rate measurements made in the mesohaline region of Chesapeake Bay.

When rates of BPP are plotted versus water column depth for the mesocosms and the field sites, there are two parallel but different patterns of exponentially decreasing rates with depth (Fig. 57, top panel). It might be anticipated that this difference is simply related to differences in light regimes in the experimental and natural environments. Although the shapes of the respective relationships between BPP and light at the sediment surface are similar for observations in the two environments, mesocosm rates at a given light level were consistently lower (Fig. 57, bottom panel). Presumably, differences between relationships of BPP versus light between mesocosms and the Bay are attributable to differences of nutrient availability or other factors between the experimental and natural habitats.

The presence of benthic microalgal communities can also affect nutrient recycling processes in experimental ecosystems because algal uptake of nutrients is proportional to light reaching the sediment, which is in turn related to water column depth. Recycling effluxes of dissolved inorganic nitrogen from sediments of shallow mesocosms with low bottom shear velocity decline significantly in the light because of assimilation by benthic microalgae (Fig. 58).

Thus, researchers must consider differences in habitat conditions when attempting to extend results from enclosed experiments to conditions in nature. On the other hand, experimental planktologists must realize that benthic communities will tend to develop at the bottom surface of all containers, and that these chamber bottoms may be sites of active organic production and consumption as well as nutrient cycling processes.

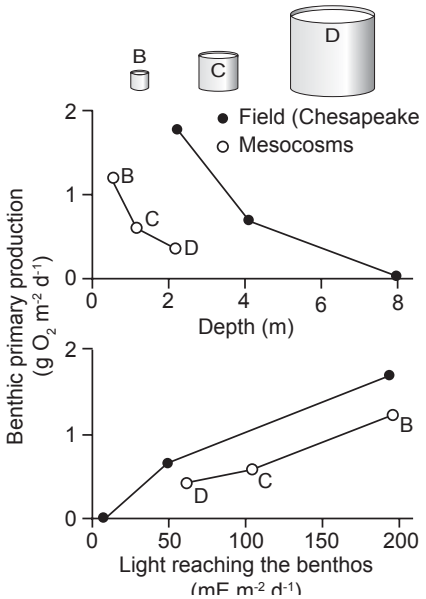

Figure 57: *Benthic primary production versus water depth in mesocosms and Chesapeake Bay (top panel). Benthic primary production versus light intensity at the sediment surface in mesocosms and Chesapeake Bay (bottom panel).*[29]

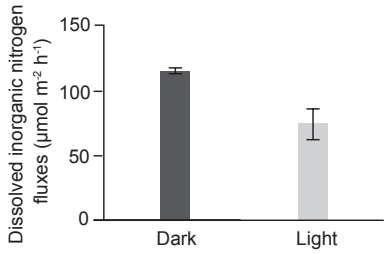

Figure 58: *Fluxes of dissolved inorganic nitrogen (nitrate + nitrite + ammonium) from sediments to overlying water under dark and light conditions in shallow experimental ecosystems with healthy benthic microalgal communities.*[30]

29. Computed from unpublished data of C.-C. Chen and Kemp 2004 for mesocosms and W. M. Kemp et al. 2005 for Chesapeake Bay
30. Cornwell unpublished

Spatial scaling: Wall artifacts vary with width of experimental ecosystems

Whereas differences in water column depth may lead to fundamental differences in ecological characteristics in experimental and natural systems, differences in mesocosm width may induce different levels of experimental artifacts. One potentially important artifact is growth of periphyton communities (including bacteria, algae, protozoa, and small metazoans) on mesocosm walls. Because walls are not normal habitats in most natural planktonic or benthic subsystems, growth of periphyton communities on container surfaces is usually considered a non-representative artifact that complicates extrapolation of results to conditions in nature. Experiments were conducted in MEERC pelagic-benthic mesocosms with tanks of different radius to quantify the artifacts of scale associated with this wall growth. If the relative contribution of wall productivity to total system productivity was proportional to the ratio of wall area to water volume (A_w:V), then it would also be inversely proportional to radius for a cylindrical container (A_w:$V = 2\pi r * z/\pi r^2 * z = 2/r$). Thus, the relative contribution of walls to total gross primary productivity among systems of different radius would be $GPP_{wall}/GPP_{total} = C_3/r$, where C_3 is a constant and r is the container radius.

In experiments without routine removal of material from container walls, periphyton biomass (normalized per water volume) was inversely proportional to mesocosm radius (Fig. 59). Similar relationships were seen for periphyton GGP and periphyton uptake of dissolved inorganic nitrogen (DIN).[31,32] Hence, the relative contribution of periphyton communities to total biomass and ecological processes in mesocosms tended to decrease with container radius. These observations led to the hypothesis that the ratio of GPP_{wall}/GPP_{total} is related to the inverse of container radius (r^{-1}). Although this ratio did decline with container radius, the exact relationship did not conform perfectly with the hypothesized model (Fig. 60). When wall productivity was expressed per unit wall surface area, periphyton were more robust in wider systems. This trend may be related to self-limitation for light or nutrients or both, with denser periphyton growth or more intense grazing pressure in narrower tanks.[31]

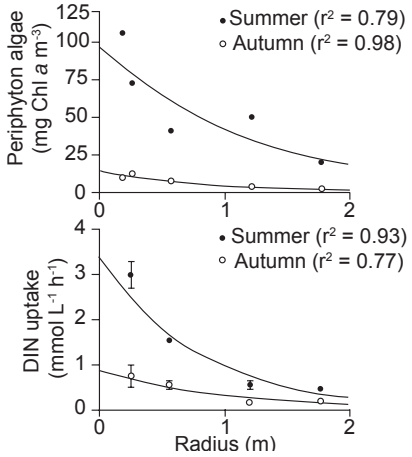

Figure 59: *Variations in periphyton community properties with increasing container radius, including algal biomass (top panel) and uptake of dissolved inorganic nitrogen (bottom panel) (both expressed per unit water column volume).*[31,32]

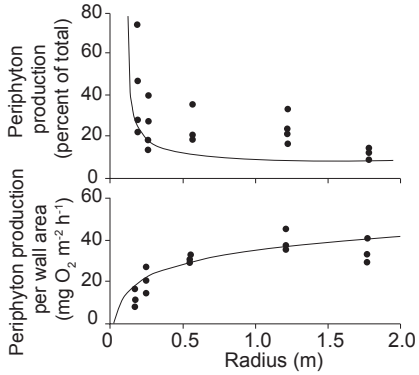

Figure 60: *Changes in relative contribution of wall periphyton to total gross primary productivity (top panel) and in productivity of wall periphyton per unit of wall area (bottom panel) with mesocosm radius. The curved lines through the data are a least-squares fit using the hypothesized inverse relationship between relative productivity and tank radius $GPP_{wall}/GPP_{total} = C_3/r$ (top panel), and a best-fit line (bottom panel).*[31,33]

31. Chen et al. 1997, 32. Chen et al. 2000, 33. Petersen et al. 2003

Spatial scaling: Mesocosm size constrains the behavior and physiology of mobile animals

The width of an experimental ecosystem also affects the behavior and physiology of fish and other swimming animals contained in that ecosystem. The frequency of encounters that a randomly swimming fish might have with container walls would be proportional to the ratio of wall area (A_w) to water volume (V), which is in turn proportional to container radius ($r = 2V/A_w$). More encounters with walls probably leads to more uncharacteristic animal behavior and associated physiological stress.[34]

A series of experiments was conducted in pelagic-benthic mesocosms[35] using the zooplantivorous bay anchovy (*Anchoa mitchilli*). In 43-day experiments, there was a consistently increasing rate of anchovy growth as the width of experimental containers increased (Fig. 61).[35]At widths exceeding 1 m diameter, growth rates began to approach those observed in the natural estuarine environment (Chesapeake Bay). Although precise mechanisms underlying this pattern are yet unknown, they presumably arise from altered swimming and feeding behavior of the bay anchovy, which may somehow increase respiration and decrease prey capture.

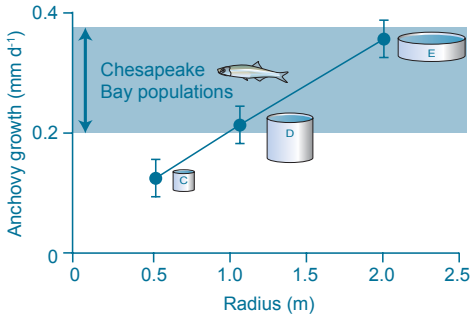

Figure 61: *Variations in growth rate (mean ± SE) of bay anchovy (*Anchoa mitchilli*) with increasing radius of experimental containers. Growth rates were measured as an increase in standard length of fish during period of captivity in container.*[35]

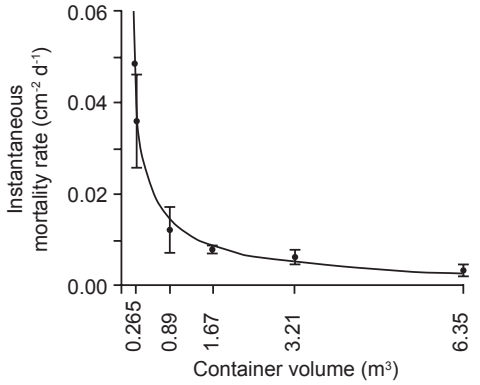

Figure 62: *Relationship between mortality rate of larval fish (capelin,* Mallotus villosus*) subjected to predation by gelatinous zooplankton (*Aurelia aurita*) at standardized size and density and volume of experimental container. Mean and standard deviation are presented for each enclosure volume.*[36]

Similar studies of predator-prey interactions have revealed aberrant behavior of the enclosed organisms in experiments conducted in small containers. For gelatinous zooplankton feeding on fish larvae, a steep inverse relationship between predation (prey mortality) rates and container volume was observed for mesocosms less than about 2 m^3 volume (Fig. 62). Conversely, other studies have reported that predatory pelagic animals appear to have threshold minimum container sizes beyond which growth rates are unaffected by container walls. This critical container volume tends to vary directly with both size and density of the consumer animals.[36]

34. Heath and Houde 2001, 35. Mowitt et al. 2006, 36. de Lafontaine and Leggett 1987

Spatial scaling: Relative variance among and within replicate experimental ecosystems is affected by container size

In addition to the average characteristics of MEERC's experimental systems varying with size, the relative variability (variance/mean) of those properties also changes with container size. The question of variance scaling can be considered in two contexts: 1) variance among replicate experimental systems and 2) variance within a given experimental system.

In the first case, researchers observed that the relative variability in phytoplankton characteristics among replicate mesocosms appears to decline with size. In fact, relative variance decreased exponentially with mesocosm length scale (Fig. 63, top panel). Variance among replicate systems was hypothesized to be controlled largely by processes occurring at container surfaces: periphyton on walls, benthic communities at the sediment surface, and neuston (minute organisms at the air-water interface). Therefore, a length-of-edge index, the square root of the sum of these three surface areas, was used for analysis (Fig. 63). Although there is surprisingly little other published information to confirm the generality of this pattern, it appears that decisions by experimentalists on the number of replicates needed for studies in mesocosms of different size are consistent with this finding. Indeed, a review of the mesocosm literature revealed an inverse relationship between size of experimental container and number of replicates used by researchers. This may reflect an understanding that larger systems are more stable and more predictable, leading to lower variability among replicates. However, this trend may be driven more by logistical considerations, including the expense of building, housing, and maintaining many replicates for larger experimental systems.

The second kind of variance-scaling involves how within-the-system variability of ecological properties changes with the size of experimental containers. In this case, MEERC researchers found that relative variability in copepod abundance tended to increase with container size (size is measured again with the length-of-edge index). In general, within-system variance tended to increase with container size (Fig. 63, bottom panel). It is likely that this relationship emerges because larger systems have more space (particularly, near edges) within which patchiness can develop. It also appears that this trend becomes more pronounced with time during the experiment, such that this scaling effect is exacerbated by experimental duration.

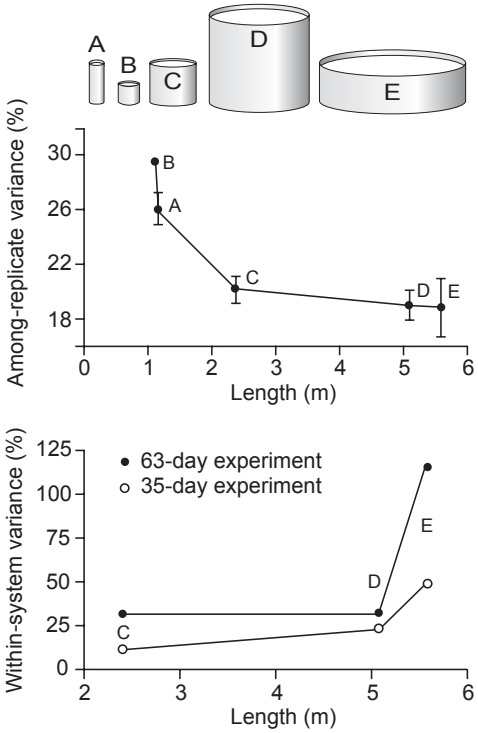

Figure 63: *Changes in relative variance for measurements of phytoplankton abundance among replicate experimental systems with changes in container size (top panel),[32] and changes in relative variance for zooplankton abundance within experimental systems with changes in container size after 35 and 63 days of experiments (bottom panel).[37,38]*

37. Kemp et al. 2001, 38. Petersen et al. 2003

Temporal scaling: Primary producer abundance in experimental ecosystems characteristically increases, then declines

Previous investigators[39] have reported a tendency of experimental planktonic communities to exhibit a characteristic temporal pattern with an initial pulse (bloom) of phytoplankton growth followed by a decline and extended period of relatively low algal biomass (bust). The duration of the bloom period tends to be 1 to 2 weeks whereas the low biomass period is protracted. This pattern presents a potential problem for conducting investigations with plankton communities because the experimental duration needs to be limited in time so as to avoid extension across the two sequential regimes (bloom and bust). If an experimental manipulation extends across the two regimes, it will be difficult to separate treatment effects statistically from these background changes in control and treated systems.

Similar temporal patterns occurred in marsh mesocosms containing emergent vascular plants, but at different scales. These mesocosms, maintained continuously for several years, exhibited exceptional growth of marsh plants in the first year, followed by a gradual decline over the subsequent 4 years.

When the phytoplankton and marsh plant biomass data are presented versus a dimensionless time-scale based on the biomass turnover-time of the plants, the patterns are virtually identical (Fig. 64, top and middle panels). Here, turnover time is the time required for plant growth to replace existing biomass, and the dimensionless 'relative time' is defined as (clock time)/(turnover time), where turnover times were taken as 1.4 days for algae and 30 days for marsh plants. For both primary producers, at high and low diversity, and in experimental containers of all sizes and shapes, peak biomass occurred after 2 to 4 relative turnovers. This sequence was hypothesized to be largely attributable to depletion of the initial nutrient supply. This idea was tested by comparing time-series of phytoplankton biomass in control containers with those receiving daily high and low rate additions of nutrients (N, Si, P at 16:16:1 proportions). In fact, added nutrients resulted in the removal of the bloom-bust cycle, with algal biomass maintained throughout the 8-week experimental duration (Fig. 64, bottom panel). Thus, it appears that these bloom-bust cycles can be eliminated with continual nutrient addition or, perhaps, by including an adequate nutrient repository (e.g., sediments) in a mesocosm.

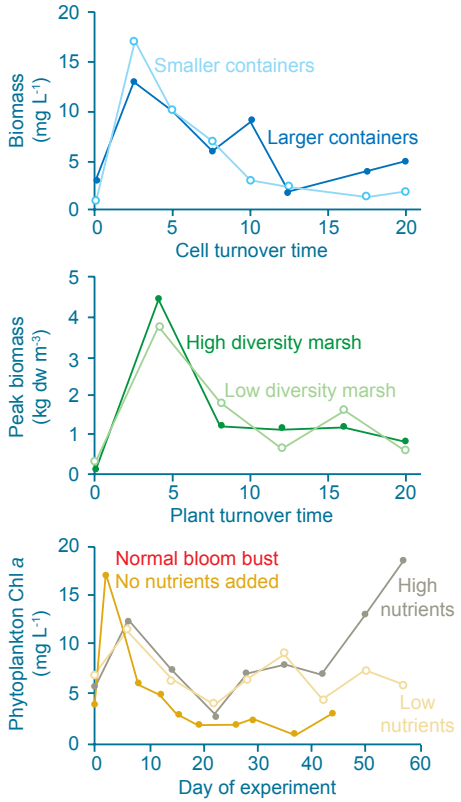

Figure 64: *Typical temporal patterns of variations in phytoplankton (top panel) and marsh plant biomass (middle panel) in mesocosms over relative time (clock time/ plant turnover time) for phytoplankton in smaller (0.1 m^3) or larger (10 m^3) containers (top panel) and for marsh plants in containers with one dominant plant species or five co-dominants (middle panel). The daily addition of nutrients (N + P + Si) at low or high rates to phytoplankton systems eliminated this bloom-bust pattern (bottom panel).*

39. Dudzik et al. 1979

Temporal scaling: Zooplankton abundance in experimental ecosystems characteristically lags phytoplankton abundance

As with phytoplankton growing in experimental ecosystems, temporal trends in zooplankton biomass in mesocosms tend to follow characteristic cycles of growth and decline. Typical examples of these cycles are depicted for mesocosms of five different size and shapes during spring and for comparable regions of Chesapeake Bay (Fig. 65). Zooplankton assemblages, which are dominated by the copepod *Acartia tonsa*, exhibit peak biomass values that lag behind phytoplankton blooms by about 2 weeks, with zooplankton values being generally higher in the smaller mesocosms (A, B, and C in Fig. 65), possibly revealing a scaling effect. Whereas zooplankton and phytoplankton biomass levels were similar to each other in mesocosms, in the natural estuary zooplankton biomass is only 10-20% of that of their phytoplankton prey. In estuaries such as Chesapeake Bay, zooplankton biomass tends to be controlled more by predators than by food supply.[40] In typical experimental ecosystems, however, most planktivorous predators are excluded, thereby allowing initial explosive zooplankton growth followed by declining growth with diminishing food supplies.

The coincidence of declining phytoplankton and increasing zooplankton in mesocosms suggests that zooplankton grazing contributes to algal losses. In fact, nutrient enrichment experiments resulted in significant increases in zooplankton biomass with little change in phytoplankton abundance, indicating food-limited conditions for zooplankton.[41] Under the extreme food limitation that typifies conditions in many experimental mesocosms, adult copepods will also prey heavily on their own juveniles. This kind of cannibalistic behavior appears to be much less common in natural estuaries where adult copepods are controlled by their predators.[41]

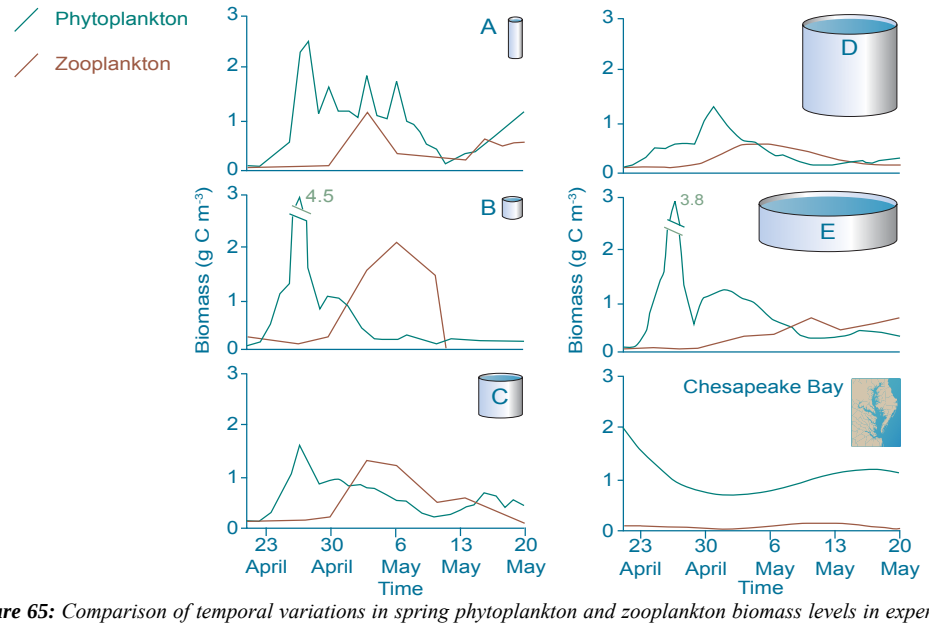

Figure 65: *Comparison of temporal variations in spring phytoplankton and zooplankton biomass levels in experimental ecosystems of different size (ranging from 0.1 m^3 to 10 m^3) and in the mesohaline region of Chesapeake Bay.*[42,43]

40. Roman et al. 2005, 41. Roman unpublished, 42. Mesocosm data from Roman unpublished, 43. Field data are adapted from Brownlee and Jacobs 1987 and Harding et al. 2002

Temporal scaling: Extended experiments lead to depleted nutrients and food, and subsequent reduced fish growth

Earlier (p. 53), we used an example from experiments with planktivorous (zooplankton-eating) bay anchovy, *Anchoa mitchilli,* to illustrate how the size of experimental containers can affect the behavior and growth of captive fish. Although these results were from a relatively short duration (43-day) experiment, a longer (90-day) experiment produced a similar pattern of increasing fish growth with increasing container radius (Fig. 66). In this longer study, however, anchovy growth rates were significantly lower than those in the shorter experiment, and all rates from the longer study were well below the range of values measured in the estuary. Given the tendency for zooplankton biomass in experimental ecosystems to decline after several weeks without supplemental nutrient additions, (p. 56), these results are not surprising. Based on observed zooplankton abundances, calculations of anchovy bioenergetic balance (i.e., consumption minus excretion minus respiration) for these two experiments revealed that growth of fish in the longer duration study was, in fact, acutely limited by food availability.[39] To minimize stress on experimental fish, growth rates had been calculated for individual fish only at the end of these experiments by comparing initial size (and inferred weight) with measured size (and weight) at the end of the experiment. It was assumed that during their first 43 days in captivity, the fish in the 90-day experiment were probably growing at rates similar to those measured in the shorter study; however, after 90 days with limited food supplies, some individuals actually shrunk.[44] Thus, duration of study in experimental estuarine ecosystems can substantially affect the observed productivity, standing stocks, feeding rates, and growth of contained organisms.

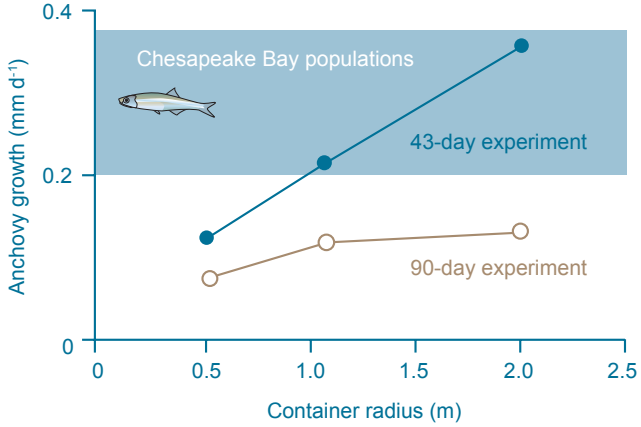

Figure 66: *Mean (± SE) growth of bay anchovy,* Anchoa mitchilli*, versus diameter of experimental ecosystems for similar studies of 43- and 90-day duration. Growth rates are calculated comparing length of fish at the beginning and end of the experiments.*[44]

44. Mowitt 1999

Temporal (and spatial) scaling: Extended experiments lead to depleted nutrients, food, and subsequent reduced oyster growth

The previous example illustrated how the size and shape of experimental containers and the duration of an experiment can substantially alter the growth of planktivorous fish. This example demonstrates a similar pattern for benthic filter-feeding oysters (*Crassostrea virginica*) when experiments are conducted without continuous nutrient additions and without resuspension of bottom sediments. These kinds of experiments are commonly used to study benthic filtration effects on plankton in aquatic ecosystems.

In these experiments, the larger mesocosms (1.0 m^3, C tanks) consistently had more phytoplankton biomass regardless of whether or not oysters were present. The smaller (0.1 m^3, A tanks) narrower containers (Fig. 67; note differences in Y-axis scale between panels) had lower light penetration through the water column, thereby supporting less algal production. As previously discussed, phytoplankton biomass exhibited an initial bloom during the first week, followed by a gradual decline in abundance over the subsequent 4 weeks.[45,46]

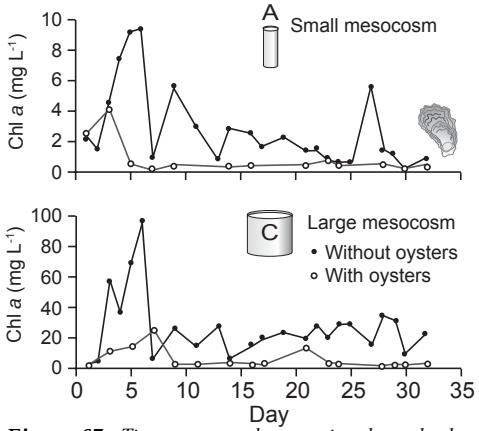

Figure 67: *Time-course changes in phytoplankton biomass (chl a) in smaller (0.1 m^3, upper panel) and larger (1.0 m^3, lower panel) mesocosms with and without benthic filter-feeding oyster populations. Notice the difference in Y-axis scale for the two experimental systems.*

In this experiment, the filter-feeding rates were scaled to container volume in the two mesocosm types by adding 120 juvenile oysters to the 1 m^3 mesocosms and 12 to the 0.1 m^3 systems. Within a week of the initiation of the experiment, oyster filtration had essentially depleted phytoplankton standing stocks in all experimental ecosystems, with chlorophyll-*a* values below 1 µg l^{-1} in the smaller systems and generally less than 5 µg l^{-1} in the larger containers. Although chlorophyll *a* levels declined in the mesocosms without oysters as well, they remained significantly higher (2-6 µg l^{-1} in the smaller systems and 10-40 µg l^{-1} in the larger containers).

At these experimental animal densities and container volumes, oysters were probably food-limited for much of the experiment, especially in the small mesocosms. Consequently, over the 4-week-long experiments, oysters grew significantly better in the larger mesocosms with higher food abundance than in the smaller systems (Fig. 68).[45,46] For a shorter experimental duration, the difference might not have been so large; however, light limitation in the smaller, narrow tanks may have created an inherently lower phytoplankton system.

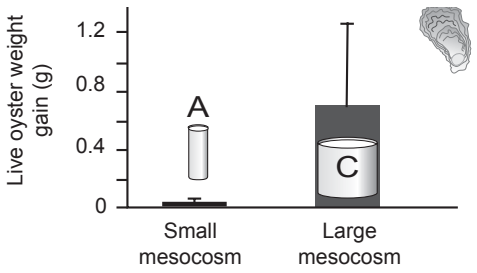

Figure 68: *Difference in weight gain (mean ± standard deviation) by oysters grown in smaller (0.1 m^3) and in larger (1.0 m^3) mesocosms. n=10 in the larger mesocosms, n=7 in the smaller mesocosms.*

45. Porter 2004a, 46. Porter 1999

References

Baker, J., R. Mason, J.C. Cornwell, J.Ashley, J. Halka and J. Hill. 1997. Final Report to Maryland Department of the Environment, Ref. No. UMCES [CBL] 97-142.

Bartleson, R. D., W. M. Kemp and J. C. Stevenson. 2005. Use of a simulation model to examine effects of nutrient loading and grazing on *Potamogeton perfoliatus L.* communities in microcosms. Ecological Modelling. 185: 483-512.

Berg, G.M., P.M. Glibert and C.-C. Chen. 1999. Dimension effects of enclosures on ecological processes in pelagic systems. Limnology and Oceanography 44:1331-1340.

Boynton, W.R., J.H. Garber, R. Summers and W.M. Kemp. 1995. Inputs, transformations, and transport of nitrogen and phosphorus in Chesapeake Bay and selected tributaries. Estuaries 18(1B):285-314.

Brownlee, P.C. and F. Jacobs. 1987. Mesozooplankton and microzooplankton in the Chesapeake Bay. Pages 217-269 in S.K. Majumdar, L.W. Hall, Jr. and H.M. Austin (eds.). Containment problems and management of living Chesapeake Bay resources. Pennsylvania Academy of Sciences, Easton.

Carpenter, S.R. 1996. Microcosm experiments have limited relevance for community and ecosystem ecology. Ecology 77:667-680.

Carpenter, S.R., J.F. Kitchell and J.R. Hodgson. 1985. Cascading trophic interactions and lake productivity. BioScience 35:634-639.

Chen, C.-C. and W.M. Kemp. 2004. Periphyton communities in experimental marine ecosystems: Scaling the effects of removal from container walls. Marine Ecology-Progress Series 271:27-41.

Chen, C.-C., J.E. Petersen and W.M. Kemp. 1997. Spatial and temporal scaling of periphyton growth on walls of estuarine mesocosms. Marine Ecology-Progress Series 155:1-15.

Chen, C.-C., J.E. Petersen and W.M. Kemp. 2000. Nutrient uptake in experimental estuarine ecosystems: Scaling and partitioning rates. Marine Ecology-Progress Series 200:103-116.

Cohen, J.E. and D. Tilman. 1996. Biosphere 2 and biodiversity: The lessons so far. Science 274:1150-1151.

Confer, J.L. 1972. Interrelations among plankton, attached algae and phosphorus cycle in artificial open systems. Ecological Monographs 42:1-23.

Cooke, G.D. 1967. The pattern of autotrophic succession in laboratory microcosms. BioScience 17:717-721.

Cornelisen, C.D and F. I. M. Thomas. 2006. Water flow enhances ammonium and nitrate uptake in a seagrass community. Marine Ecology-Progress Series 312:1-13.

Cornwell, J.C. Unpublished data. MEERC report, U.S.E.P.A. Star Program.

Cowan, J.L.W. and W.R. Boynton. 1996. Sediment-water oxygen and nutrient exchanges along the longitudinal axis of Chesapeake Bay: Seasonal patterns, controlling factors and ecological significance. Estuaries 19:562-580.

Crawford, S.M. and L.P. Sanford. 2001. Boundary shear velocities and fluxes in the MEERC experimental ecosystems. Marine Ecology-Progress Series 210:1-12.

de Lafontaine, Y. and W.C. Leggett. 1987. Effect of container size on estimates of mortality and predation rates in experiments with macrozooplankton and larval fish. Canadian Journal of Fisheries and Aquatic Sciences 44:1534-1543.

Dudzik, M., J. Harte, A. Jassby, E. Lapan, D. Levy and J. Rees. 1979. Some considerations in the design of aquatic microcosms for plankton studies. International Journal of Environmental Studies 13:125-130.

Eppley, R.W., P. Koeller and G.T. Wallace, Jr. 1978. Stirring influences the phytoplankton species composition within enclosed columns of coastal sea water. Journal of Experimental Marine Biology and Ecology 32:219-239.

Estrada, M., M. Alcaraz and C. Marrasé. 1987. Effects of turbulence on the composition of phytoplankton assemblages in marine microcosms. Marine Ecology-Progress Series 38:267-281.

Fee, E.J. and R.E. Hecky. 1992. Introduction to the northwest Ontario lake size series (NOLSS). Canadian Journal of Fisheries and Aquatic Sciences 49:2434-2444.

Fonseca, M.S. and W. J. Kenworthy. 1987. Effects of current on photosynthesis and distribution of seagrasses. Aquatic Botany 27:59-78.

Fukuda, M.K. and Lick, W., 1980. The Entrainment of Cohesive Sediments in Freshwater. Journal of Geophysical Research, 85(C5): 2813-2824.

Gallagher, J.L and F.G. Daiber. 1973. Diel rhythms in edaphic community metabolism in a Delaware salt marsh. Ecology 54:1160-1163.

Grice, G.D. and M.R. Reeve (eds.). 1982. Marine Mesocosms: Biological and Chemical Research in Experimental Ecosystems. Springer-Verlag, New York.

Gust, G. and Mueller, V., 1997. Interfacial hydrodynamics and entrainment functions of currently used erosion devices. pp. 149-174 in: N. Burt, W.R. Parker and J. Watts (ed.s), Cohesive Sediments. John Wiley and Sons, New York,

Harding L.W., Jr., M.E. Mallonee and E.S. Perry. 2002. Toward a predictive understanding of primary productivity in a temperate, partially stratified estuary. Estuarine and Coastal Shelf Science 55:437-463.

Harte, J., D. Levy, J. Rees and E. Saegebarth. 1980. Making microcosms an effective assessment tool. Pages 105-137 in J.P. Giesy, Jr. (ed.). Microcosms in Ecological Research. National Technical Information Service, Springfield VA.

Heath, M.R. and E.D. Houde. 2001. Evaluating and modeling foraging performance of planktivorous and piscivorous fish: Effects of containment and issues of scale. Pages 191-250 in R.H. Gardner, W.M. Kemp, V.S. Kennedy and J.E. Petersen (eds.). Scaling Relations in Experimental Ecology. Columbia University Press, New York.

Houde, E.D. Unpublished data. MEERC report, U.S.E.P.A. Star report.

Huettel, M. and A. Rusch. 2000. Transport and degradation of phytoplankton in permeable sediment. Limnology and Oceanography 45:534-549.

Kadlec, R.H. and R.L. Knight. 1995. Treatment Wetlands. Lewis Publishers: Boca Raton FL.

Kemp, W.M., R. Batiuk, R. Bartleson, P. Bergstrom, V. Carter, G. Gallegos, W. Hunley, L. Karrh, E. Koch, J. Landwehr, K. Moore, L. Murray, M. Naylor, N. Rybicki, J. C. Stevenson, and D. Wilcox. 2004. Habitat requirements for submerged aquatic vegetation in Chesapeake Bay: Water quality, light regime, and physical-chemical factors. Estuaries 27:363-377.

Kemp, W.M. and W.R. Boynton. 1984. Spatial and temporal coupling of nutrient inputs to estuarine primary production: The role of particulate transport and decomposition. Bulletin of Marine Science 35:522-535.

Kemp, W.M., W.R. Boynton, J.E. Adolf, D.F. Boesch, W.C. Boicourt, G. Brush, J.C. Cornwell, T.R. Fisher, P.M. Glibert, J.D. Hagy, L.W. Harding, E.D. Houde, D.G. Kimmel, W.D. Miller, R.I.E. Newell, M.R. Roman, E.M. Smith and J.C. Stevenson. 2005. Eutrophication of Chesapeake Bay: Historical trends and ecological interactions. Marine Ecology-Progressive Series 303:1-29.

Kemp, W.M., M.R. Lewis, J.J. Cunningham, J.C. Stevenson and W.R. Boynton. 1980. Microcosms, macrophytes, and hierarchies: Environmental research in the Chesapeake Bay. Pages 911-936 in J.P. Giesy, Jr. (ed.). Microcosms in Ecological Research. National Technical Information Service, Springfield, VA.

Kemp, W.M., J.E. Petersen and R.H. Gardner. 2001. Scale-dependence and the problem of extrapolation: Implications for experimental and natural coastal ecosystems. Pages 3-57 in R.H. Gardner, W.M. Kemp, V.S. Kennedy and J.E. Petersen (eds.). Scaling Relations in Experimental Ecology. Columbia University Press, New York.

Kemp, W.M., R.R. Twilley, J.C. Stevenson, W.R. Boynton and J.C. Means. 1983. The decline of submerged vascular plants in upper Chesapeake Bay: Summary of results concerning possible causes. Marine Technology Society Journal 17:78-89.

Kerhin, R.T., P.J. Blakeslee, N. Zoltan and R. Cuthbertson. 1988. The surficial sediments of the Chesapeake Bay, Maryland: Physical characteristics and sediment budget. Report of Investigation 48, Maryland Geological Survey. 82 pages.

Kitchens, W.M. 1979. Development of a salt marsh microecosystem. International Journal of Environmental Studies 13:109-118.

Kuiper, J. 1981. Fate and effects of mercury in marine plankton communities in experimental enclosures. Ecotoxicology and Environmental Safety 5:106-134.

Lewis, M.R. and T. Platt. 1982. Scales of variability in estuarine ecosystems. Pages 3-20 in V.S. Kennedy (ed.). Estuarine Comparisons. Academic Press, New York.

Luckett, C., W.H. Adey, J. Morrissey and D.M. Spoon. 1996. Coral reef mesocosms and microcosms - successes, problems and the future of laboratory models. Ecological Engineering 6:57-72.

Luckinbill, L.S. 1973. Coexistence in laboratory populations of Paramecium aurelia and its predator Didinium nasutum. Ecology 54:1320-1327.

Madsen, T.V. and M. Søndergaard. 1983. The effects of current velocity on the photosynthesis of *Callitriche stagnalis* scop. Aquatic Botany 15: 187-193.

Marvin-DiPasquale, M.C. and D.G. Capone. 1998. Benthic sulfate reduction along the Chesapeake Bay central channel. I. Spatial trends and controls. Marine Ecology-Progress Series 168:213-228.

Merrell, K.S. 1996. The effects of flow and mixing on *Vallisneria* and its associated community in experimental mesocosms. MS thesis. University of Maryland, College Park. 83p.

Mowitt, W.P. 1999. Scale-dependence of bay anchovy (*Anchoa mitchilli*) growth and top-down control by anchovies of plankton communities in estuarine mesocosms. MS thesis. University of Maryland, College Park.

Mowitt, W.P., E.D. Houde, D.C. Hinkle and A. Sanford. 2006. Growth of planktivorous bay anchovy *Anchoa mitchilli*, top-down control, and scale-dependence in estuarine mesocosms. Marine Ecology-Progress Series 308:255-269.

Muffley, B.W. 2002. Scale-dependent predatory effects of the Atlantic silversides, *Menidia menidia*, and lobate ctenophore, *Mnemiopsis leidyi*, on plankton communities in estuarine mesocosms. MS thesis. University of Maryland, College Park.

Murray, L., R.B. Sturgis, R.D. Bartleson, W. Severn and W.M. Kemp. 2000. Scaling submersed plant community responses to experimental nutrient enrichment. Pages 241-257 in S. A. Bortone (ed.). Seagrasses: Monitoring, Ecology, Physiology, and Management. CRC Press, New York.

Naeem, S. and S. Li. 1997. Biodiversity enhances ecosystem reliability. Nature 390:507-509.

Neckles, H.A., R.L. Wetzel and R.J. Orth. 1993. Relative effects of nutrient enrichment and grazing on epiphyte-macrophyte (*Zostera marina L.*) dynamics. Oecologia 93:285-295.

Neundorfer, J.V. and W.M. Kemp. 1993. Nitrogen versus phosphorus enrichment of brackish waters: Responses of the submersed plant Potamogeton perfoliatus and its associated algal community. Marine Ecology-Progress Series 94:71-82.

Nixon, S.W. 1969. A synthetic microcosm. Limnology and Oceanography 14:142-145.

Nixon. S. W. and C.A. Oviatt. 1973. Ecology of a New England salt marsh. Ecological Monographs 43:463-498.

Odum, E.P. 1961. The role of tidal marshes in estuarine production. Conservationist 15:12-15.

Øiestad, V. 1990. Specific application of meso- and macrocosms for solving problems in fisheries research. Pages 136-154 in C.M. Lalli (ed.). Enclosed Experimental Marine Ecosystems: A Review and Recommendations. Springer-Verlag, New York.

Parsons, T.R. 1982. The future of controlled ecosystem enclosure experiments. Pages 411-418 in G.D. Grice and M.R. Reeve (eds.). Marine Mesocosms: Biological and Chemical Research in Experimental Ecosystems. Springer-Verlag, New York.

Petersen, J.E., C.-C. Chen and W.M. Kemp. 1997. Scaling aquatic primary productivity: Experiments under nutrient- and light-limited conditions. Ecology 78:2326-2338.

Petersen, J.E., J.C. Cornwell and W.M. Kemp. 1999. Implicit scaling in the design of experimental aquatic ecosystems. Oikos 85:3-18.

Petersen, J.E., W.M. Kemp, R. Bartleson, W.R. Boynton, C.-C. Chen, J.C. Cornwell, R.H. Gardner, D.C. Hinkle, E.D. Houde, T.C. Malone, W.P. Mowitt, L. Murray, L.P. Sanford, J.C. Stevenson, K.L. Sundberg and S.E. Suttles. 2003. Multiscale experiments in coastal ecology: Improving realism and advancing theory. BioScience 53:1181-1197.

Petersen, J.E., L.P. Sanford and W.M. Kemp. 1998. Coastal plankton responses to turbulent mixing in experimental ecosystems. Marine Ecology-Progress Series 171:23-41.

Porter, E.T. 1999. Physical and biological scaling of benthic-pelagic coupling in experimental ecosystem studies. PhD dissertation, University of Maryland, College Park.

Porter, E.T., J.C. Cornwell, L.P. Sanford and R.I.E. Newell. 2004a. Effect of oysters *Crassostrea virginica* and bottom shear velocity on benthic-pelagic coupling and estuarine water quality. Marine Ecology-Progress Series 271:61-75.

Porter, E.T., M.S. Owens and J.C. Cornwell. 2006. Effect of manipulation on the biogeochemistry of experimental sediment systems. Journal of Coastal Research 22:1539-1551.

Porter, E.T., L.P. Sanford, G. Gust and F.S. Porter. 2004b. Combined water-column mixing and benthic boundary-layer flow in mesocosms: Key for realistic benthic-pelagic coupling studies. Marine Ecology-Progress Series 271:43-60.

Porter, E.T., L.P. Sanford and S.E. Suttles. 2000. Gypsum dissolution is not a universal integrator of 'water motion'. Limnology and Oceanography 45:145-158.

Purcell, J.E., U. Båmstedt and A. Båmstedt. 1999. Prey, feeding rates, and asexual reproduction rates of the introduced oligohaline hydrozoan Moerisia lyonsi. Marine Biology 134:317-325.

Reeve, M.R., G.D. Grice and R.P. Harris. 1982. The CEPEX approach and its implications for future studies in plankton ecology. Pages 389-398 in G.D. Grice and M.R. Reeve (eds.). Marine Mesocosms: Biological and Chemical Research in Experimental Ecosystems. Springer-Verlag, New York.

Resetarits, W.J., Jr. and J.E. Fauth. 1998. From cattle tanks to Carolina bays: the utility of model systems for understanding natural communities. Pages 133-151 in W.J. Resetarits, Jr. and J. Bernardo (eds.). Experimental Ecology: Issues and Perspectives. Oxford University Press, New York.

Ringelberg, J. and K. Kersting. 1978. Properties of an aquatic microecosystem: I. General introduction to the prototypes. Archiv für Hydrobiologie 83:47-68.

Roman, M.R. Unpublished data. MEERC report, U.S.E.P.A. Star report.

Roman, M., X. Zhang, C. McGilliard and W. Boicourt. 2005. Seasonal and annual variability in the spatial patterns of plankton biomass in Chesapeake Bay. Limnology and Oceanography 50:480-492.

Roush, W. 1995. When rigor meets reality. Science 269:313-315.
Sanford, L.P. 1997. Turbulent mixing in experimental ecosystem studies. Marine Ecology-Progress Series 161:265-293.
Sanford, L.P. and S.M. Crawford. 2000. Mass transfer versus kinetic control of uptake across solid-water boundaries. Limnology and Oceanography 45:1180-1186.
Santschi, P.H., U. Nyffeler, R. Anderson and S. Schiff. 1984. The enclosure as a tool for the assessment of transport and effects of pollutants in lakes. Pages 549-562 in H.H. White (ed.). Concepts in Marine Pollution Measurements. Maryland Sea Grant College, College Park.
Schindler, D.E. and M.D. Scheuerell. 2002. Habitat coupling in lake ecosystems. Oikos 98:177-189.
Schindler, D.W. 1998. Replication versus realism: The need for ecosystem-scale experiments. Ecosystems 1:323-334.
Schmitz, J.P. 2000. Meso-scale community organization and response to burning in mesocosms and a field salt marsh. MS thesis. University of Maryland, College Park.
Short, F.T., D.M. Burdick and J.E. Kaldy III. 1995. Mesocosm experiments quantify the effects of eutrophication on eelgrass, *Zostera marina*. Limnology and Oceanography 40:740-749.
Steele, J.H. and J.C. Gamble. 1982. Predator control in enclosures. Pages 227-237 in G.D. Grice and M.R. Reeves (eds.). Marine Mesocosms: Biological and Chemical Research in Experimental Ecosystems. Springer-Verlag, New York.
Sturgis, R.B. and L. Murray. 1997. Scaling of nutrient inputs to submersed plant communities: Temporal and spatial variations. Marine Ecology-Progress Series 152:89-102.
Tatterson, G.B. 1991. Fluid Mixing and Gas Dispersion in Agitated Tanks. McGraw-Hill, New York.
Twilley, R.R., W.M. Kemp, K.W. Staver, J.C. Stevenson and W.R. Boynton. 1985. Nutrient enrichment of estuarine submersed vascular plant communities. 1. Algal growth and effects on production of plants and associated communities. Marine Ecology-Progress Series 23:179-191.
Wiens, J.A. 2001. Understanding the problem of scale in experimental ecology. Pages 61-88 in R.H. Gardner, W.M. Kemp, V.S. Kennedy and J.E. Petersen (eds.). Scaling Relations in Experimental Ecology. Columbia University Press, New York.
Zelenke, J. 1999. Tidal freshwater marshes as nutrient sinks: Nutrient burial and denitrification. PhD dissertation. University of Maryland, College Park.
Zieman, J.C., S.A. Macko, and A.L. Mills. 1984. Role of seagrasses and mangroves in estuarine food webs: Temporal and spatial changes in stable isotope composition and amino acid content during decomposition. Bulletin of Marine Science 35:380-392.