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THE ROLE OF ENCLOSED EXPERIMENTAL ECOSYSTEMS ("MESOCOSMS") IN OCEAN SCIENCE

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200 word synopsis: Enclosed experimental ecosystems ("mesocosms" and "microcosms") have become widely used research tools in aquatic sciences because they allow for a relatively high degree of experimental control and replication necessary for hypothesis testing while still capturing dynamics that emerge from ecosystem-level interactions between organisms and their physical and chemical environments. Mesocosms provide a bridge between observational field studies and process-oriented lab research. Over the last 30 years, mesocosms have become important tools in the marine environment to address critical research questions in the fields of chemical and physical oceanography, ecotoxicology, fisheries science, and basic and applied ecology. To be effective as research tools, great care must be given to the design, operation and interpretation of investigations conducted in experimental ecosystems. Problems of scale necessitate consideration of two key questions for researchers who employ experimental ecosystems. First, how does one design experiments that accurately capture essential chemical, physical and biological characteristics of the "real world" that is being modeled? Second, how can results from experiments conducted in these simplified systems be systematically and quantitatively extrapolated to improve our understanding of nature?

Experimental Ecosystems as Tools for Aquatic Research

Within the last few decades there has been a clear trend within ecological science of growing reliance on manipulative experiments as a means of testing ecological theory. Many approaches are available for experimentation. An important distinction can be drawn between field and laboratory based experiments. In field experiments, either parts of nature or whole, naturally bounded ecosystems are manipulated in place while similar areas are left as controls. In laboratory experiments, organisms, communities, and the physical substrate are transported to controlled facilities. A second distinction can be drawn between experiments in which organisms and materials freely exchange between the experiment and surrounding environment and those in which organisms and materials are enclosed and isolated either in a laboratory setting or with physical boundaries imposed in the field. The term "enclosed experimental ecosystem" is used when the goal of an enclosure experiment, conducted in either laboratory or field conditions, is to explore interactions among organisms or between organisms and their chemical and physical environment. Because enclosed experimental ecosystems are intended to serve as miniaturized worlds for studying ecological processes, they are often called "microcosms" or "mesocosms".

Enclosed experimental ecosystems have become widely used research tools in oceanographic and freshwater sciences because they allow for a relatively high degree of experimental control and replication necessary for hypothesis testing while still capturing dynamics that emerge from ecosystem-level interactions between organisms and their physical and chemical environments. They provide a bridge between observational field studies and process-oriented lab research. Mesocosms have been used to conduct experiments on a broad range of aquatic habitats. Over the last 30 years, enclosed experimental ecosystems have become important tools in both coastal and open ocean contexts to address critical research questions in the fields of chemical and physical oceanography, ecotoxicology, fisheries science, and basic and applied ecology (figure 1).

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Two fundamental objectives of ecological experiments are to achieve high levels of control and realism. Control refers to the ability to relate cause and effect, to manipulate, to replicate, and to repeat experiments, realism is a measure of the degree to which results accurately mimic the dynamics of particular natural ecosystems. Tradeoffs between control and realism are inherent in different experimental approaches; experiments conducted within nature tend to maximize realism, whereas physiological experiments in the laboratory allow for the highest degree of experimental control. In theory, mesocosms provide intermediate levels of both control and realism (figure 2).

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Scale is a Crucial Issue in Mesocosm Research

Scale is a crucial issue for all ocean scientists and has particular implications for researchers using enclosed experimental ecosystems. How can large-scale processes be simulated and incorporated into enclosed experimental ecosystems so as to maximize realism? How can research findings be quantitatively extrapolated from small, often simplified experimental ecosystems up to whole natural ecosystems? For that matter, how can information gleaned from research in one type of ecosystem be extrapolated to other natural ecosystems that differ in scale? Recent research indicates that scale effects can be parsed into "fundamental effects", that are evident in both natural and experimental ecosystems, and "artifacts of enclosure", that are solely attributable to the artificial environment in mesocosms. A key objective of this contribution to the Encyclopedia is to review the ways in which mesocosm experiments have been used to study the marine environment and to suggest ways in which scaling considerations can be used to improve the use of mesocosms research tools.

History and Applications

There is a rich history in the use of enclosed experimental ecosystems. The initial concept of microcosms, as hierarchically nested miniature worlds contained successively within larger worlds, has been credited to early Greek philosophers including Aristotle. Although it is difficult to date the initial scientific uses of enclosed experimental ecosystems, small glass jars and other containers were routinely used as experimental ecosystems by the middle of the 20th century. H. T. Odum and his colleagues were pioneers and proponents of the use of mesocosms to study aquatic ecosystems. They constructed a wide variety of experimental ecosystems including laboratory streams, containers with planktonic and vascular plant communities, and shallow outdoor ponds containing oysters and/or seagrasses. Although the word, microcosm, was used initially to describe virtually all experimental ecosystems, the term mesocosm was later adopted to distinguish larger experimental units from smaller bench-top laboratory systems.

Some have suggested that experimental manipulations of whole aquatic ecosystems in nature are always preferable to mesocosm studies. However, the characteristically steep spatial gradients, three dimensional water exchanges, lack of boundaries and natural variability make such whole ecosystem manipulations extremely difficult to accomplish in coastal and open ocean environments, leaving mesocosms as critical tools for controlled experimentation. A series of books devoted to aspects of experimental aquatic ecosystems mark recent progress with this research approach (see “further readings” at the close of article).

There are diverse styles and applications of enclosed experimental ecosystems (figure 3). During the last four decades, experimental microcosms and mesocosms have been developed in a diversity of sizes, shapes, and habitats to address a broad range of research questions. Small (~0.5 L) laboratory chemostat flasks have been widely used by R. Margalef and others to study plankton community dynamics, while large (30-1300 m^3) plastic bag enclosures have been deployed *in situ* by J. Gamble, G. Grice, D. Menzel, T. Parsons, M. Reeve, J. Steele, J. Strickland and others to study pelagic (in some cases including benthic) coastal ecosystems in Europe and North America. Similarly, mesocosm shapes vary from the tall and relatively narrow (23 m high x 9.5 m deep) in situ plankton bags used by Gamble, Steele and their colleagues to broad (350 m^2 surface), shallow (1 m deep) estuarine ponds used by R. Twilley and others. Mesocosms have been constructed to study diverse marine habitats, including planktonic regions of oceans and estuaries, deep benthos, shallow tidal ponds, coral reefs, salt marshes, and seagrasses.

Composition and organization of experimental ecological communities range broadly and include: simple “gnotobiotic” ecosystems where all species are selected and identified; interconnected microcosms, each containing a different trophic-level; intact “undisturbed” columns of sediment and overlying water extracted and contained; and tidal ponds with “self-organizing” communities developed by seeding with diverse inoculant communities taken from different natural ecosystems.

<Figure 3 near here>

Marine mesocosms have been used effectively to address a range of theoretical and applied scientific questions. Early studies using in situ bag enclosures (e.g., CEPEX, Loch Ewe Enclosures, Kiel Plankton Towers) examined planktonic food web responses to nutrient enrichment and introduction of toxic contaminants (e.g., copper, mercury). These experiments were designed to assess the effects of both “bottom-up” (resource limited) and “top-down” (herbivore and predator determined) controls (e.g., figures 3a and 4). Although these studies were very instructive, difficulties in controlling mixing regimes and lack of replication of treatments tended to limit interpretation of results. Later studies, notably the land-based Marine Ecosystem Research Laboratory (MERL), employed mechanical mixing, added intact sediments, and increased replication (figure 3b). MERL systems were used by S. Nixon, C. Oviatt and their colleagues to investigate trophic and biogeochemical responses to similar treatments including N, P, and Si enrichment, crude oil contamination, filter-feeding, and storm mixing events. The versatile and permanent MERL facility allowed investigators to explore interactions between pelagic and benthic communities that are critical in the dynamics of shallow coastal ecosystems (e.g., figure 5).

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The Challenges and Opportunities of Scale in Mesocosm Research

Two parallel trends in ecology during the last 20 years have been an increased use of mesocosms as research tools (figure 6a) and an increased recognition of the importance of scale as a determinant of the patterns and processes observed in natural ecosystems (figure 6b). As we have discussed, mesocosms have become widely-used and accepted tools in ocean science because they provide a means of conducting ecosystem level experiments under replicated, controlled, and repeatable conditions. The focus on scale can be traced to a number of factors including: theoretical and technological advances that increase our understanding of causal linkages between local, regional and global phenomena; a growing awareness of human impact at all scales; and the formalization of scale as a legitimate topic of inquiry within the emerging field of landscape ecology. This emphasis on scale is evidenced by the steady increase in the number of journal articles listing "scale" as a keyword (figure 6b) and in the publication of a number of new books devoted to scaling theory.

<Figure 6 near here>

It has long been recognized that scale is an inherent design problem that may confound the interpretation of results from experimental ecosystem studies. Since their use first became prevalent in the 1970s, researchers have expressed concerns regarding scaling problems associated with mesocosms including the effects of: reduced system size and short time scale of experiments, reduced ecological complexity, wall growth, limitations on animal movements, distorted mixing regimes, and unrealistic water exchange rates. A few investigators have used a simple idea of mesocosm calibration, where key properties are adjusted in experimental systems to mimic conditions in the natural environment. However, the majority of early mesocosm studies skirted the question of scaling and the problem of extrapolation altogether. By the end of the 1980's it was clear that further progress in the application of experimental ecosystem methods to aquatic science would require focused quantitative study of how scale affects behavior in natural and experimental ecosystems and how experimental ecosystems might be better designed to account for scale. The development of systematic techniques for extrapolating results from small experimental ecosystem studies to conditions in nature at large remains an active area of research. Recent research (e.g., at the Multiscale Experimental Ecosystem Research Center, "MEERC") has focused on developing quantitative and systematic approaches for the design and interpretation of experimental ecosystem research with a particular focus on the problem of scale.

Several scaling concerns must be addressed when using mesocosm results to predict effects in natural aquatic ecosystems. The first and most obvious is that experimental systems are constrained in size and duration. An extensive literature review revealed a median experimental duration of 49 days and median volume of 1.7 m^3; aquatic mesocosm experiments are brief and small relative to the natural scales that characterize many important ecological processes of interest. A second problem is the presence of walls, which restrict biological, material and energy exchange with the outside world and provide a substrate for growth of undesirable but potentially influential organisms on this artificial edge habitat. A third problem is that a host of experimental design decisions – such as how many replicates to include per treatment and whether to control light, mixing and other properties – tend to vary together with choices of size, duration and ecological complexity (figures 7 and 8). Finally, the relative importance of the air-water area, sediment-water area, and wall area, in relation to each other and to water and sediment volume change with physical dimensions. Unfortunately, parallel scaling problems also exist for field experiments. For example, replication tends to decrease with increasing plot size and experimental lakes and field plots tend to be orders of magnitude smaller than the natural systems for which inferences are drawn.

<Figure 7 near here>

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An analysis of aquatic studies conducted in cylindrical planktonic-benthic mesocosms reveals that in designing experimental ecosystems, researchers gravitate towards a depth/radius ratio of approximately 4.5 (figure 9). As a consequence of this bias, in general larger mesocosms are simultaneously less influenced by wall artifacts, have less sediment area per unit volume, and have less surface area available for gas and light exchange per unit volume than do smaller systems (Fig. 9 b, c). Collectively, these scaling attributes can potentially confound interpretation, comparison and extrapolation of findings from mesocosm experiments.

<Figure 9 near here>

One might conclude from the preceding figures and discussion that reductions, artifacts, co-variation and distortions in scale pose an almost insurmountable obstacle to designing mesocosm studies to examine oceanic processes. Alternatively, these problems can be viewed as interesting research opportunities to advance our theoretical and practical understanding of the “science of scale”. A variety of mesocosm scaling experiments have been designed to shed light on two classes of effects: “fundamental effects of scale” evident in both natural and experimental ecosystems (e.g., the effects of water depth), and “artifacts of enclosure” attributable to the artificial environment in experimental ecosystems (e.g., the effects of wall growth). In these experiments, ecological responses are measured in relation to manipulations in experimental scales (i.e., time, space and complexity) for a variety of coastal habitat types. Such studies suggest that it is possible to improve substantially the design of experimental ecosystems. Selected examples are discussed in the sections that follow.

Effective Design of Enclosed Experimental Ecosystems

There are a host of issues and questions that must be considered in the design of enclosed experimental ecosystems. Design decisions are important because they affect how results can be interpreted and extrapolated to nature. Optimal design is determined by the research question under consideration. The processes, organisms, and habitats associated with this question determine the appropriate size, shape, duration and complexity for the experimental ecosystem. Even within a given ecosystem type, there is no single best design that will suit all research goals. Typically, the choices made will reflect a balance between three competing objectives: 1. control (the ability to relate cause and effect, to manipulate, to replicate, and to repeat experiments), 2. realism (the degree to which results accurately mimic nature), and 3. generality (the breadth of different systems to which results are applicable). There are, however, specific tools and guidelines available to aid in the experiment design process for enhancing the probability of research success. The sections below provide guidance on critical issues that must be considered.

Design choices: Degree of abstraction:

Experimental ecosystems are a type of model. Models are, by definition, simplifications and abstractions of the reality that we hope to represent with them. As modelers, researchers select a level of abstraction that is appropriate to their research question, and the choices made have direct bearing on tradeoffs between control, realism, and scale.

One can distinguish between “generic” and “ecosystem-specific” models, which represent the two extremes in this tradeoff. Generic mesocosms are used to test broad theories that potentially apply to many different kinds of ecosystems. These systems tend to be small, highly artificial, have minimal physical and biological complexity, and are not designed to represent particular natural ecosystems. This is the ecological analog of using a worm as a model for studying human physiology or behavior. In ecology, generic mesocosms have been successfully applied to address research questions pertaining to ecosystem development, predator-prey relations, stress, system stability and species diversity. Because precise correspondence with particular ecosystems is not an objective, the researcher has considerable design flexibility in constructing generic models. The downside is that extrapolation from simplified, abstract systems to particular natural ecosystems is challenging.

Ecosystem-specific mesocosms are used to test hypotheses linked to particular types of ecosystems. This is the ecological analog of using chimpanzees to study human physiology and behavior. To achieve the higher degree of realism required, these systems must incorporate the essential physical and biological features that control the dynamics in the systems that they represent. Various ecosystem-specific models have been constructed, ranging from coral reefs to coastal plain estuaries. As the desired degree of specificity and desired level of realism increase, so does the complexity of engineering necessary to achieve realistic ecological conditions (e.g., figure 10).

<Figure 10 near here>

<u>Design choices: Physical characteristics</u>:
In addition to questions related to appropriate degree of abstraction and ecosystem type, researchers face crucial design questions regarding the physical characteristics of the experimental ecosystem. For example, what are the minimum system size, experimental duration, and ecological complexity necessary to answer the research question? How will the experimental system address each of the following design decisions: light source, mixing, temperature, exchange of water and constituents, inclusion of sediments, organism source and introduction mode? We provide a list (Table 1) of some of the key variables associated with these questions that must be considered, the design decisions associated with these variables, and the ecological properties that are potentially affected by these design decisions. Choices related to physical characteristics are obviously also dependent on resources available in terms of funds, time, equipment, and support personnel.

<Table 1 near here>

<u>Design choices: Mixing and exchange:</u>
Mixing and exchange of water and associated constituents are particularly important factors to consider in the design of enclosed experimental ecosystems. A core objective of mesocosm experiments is to isolate biological, chemical and physical conditions to facilitate controlled manipulative experiments. This act of isolation can, however, create conditions within the mesocosm that are very different from those in nature, thereby distorting the dynamics observed in these experiments. Exchange can be defined as the net transport of water and its constituents through a system. Mixing can be defined as the physical movement of the water and its constituents within the system, generating turbulence within the fluid and homogenization of the constituents. Mixing and exchange are important aspects of natural marine ecosystems from the largest to the smallest of scales. Depending on how the system of interest is defined, mixing at one scale can sometimes be considered exchange at another scale. For example, mixing of surface and bottom waters can be thought of as an exchange that delivers nutrient rich water to the surface. Mesocosms need to be designed to either include or simulate the variety and magnitude of exchange and mixing that occur in the natural ecosystems that they are designed to represent.

At intermediate (meso) scales, mixing and exchange are crucial in estuaries and coastal waters where fresh and saltwater interact. Exchange and mixing of water are intricately linked processes that determine the estuary's flushing rate, and in so doing they play a major role in its biological productivity and its susceptibility to pollution effects.

At very small scales, microscopic organisms are influenced by relative motion of the fluid (shear) that is directly related to mixing intensity. Small-scale mixing renews nutrient and food supplies, affects contact between predators and prey, and may be a source of physical stress at high levels (Table 2). Mesocosm experiments indicate that mixing intensity can have a negative effect on copepod abundance and a highly negative effect on gelatinous zooplankton (figure 11).

<Table 2 near here>

<Figure 11 near here>

At the interfaces between water and fixed solid surfaces, boundary layers (regions of reduced mixing) are formed due to effects of friction. Experimental ecosystems will generally require special mixing mechanisms to minimize boundary layers at their walls and mimic natural boundary layers near the sediment surface (benthic boundary layers).

A variety of engineering approaches can be taken to mix water in mesocosms. Spinning paddles and discs, mechanical plungers, bubbling, and water pumping have all been used as approaches to generating mixing in the water column (figure 12). A range of techniques can be used to characterize the mesocosm mixing environment, including current meters and acoustic Doppler current profilers, as well as measurements of dye dispersion and gypsum dissolution. Scale-models can be developed and used to explore mixing characteristics before full scale experimental ecosystems are built. A range of investigations in various mesocosm systems (e.g., CEPEX, Loch Ewe, MERL, MEERC) have demonstrated the physical and ecological effects of alternative mixing regimes. The goal of these studies is to characterize the mixing environment within the water column and the mixing and flow environment across the bottom so that key mixing parameters (e.g., turbulent energy dissipation, vertical mixing rate) can be matched to natural conditions. Mesocosm researchers should familiarize themselves with the mixing literature as it relates to the design of mesocosms (see “Further Reading” below).

The rate at which water is exchanged with surrounding ecosystems is a physical feature that controls many important processes in marine systems. Indeed, the relatively high rate of primary and secondary productivity typical of coastal ecosystems is often attributed to large material exchange resulting from their position at the interface between the watershed and open ocean. Although exchange incorporates both temporal and spatial scale, it is often convenient to express water exchange in terms of “residence-time” (i.e. time required for incoming water to replace the entire volume of the basin or container), or alternatively as “exchange-rate” (i.e. residence-time^{-1}).

Residence time is an important scaling factor to consider in natural and experimental ecosystems because it determines whether a system is dominated by internal or external processes. The residence time of a substance or organism in the system depends on the combination of flow rate and the rate of reaction, growth, or death inside the system. Flow-through “chemostat” experiments are commonly used to study phytoplankton growth, however, few ecosystem-level studies have attempted to simulate exchange-rates that characterize specific natural ecosystems, and fewer still have explicitly assessed the effects of different exchange-rates on ecological dynamics.

The studies that have been conducted indicate that variations in water exchange rate can have substantial effects on ecological dynamics observed in both planktonic and seagrass mesocosms (figure 13). The specific impacts of exchange rates are regulated by the nature of the constituents being exchanged with the water, by the overall water residence time and by the organisms present within the system. Depending on the actual conditions and the organisms involved, variations in water exchange sometimes have counteracting effects. For example, exchange can deliver nutrients or other resources to a system and at the same time flush out mobile organisms that might utilize those resources. The effects of exchange are distinct for systems dominated by planktonic primary producers from those that are dominated by stationary producers. It is also important to recognize that variability in exchange rates can be as important in controlling ecological dynamics as the mean rates of exchange. The various effects of exchange must be taken into careful consideration in the design of experimental ecosystems.

<Figure 13 near here>

Scaling considerations in design and extrapolation:

Even in the case of "ecosystem specific" mesocosms that are designed to match precisely certain natural habitats (see section above on abstraction), experimental systems will generally be far smaller than the natural ecosystem that they are intended to represent. Scaling theory suggests that certain patterns and processes only become evident as system size and duration are increased beyond thresholds. Furthermore, scaling responses are often non-linear and unique for specific variables. Thus, for example, patterns determined to be scale-dependent in mesocosm experiments may become scale-independent at the larger scales of natural systems (solid line in figure 14). Likewise, relationships seen as scale-independent in mesocosms may change with scale in larger natural ecosystems (dashed line in figure 14). Finally, it is possible that thresholds exist over which small changes in scale result in dramatic and possibly discontinuous changes in ecological dynamics.

<Figure 14 near here>

Given these possibilities, special attention is necessary to account for the potential scale-dependence of observations made in mesocosms. Spatial scaling relationships such as those established between water depth and both phytoplankton primary productivity and zooplankton biomass (figures 14, 15) provide a basis for quantitative extrapolation. Although less information is available, it is clear that temporal as well as spatial dynamics can also profoundly affect experimental outcomes (figure 16). In most cases experimental interpretations and conclusions must be qualified with the acknowledgement that precise effects of scale are yet known.

<Figure 15 near here>

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The evidence that we have presented thus far implies that mesocosms are inherently distorted representations of nature. A key question then is, can we somehow compensate for these distortions in the design and interpretation of experiments? The term "dimensional analysis" encompasses a variety of techniques that are based on the proposition that universal relationships should apply regardless of the dimensions of a particular system under investigation. In general, the technique involves developing dimensionless relationships that capture the balance between processes or forces governing the dynamics of a particular system. Dimensional analysis provides a potentially valuable tool for designing experimental ecosystems so that they retain key features of nature. For example, spatially patchy distributions of resources and predators in natural ecosystems may be simulated in mesocosms by creating an exchange regime that is pulsed over time. Similarly, the effects of patchy schools of plankton-eating fish on plankton community dynamics can be simulated experimentally with periodic additions and then removal of fish from the tank. In these cases, temporal variability is substituted for spatial heterogeneity, and the dimensional properties conserved in the mesocosm study are both the duration and frequency of contact between organisms, resources and predators.

Simulation models provide an additional tool that can be used to improve both the design and interpretation of mesocosm research. Given the importance of spatial heterogeneity in controlling ecological dynamics, coupling mesocosms with spatially explicit dynamic simulation models may become an increasingly valuable approach to ecological research. In this approach, mesocosms can be thought of as individual cells (grain) within a heterogeneous matrix of different habitats that cover broad spatial extent. Likewise, models can be used to explore effects of temporal variability that are difficult to incorporate in the design of mesocosm studies. Numerical models offer an excellent tool for exploring non-linear feedback effects at scales that are larger than individual mesocosms.

Conclusions

Enclosed experimental ecosystems have become crucial tools for conducting controlled and repeatable studies of the ocean environment. Those who use mesocosms as research tools and those who use the results of mesocosms experiments need to understand that experimental design choices have important implications for interpretation. Mesocosms are model ecosystems and as such they represent imperfect representations of nature. A great deal is now known about how to design these experimental ecosystems so that they capture the essential features of nature. Much remains to be learned. The information presented in this chapter is intended to provide the reader with an introduction to some of the key issues in mesocosm research. The interested reader is encouraged to explore the more detailed information that is referenced in the reading listed below.

Figure Legends

Figure 1: Enclosed experimental ecosystems provide a means of conducting controlled, replicated experiments to reveal processes and interactions that occur within different marine habitats. Adapted from Petersen et al. 2007 (see "further readings").

Figure 2: As the scale of experiments increases from simple laboratory experiments to complex whole ecosystem manipulations, greater realism is possible, but control over experimental conditions declines. Simulation models can be used to synthesize and integrate results from all types of studies. Adapted from Petersen et al. 2007.

Figure 3: Marine mesocosm facilities have taken diverse forms including (a) Controlled Ecosystem Pollution Experiment (CEPEX , 1300 m^3, 17 m deep, 3 m diameter) system in Saanich Inlet, British Columbia 1978, (b) Marine Ecosystem Research Laboratory (MERL, 13 m^3, 5 m deep, 1.8 m diameter) experimental ecosystems established in 1980, (c) Rocky littoral mesocosms (23 m^3, 4.7 m long, 3.6 m wide, 1.3 m deep) at Solbergstrand Norway, (d) Plankton community mesocosms (55L, 0.77 m deep, 0.30 m diameter) with Neuse estuary water from University of North Carolina. Adapted from Petersen et al. 2007.

Figure 4: Example results of in situ mesocosm experiments (CEPEX) designed to investigate "top-down" (predator) and "bottom-up" (nutrient) controls on phytoplankton. Inorganic nutrients were added (on days 25, 37 and 53) to two of three mesocosms to stimulate primary productivity (a). Mercury was added to one of these mesocosms (on day 9) to reduce zooplankton abundance (b). Although the experiments incorporated no replication, the findings contributed to our understanding of the importance of top-down control. Figure redrawn from Grice, G.D., M. R. Reeve, P. Koeller, and D. W. Menzel. 1977. The use of large volume, transparent, enclosed sea-surface water columns in the study of stress on plankton ecosystems. Helgolander wiss. Meresunters. 30: 118-133.

Figure 5: Example results of land-based mesocosm experiments (MERL) examining plankton-benthic responses to different levels of nutrient enrichment. Total productivity and total system respiration both respond positively to enrichment (a). However, the relative importance of polychaetes worms and macro-infauna change across the gradient. Figure redrawn from Nixon, S.W. et al. pp.105-135, In: M.J.R. Fasham (ed.) Flows of energy and materials in marine ecosystems. Theory and practice. Plenum Press, New York.

Figure 6: (a) Trends in use of field experiments and mesocosms in ecological studies as revealed from key-word searches in ecological journals. Note that field experiments and mesocosm studies are not mutually exclusive categories because the latter can be used in the field. The patterns suggests an increasing reliance on both categories of experimentation. (b) Trends in scale studies in ecology based on separate searches conducted by year for the term ‘scale’ in key-words and abstracts of journals emphasizing terrestrial research (*Ecology, Oikos, Oecologia*) and journals publishing only aquatic research (*Limnology and Oceanography, Marine Ecology Progress Series*). The number of papers identified in each year was then standardized to the total number of papers published for that year in those journals and expressed in the graph as a percent. Adapted from Petersen, J. E., Cornwell, J. C., and Kemp, W. M. 1999. Implicit scaling in the design of experimental aquatic ecosystems. Oikos 85:3-18.

Figure 7: Relationship between mesocosm size and the presence of various design characteristics in a quantitative review of the mesocosm literature. Size categories (small, medium, or large, in cubic meters) are indicated in the legend. The y-axis represents the percentage of articles in a given size class for which the design characteristic indicated is present. The overall percentage of experiments for which a given characteristic is present is indicated in parentheses within the key. “Defined community” indicates that individual populations were selectively added to create the mesocosm community. Adapted from Petersen, J. E., Cornwell, J. C., and Kemp, W. M. 1999. Implicit scaling in the design of experimental aquatic ecosystems. Oikos 85:3-18.

Figure 8. Plot of mesocosm volume versus number of replicates per treatment. Median values are represented by the bar within a box, and the 75th and 25th percentiles (i.e., the interquartile range) by the top and bottom of the box. The ends of the “whiskers” represent the farthest data point within a span that extends 1.5 times the interquartile range from the 75th and 25th percentiles. Data outside this span are graphed with asterisks Adapted from Petersen, J. E., Cornwell, J. C., and Kemp, W. M. 1999. (see “further readings”).

Figure 9: a) Available options for conserving characteristic length relationships as the size of a cylindrical mesocosm is increased. b) Relations between depth and radius for the cylindrical mesocosms in the ecological literature. Dots are physical dimension data from a comprehensive literature review of experiments conducted in mesocosms. c) Surface areas of the vertical walls versus volume. d) Surface area of bottom and top versus mesocosm volume. Dotted (green) lines represent scaling for constant depth and are placed at values corresponding with median depth. Dashed (red) lines that represent scaling for constant-radius are placed at median radius. The solid (blue) lines represent scaling for constant shape and are derived from linear regression of radius (r) versus depth (z), with statistics provided in panel b. A clear implicit biases is evident towards scaling for constant shape. Adapted from Petersen, J. E., Cornwell, J. C., and Kemp, W. M. 1999.

Figure 10: Experimental ecosystems are typically simplified relative to nature in terms of biodiversity and trophic (feeding) complexity. Inclusion of higher trophic levels (increased trophic depth) or more species diversity at each trophic level (increased trophic breadth) is not always feasible or desirable. Predators at high trophic levels are often large and may not exhibit normal behavior in small enclosures. Adapted from Petersen et al. 2007.

Figure 11: Relationships between the abundance of *Moerisia lyonsia* and *Acartia tonsa*, and the turbulent energy dissipation rate (ε) in the 3 mixing treatments. Turbulent energy dissipation is one of a number of important parameters that can be used to match conditions in nature and mesocosms. Data from Petersen, J. E., L. Sanford and W. M. Kemp. 1998. Coastal plankton responses to turbulent mixing in experimental ecosystems. Marine Ecology Progress Series 171: 23-41.

Figure 12: Typical water flow patterns generated in a mesocosm provided with a single rotating axial impeller. Adapted from Petersen et al. 2007.

Figure 13: Effects of water exchange rate and nutrient concentration of inflowing waters on gross primary productivity and zooplankton biomass in planktonic experimental ecosystems (left panels) and on competition between aquatic grasses and epiphytes growing on plant leaves (right panels). Values presented are experimental means ± SE. Adapted from Petersen et al. 2007.

Figure 14: Hypothetical responses of two distinct ecological properties to changes in the scales over which they are observed. Mesocosms 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. From 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, pp. 3-57, In: R. Gardner, W. M. Kemp, V. Kennedy and J. Petersen (eds.) Scaling relations in experimental ecology. Columbia Univ. Press, New York.

Figure 15: Variations in primary productivity and depth 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 for gross primary productivity (GPP per unit water volume) are mean values measured from changes in dissolved oxygen concentration. Data are from 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, and from 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, pp. 3-57, In: R. Gardner, W. M. Kemp, V. Kennedy and J. Petersen (eds.) Scaling relations in experimental ecology. Columbia Univ. Press, New York.

Figure 16: Variations in mean growth of bay anchovy, *Anchoa mitchelli*, with size (radius) of cylindrical mesocosms and with duration of experiment. In smaller containers and in longer experiments fish exhibit lower growth rate. Shaded area indicates the range of growth rates measured in natural coastal waters. Only in the larger containers and shorter experiments were bay anchovy growth rates comparable to those reported for the estuarine waters that serve as natural habitat for these fish. Adapted from Mowitt, W.P., E.D. Houde, D. Hinkle, A. Sanford. 2006. Growth of planktivorouos bay anchovy *Anchoa mitchelli*, top-down control, and scale-dependence in estuarine mesocosms. Marine Ecology Progress Series 308: 255-269.

Additional Resources

Further Reading:

Adey, W. H., and Loveland, K. (1991). *Dynamic aquaria: building living ecosystems*. San Diego: Academic Press.

Beyers, R. J., and Odum, H. T. (1993). *Ecological microcosms*. New York: Springer-Verlag.

Gardner, R. H., Kemp, W. M., Kennedy, V. S., and Petersen, J. E., (eds.) (2001). *Scaling relations in experimental ecology*. New York: Columbia University Press.

Giesy, J. P. J., (ed.) (1980). *Microcosms in ecological research*. Springfield, VA: National Technical Information Service.

Graney, R. L., Kennedy, J. H., and Rodgers Jr., J. H., (eds.) (1994). *Aquatic mesocosm studies in ecological risk assessment*. Boca Raton, FL: CRC Press, Inc.

Grice, G. D., and Reeve, M. R., (eds.) (1982). *Marine mesocosms: Biological and chemical research in experimental ecosystems*. New York: Springer-Verlag.

Kemp, W. M., Lewis, M. R., Cunningham, F. F., et al. (1980). Microcosms, macrophytes, and hierarchies: environmental research in the Chesapeake Bay. Pages 911-936 in Giesy, J. P.

(ed.), *Microcosms in ecological research*. Springfield, VA: National Technical Information Service.

Lalli, C. M., (ed.) (1990). *Enclosed experimental marine ecosystems: a review and recommendations*. New York: Springer-Verlag.

Odum, E. P. (1984). The mesocosm. *BioScience* 34:558-562.

Oviatt, C. (1994). Biological considerations in marine enclosure experiments: Challenges and revelations. *Oceanography* 7:45-51.

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

Petersen, J. E., and Hastings, A. (2001). Dimensional approaches to scaling experimental ecosystems: designing mousetraps to catch elephants. *American Naturalist* 157:324-333.

Petersen, J. E., Kemp, W. M., Bartleson, R., et al. (2003). Multiscale experiments in coastal ecology: Improving realism and advancing theory. *BioScience* 53:1181-1197.

Petersen, J. E., Kennedy, V. S., Dennison, W. C., and Kemp, W. M., (eds.) (2007). *Enclosed experimental ecosystems and scale: Tools for understanding and managing coastal ecosystems*. New York: Springer-Verlag.

Sanford, L. P. (1997). Turbulent mixing in experimental ecosystem studies. *Marine Ecology-Progress Series* 161:265-293.

See Also: 134, 290, 500, 616, 620, 741, 742.

Tables:

Table 1: Key variables to consider in the design of experimental ecosystemsa[a].

Variable	Design Decisions	Properties Affected
Size	Volume, depth, radius, surface area	Relative dominance of pelagic, benthic, and emergent producer communities, wall growth, temperature oscillations
Time	Duration, timing of perturbation, sampling frequency	Ecological dynamics and life cycle of organism included in experiment, ability to detect seasonal and long term effects, influence of experimental artifacts
Mixing	Vertical and horizontal mixing environment, mechanical mixing apparatus employed	Pelagic-benthic interactions, feeding rates and behaviour, access to nutrients, artifacts, and potential mortality associated with mechanical devices
Materials exchange	Frequency, magnitude, variability chemical composition, biological composition	Re-colonization rates, flushing of planktonic organisms, selection for particular organisms and communities
Light	Natural or artificial, intensity, spectral properties	Primary productivity, producer community composition, water temperature
Walls	Construction materials, whether to clean, cleaning frequency	Relative dominance of wall growth, light environment
Temperature	Whether to control, how to control	Rate of biogeochemical activity, selection for particular organisms
Ecological complexity	Species and functional group diversity, number of habitats and biogeochemical environments included	Primary productivity, trophic dynamics, biogeochemical pathways
Sediments	From nature or synthesized, intact or homogenized, particle size, organic matter content, organisms included	Pelagic-benthic interactions, vascular plant growth, primary productivity

[a]Adapted from Petersen et al. 2007 (see "further readings").

Table 2: Empirically determined effects of mixing on phytoplankton, zooplankton, and ecosystem processes.

Variable	Relationship
Phytoplankton	
Settling rate	[a](-)
Cell size	(+)
Cell abundance	(+) or (0)
Chlorophyll *a*	(+)
Cell growth	(+) or (-)
Diatom/flagellate	(+)
Species composition	(√)
Nutrient uptake	(+) or (-)

Timing of bloom	(√)
Microzooplankton (protozoa)	
Predation/grazing rate	(+) , (-) or (0)
Growth rate (numbers)	(+)
Cell size	(-)
Macrozooplankton (copepods)	
Abundance/biomass	(-) or (+)
Metabolic rate	(+)
Excretion rate	(+)
Predation/grazing rate	(+) or (-)
Growth rate	(+)
Development rate	(+)
Age structure	(√)
Sex ratio	(√)
Ecosystem	
Community productivity	(+), (-) or (0)
Ecosystem productivity	(+)
Ecosystem R	(+)
Nutrient dynamics	(√)

[a] (+) symbol indicates a positive relationship between the variable and turbulence, (-) indicates a negative relationship, (√) indicates the presence of a relationship, (0) indicates no relationship. Because mixing levels used in individual experiments included in this analysis ranged from no mixing to levels atypical of nature, this table can only be considered a rough summary of findings. Citations to studies in this analysis are included in Petersen, Sanford and Kemp, (1998) Coastal plankton responses to turbulent mixing in experimental ecosystems. Marine Ecology Progress Series. 171: p23-41

Figures:

Fig. 1

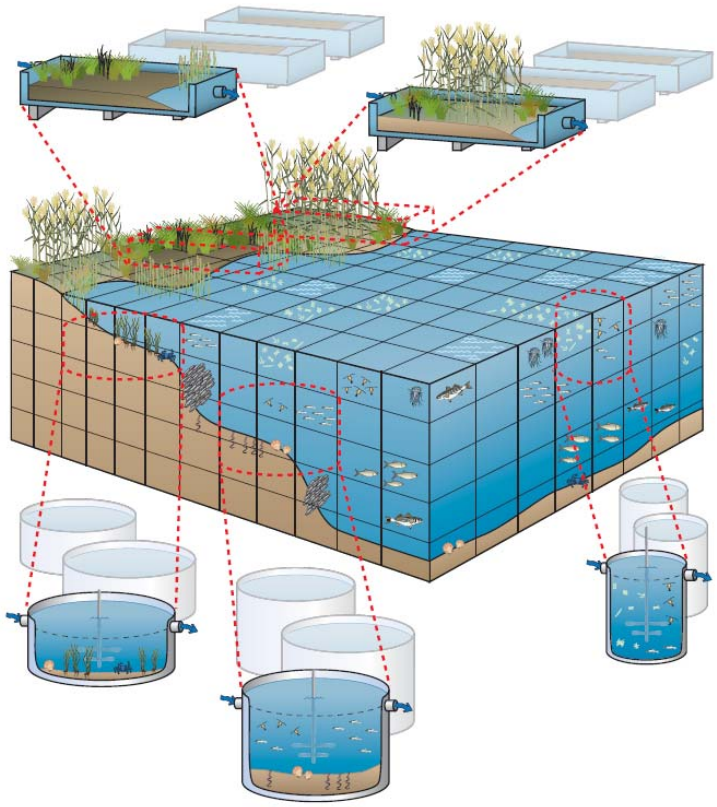


Fig. 2

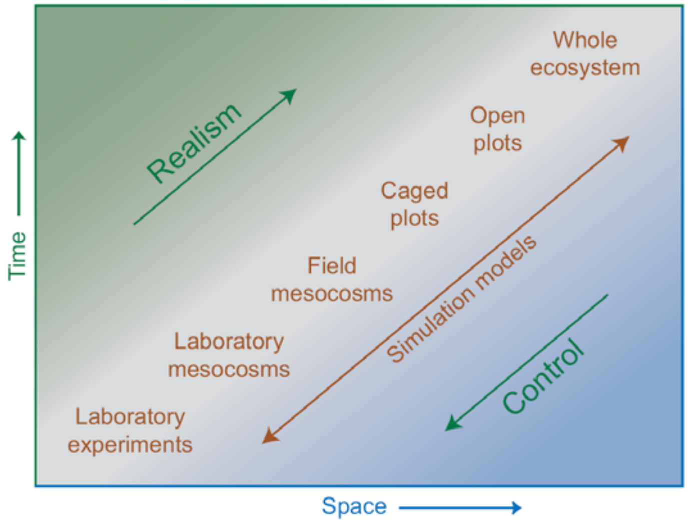


Fig. 3a

Fig. 3b

Fig. 3c

Fig. 3d

Fig. 4

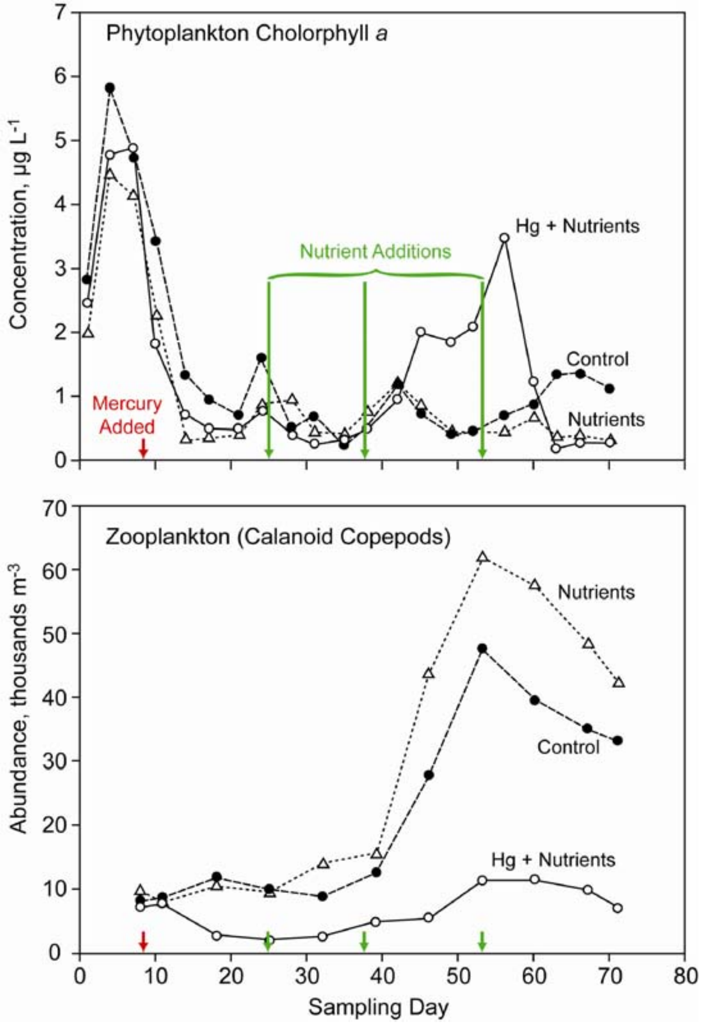

Phytoplankton Cholorphyll *a*
Concentration, µg L-1
7
6
5
4
3
2
1
0
Nutrient Additions
Hg + Nutrients
Control
Nutrients
Mercury Added
Zooplankton (Calanoid Copepods)
Abundance, thousands m-3
70
60
50
40
30
20
10
0
Nutrients
Control
Hg + Nutrients
0
10
20
30
40
50
60
70
80
Sampling Day

Fig. 5

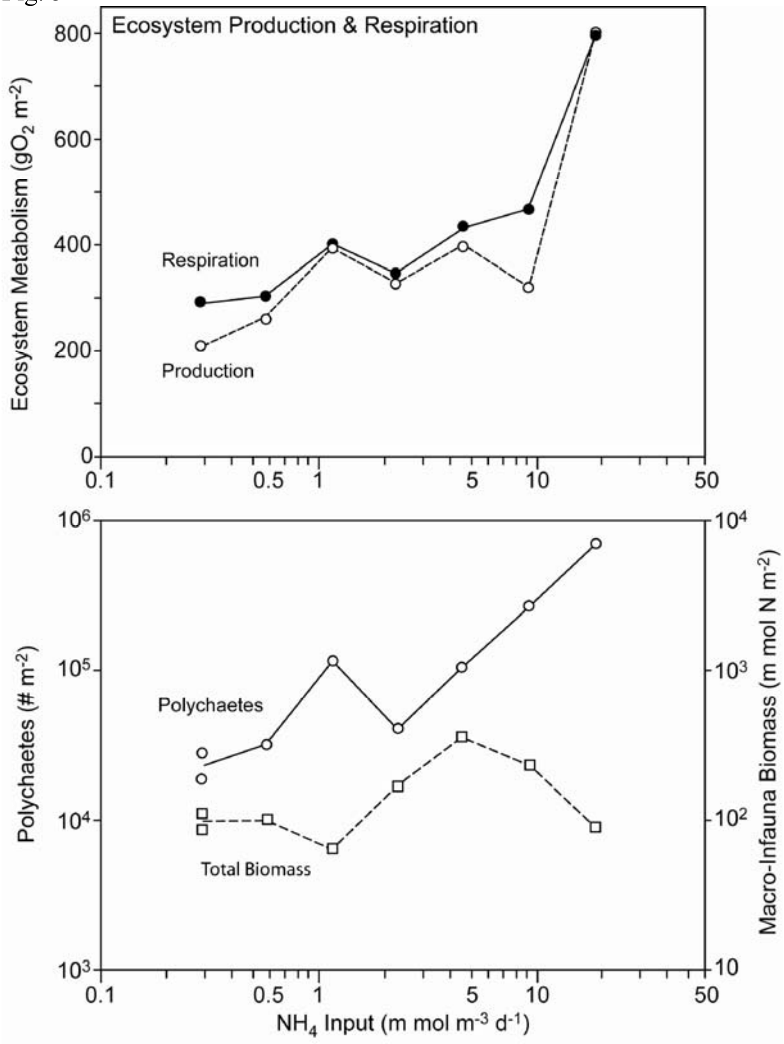

Ecosystem Production & Respiration
Ecosystem Metabolism (gO$_2$ m^{-2})
800
600
400
200
0
Respiration
Production
0.1
0.5
1
5
10
50
10^6
10^5
10^4
10^3
Polychaetes (# m^{-2})
Polychaetes
Total Biomass
10^4
10^3
10^2
10
Macro-Infauna Biomass (m mol N m^{-2})
NH$_4$ Input (m mol m^{-3} d^{-1})

Fig. 6a

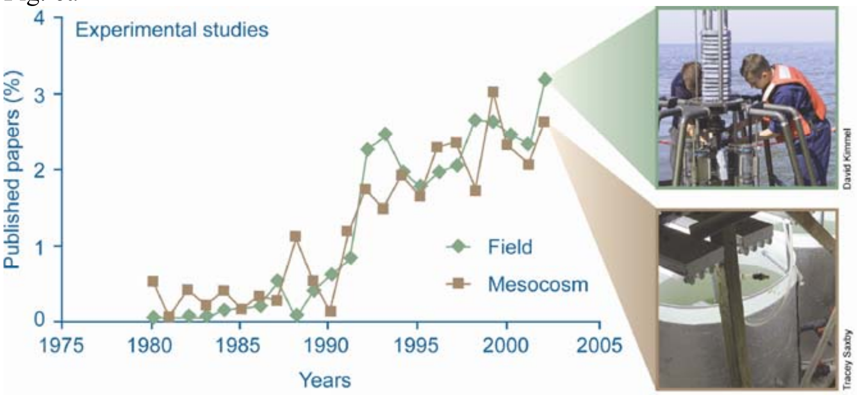


Fig. 6b

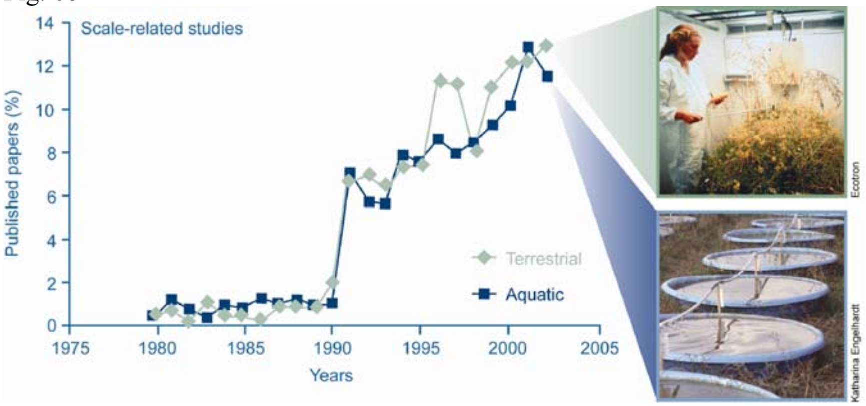


Fig. 7

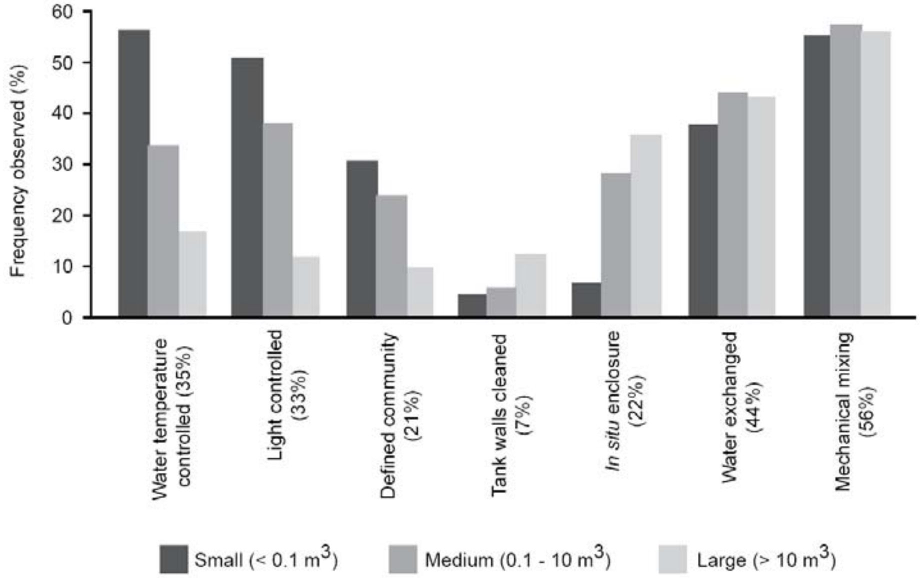


Fig. 8

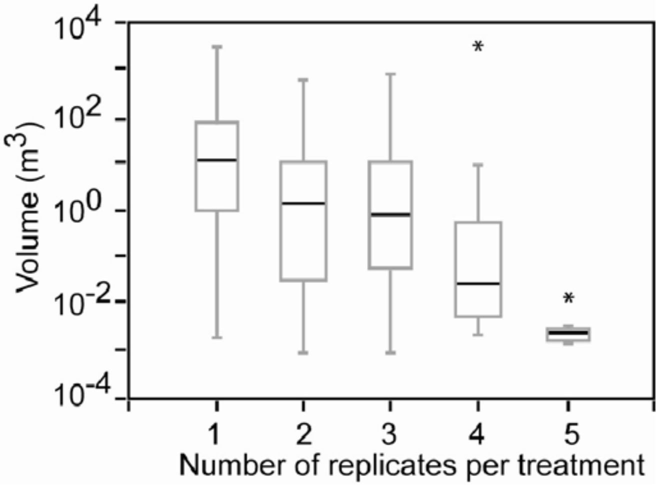

Volume (m³)
10⁴
10²
10⁰
10⁻²
10⁻⁴
*
*
1
2
3
4
5
Number of replicates per treatment

Fig. 9

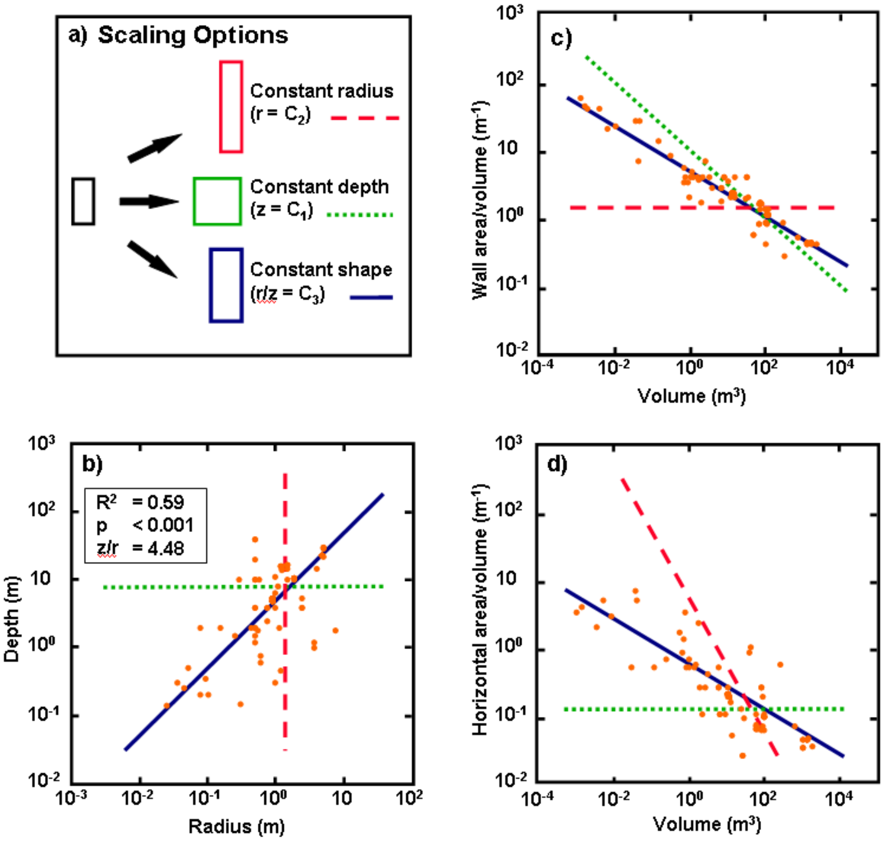

a) Scaling Options
Constant radius
(r = C₂)
Constant depth
(z = C₁)
Constant shape
(r/z = C₃)
c)
Wall area/volume (m⁻¹)
10³
10²
10
10⁰
10⁻¹
10⁻²
10⁻⁴
10⁻²
10⁰
10²
10⁴
Volume (m³)
b)
R² = 0.59
p < 0.001
z/r = 4.48
Depth (m)
10³
10²
10
10⁰
10⁻¹
10⁻²
10⁻³
10⁻²
10⁻¹
10⁰
10
10²
Radius (m)
d)
Horizontal area/volume (m⁻¹)
10³
10²
10
10⁰
10⁻¹
10⁻²
10⁻⁴
10⁻²
10⁰
10²
10⁴
Volume (m³)

Fig. 10

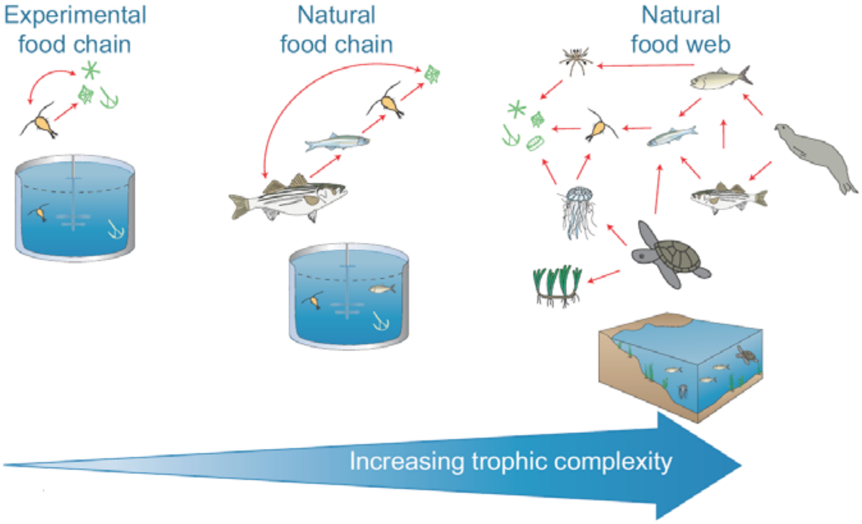


Fig. 11

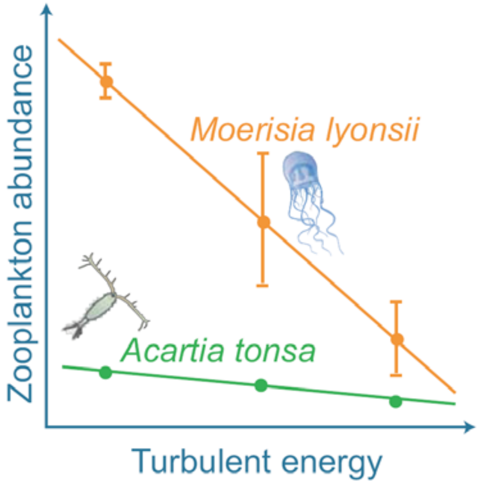


Fig. 12

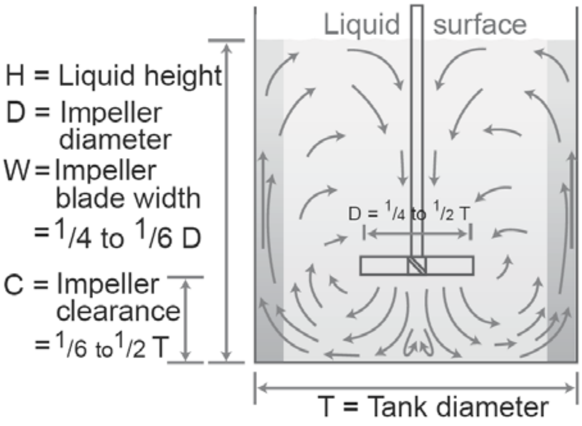


Fig. 13

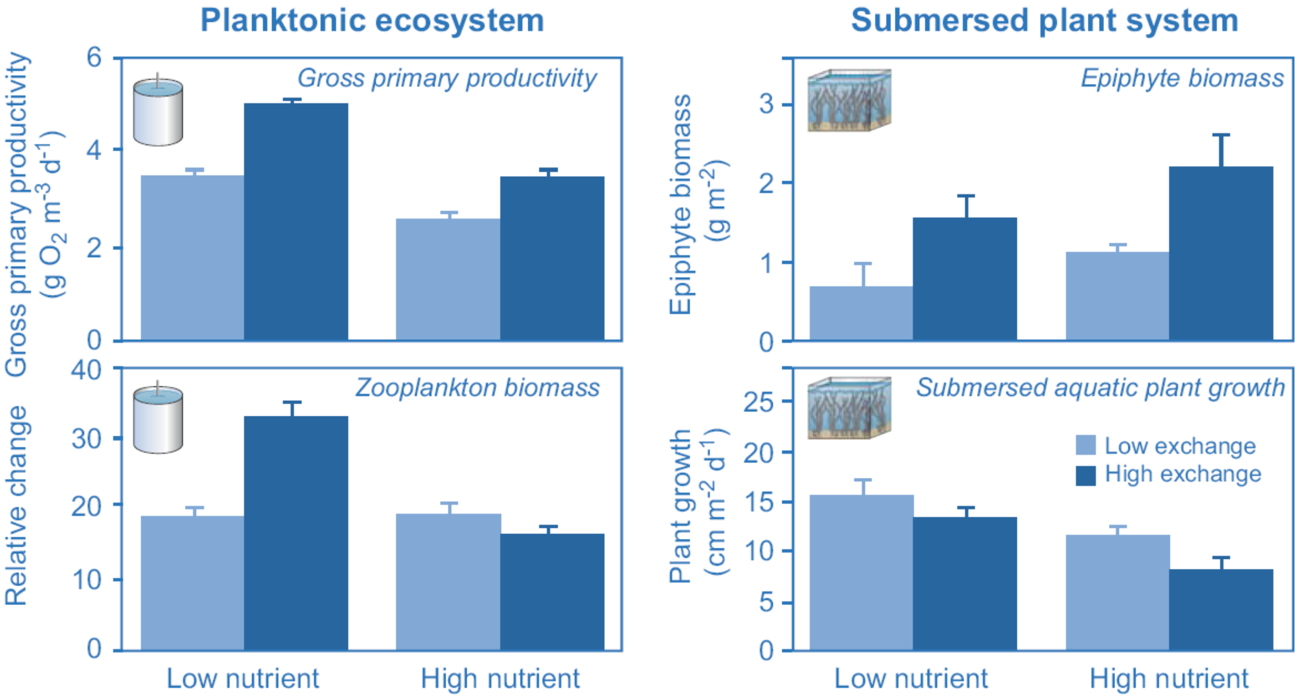
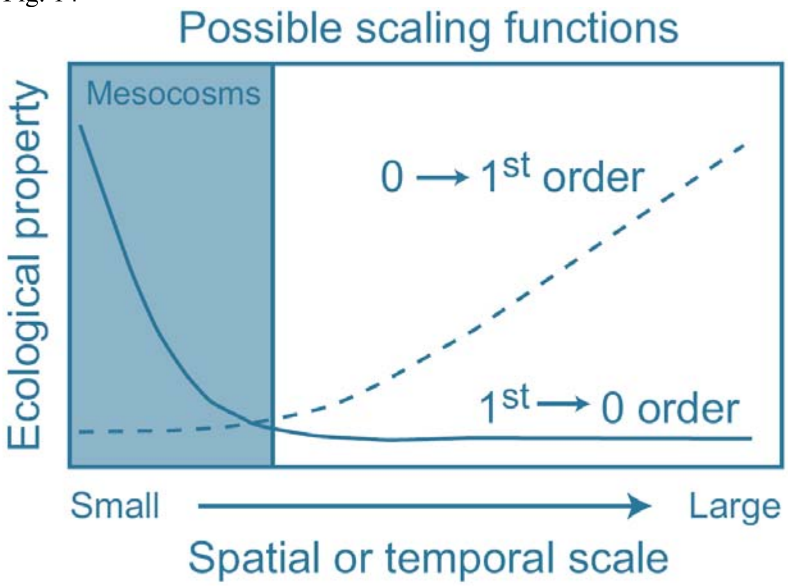


Fig. 14



615

Fig. 15

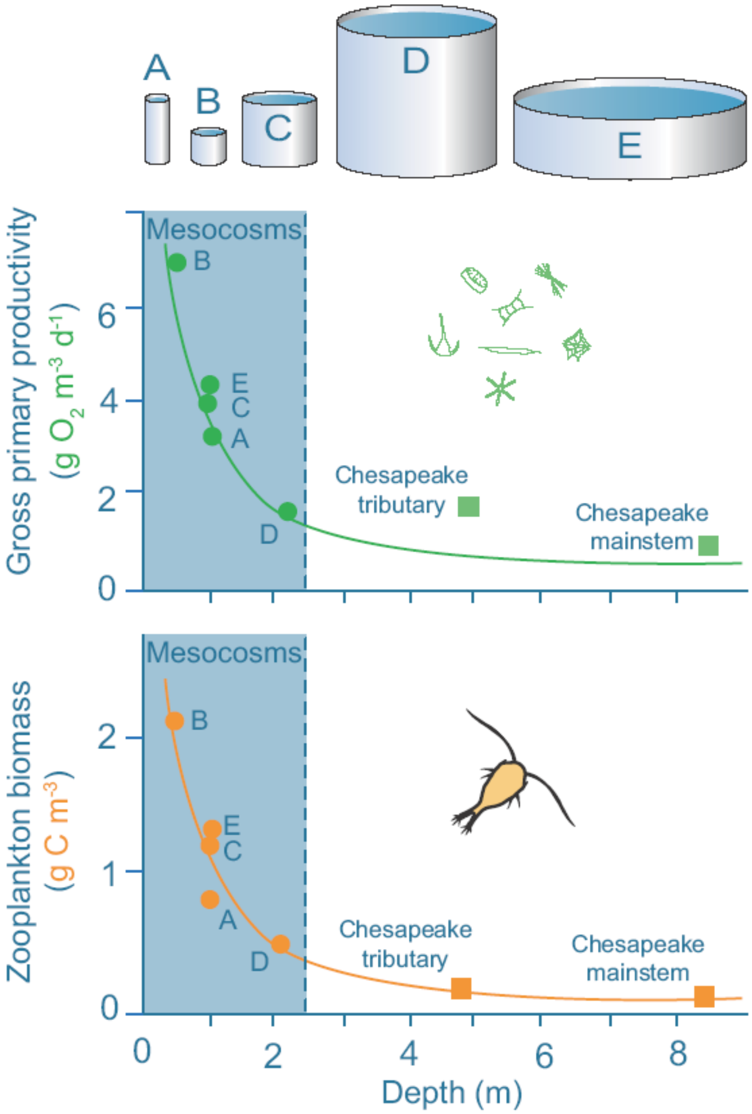
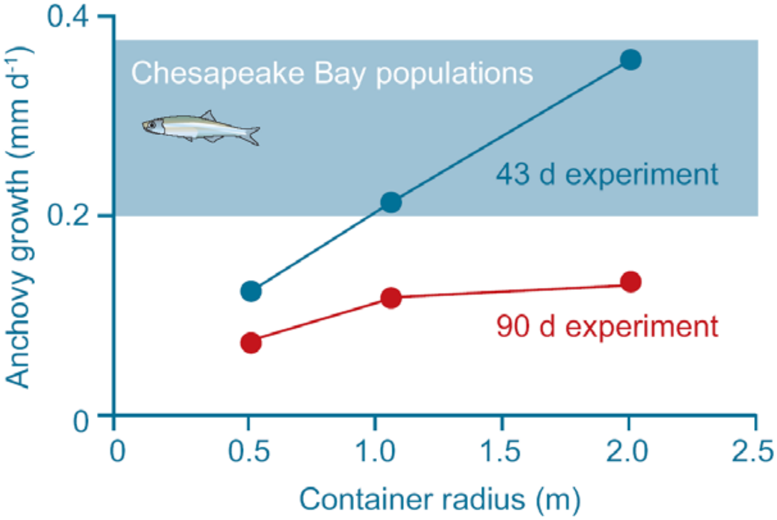

A
B
C
D
E
Mesocosms
Gross primary productivity
(g O_2 m^{-3} d^{-1})
0
2
4
6
B
E
C
A
D
Chesapeake tributary
Chesapeake mainstem
Mesocosms
Zooplankton biomass
(g C m^{-3})
0
1
2
B
E
C
A
D
Chesapeake tributary
Chesapeake mainstem
0
2
4
6
8
Depth (m)

Fig. 16


0.4
0.2
0
Anchovy growth (mm d^{-1})
Chesapeake Bay populations
43 d experiment
90 d experiment
0
0.5
1.0
1.5
2.0
2.5
Container radius (m)