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## Microcosmology: Introductory Comments

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This volume is a compilation of the research of numerous investigators who have used microcosms to address diverse theoretical and applied ecological questions. Before considering these studies, we believe that it is necessary to address some of the assumptions and questions that are the theoretical basis of microcosmology. Specifically, we hope to address the questions: What are the goals of microcosm research? How can the results of microcosm research be interpreted and applied to complex ecosystem-management questions? What is the meaning of variability in microcosm studies? How much and which components of this variability can be controlled? What are the consequences of restricting variability, scale, surface-to-volume ratios, and particular biotic or abiotic components?

The strategy of protecting target organisms or monitoring indicator species has been implemented because of the relative ease with which single species can be tested in the laboratory and single populations can be monitored in the environment. It is often not understood that management strategies implemented to protect "target species" (generally herbivores or carnivores, such as fish) are based on the assumptions that they are the most sensitive species and that protection of the target species somehow preserves enough of the other components of the community to maintain a viable environment for the target species (Cairns, Lanza, and Parker, 1972). Target organisms protected under these schemes are generally economically or aesthetically important species that may not exert much influence on ecosystem functioning as a whole. That is, they may play minor roles in processing nutrients or energy and have

mostly a "fine-tuning" effect on the structure and function of the entire system. Organisms of higher trophic levels may be involved in compensatory behavior or negative feedback loops and, thus, be inseparably linked to other components of their environment and be thought to be integrators of environmental perturbation. Effects seen at this level are filtered through so many interfaces and transfers, however, that the responses of target species to subtle environmental perturbations are often slow, resulting in a posteriori and often irreversible effects on the system before effects on target species are measurable.

Predictive toxicity testing has been based on acute single-species laboratory toxicity tests on target species. This type of toxicity evaluation or autecology is insensitive to important interactions or compensatory reactions and eliminates the important interactions between an organism and its environment, both abiotic and biotic. This type of testing also suffers from a lack of information on chronic effects and dose-response relationships. This is accentuated by the relatively long life spans of the larger organisms usually used as target species. Cairns, Lanza, and Parker (1972) stated that a complex community with many interlocking reciprocal cause-effect pathways cannot be preserved by protecting one of a few target species and that monitoring the effects of stressors should consider more important aspects of ecosystem structure and function. [We use the terms structure and function as defined by Odum (1962).] The concept of structure involves "(1) the composition of the biological community, including species, numbers, biomass, life history and distribution in space of populations; (2) the quantity and distribution of the abiotic (non-living) materials such as nutrients, water, etc.; (3) the range, or gradient, of conditions of existence such as temperature, light, etc." Ecosystem function involves "(1) the rate of biological energy flow through the ecosystem, that is, the rates of production and the rates of respiration of the populations and the community; (2) the rate of material or nutrient cycling, that is, the biogeochemical cycles; (3) biological or ecological regulation, including both regulation of organisms by environment (as, for example, in photoperiodism) and regulation of environment by organisms (as, for example, in nitrogen fixation by microorganisms)."

Our basic rationale for assessing environmental effects is the stability of the ecosystem and, thus, the magnitude of change that can be expected from a particular perturbation. Since stability is a function of the structure and kinetics of a system, the impacts of the planned action should be assessed for both structural and functional properties in the context of their coupling to other biotic and abiotic processes. Although ecosystem level properties may be slower to

respond than those of individuals or populations for the most critical biological function, the probability of choosing the most critical portion of the ecosystem to measure is low. Thus we suggest that the holistic approach of measuring ecosystem responses may be a more sensitive way of evaluating impacts than measuring a few parameters and hoping that the most critical have been chosen. Hurd et al. (1971) found that an old field plot in a late stage of succession with a rich assemblage did not buffer the effects on primary and secondary consumers of a perturbation to the base of the food web. This indicates that system-level parameters may indeed be sensitive indicators of environmental perturbations.

Most environmental assessments have been done at either the population or the community level, and detailed information on the structural and functional properties of ecosystems is seldom collected. We submit that ecosystems have emergent properties such that the whole system is greater than the sum of its parts. The many nonadditive interactions observed in ecological studies are evidence of this. Thus studies of ecosystem components, such as populations or individuals, will not adequately describe or allow assessment of the effects of perturbations on the entire system, or even individuals or populations. Individuals and populations in ecosystems do not exist in isolation from the surrounding biotic and abiotic components. They are intimately associated with them and actively exchange energy and materials with them. It is these exchanges that determine the fates of the individuals and populations. Any serious assessment of the impacts of a given pollutant or physical stressor on individuals and populations must consider these exchanges. Exchange processes or systems parameters, as well as traditional population parameters, can be studied for an indication of the more complex processes and effects of a stressor on biota and will give a more powerful extrapolation to the real world. We suggest that such ecosystem-level functions as total community metabolism, nutrient cycling, and energy flow be measured. Community function can be evaluated by measuring primary productivity, respiration, carbon export from the systems, decomposition rates, nutrient cycling, and rates of nitrification and denitrification.

Community composition and diversity of an aquatic community can be extremely sensitive biological indexes of environmental change. Even slight changes in environmental conditions, if persistent, can lead to changes in community structure and diversity (Gaufin, 1973). However, knowledge of the dynamics of specific populations may provide insight into specific stressor mechanisms that may not be apparent from changes in diversity. Community structure can be investigated by measuring numbers and densities of

taxa, community diversity, colonization rate, and standing crop biomass.

Because of the vast difference between simple laboratory tests and complex field situations, scientists have formed conceptual and operational bridges between the two systems. These include models of theoretical conceptualization of how complex systems operate, with computer science providing the bookkeeping capacity to describe these systems with complex linear and nonlinear functions. Not only a conceptual bridge but also an operational bridge has been necessary. Microcosms have been developed to fill this role. The study systems developed are diverse because of the questions addressed and the training of the scientists conducting them. All have one characteristic in common, however; i.e., they are all subsets or simplifications of the real world.

For the sake of argument, we have defined microcosms as artificially bounded subsets of naturally occurring environments which are replicable. Additional restrictions are that a microcosm cannot be a pure culture system and that it is generally required to have several trophic levels. In fact, we might say that, to qualify as a microcosm, an experimental unit should exhibit system-level properties. Various workers will take issue with every word of this definition, depending on the systems they study or the questions they ask. Modelers may view microcosms as the initial "biologicalification" of their hypotheses, which are described mathematically. Biologists view microcosms as orderly and logical simplifications of ecosystems which maintain the complexity not found in mathematical models.

Microcosms can be divided into two types—those which provide information on a single property, such as leaching, volatility, or damage to microorganisms, and those which seek evidence of interactions on such processes as bioaccumulation or structural or functional changes of communities. A soil column, such as that described by Bond, Lighthart, and Vulk (1979); the soil-plant system of Nash and Beall (1979); and the soil-microorganism segment used by Draggan (1976) are examples of the first type. The second is represented by the model ecosystem of Lichtenstein (this volume), the terrestrial microcosm system described by Gillett and Witt (this volume), and the aquatic channel microcosms at the Savannah River Ecology Laboratory (SREL) (Bowling et al., this volume). The essential difference between the two types is the number of trophic levels that researchers have attempted to model and include.

Microcosms can be structurally simple, e.g., flasks containing several microbial populations (Taub and Crow, this volume), or

completely colonized stream channels or ponds. Microcosms can be large or small, e.g., CEPEX type enclosures 30 m deep by 10 m wide or a soil column 2 cm in diameter and 10 cm long. Levels of control range from systems that are completely controlled, e.g., EPA-ECOS in Athens, Ga. (Sanders and Falco, 1973), to systems subject to stochastic environmental and natural colonization, e.g., the SREL channels.

An attractive attribute of microcosms is their replicability, which is amenable to statistical testing of the effects of manipulation. However, there are many variables that cannot be adequately controlled in microcosms to make them analogous to natural systems. These include such physical factors as light intensity and spectral quality; temperature regime, including stratification; turbulence and mixing; water-to-sediment-area ratios; primary-to-secondary-productivity ratios; and species controlling species pairings. The papers collected in this volume discuss many of the advantages and limitations of microcosms, consequences of their use, and restraints on the usefulness of the results of microcosm studies. Several of the papers discuss particular physical, chemical, or biotic parameters that the authors felt were very important in the particular use to which their microcosm was put and in their attempts to design in the required complexity.

Microcosms can be either synthetic or natural, i.e., a size and supporting structure defined and allowed to colonize naturally or component species added and allowed to equilibrate (Beyers, 1963). Only a few of the possible synthetic combinations are allowable, however. If the microcosm is completely defined, it is said to be "gnotobiotic" (Dougherty, 1959). This is not to say that specific components and colonization seeding cannot be done to facilitate rapid colonization. Microcosms can be constructed so that they are structural simplifications in a naturally occurring system (Wiegert, 1979). The system should be allowed to come to dynamic equilibrium since it is recognized that systems, especially young systems, undergo succession and cyclical changes.

In laboratory-scale microcosms, the dimensions of size, time, and mass of both biotic and abiotic components must, of necessity, be limited. Additionally, processes and environmental factors (e.g., light) may be somewhat modified, depending on the degree of complexity and control designed into the system. Laboratory-scale microcosms, of necessity, have boundaries; consequently, the "wall effects" become important. This limits interaction with the rest of the universe, including energy and matter flow, and probably constrains normal cycling as a consequence. Thus laboratory-scale

microcosms are metastable systems, which are often incapable of self-perpetuation.

Microcosms need not exactly mimic natural systems at all levels of organization but, for the study of general ecological principles or gross toxicological effects, can be thought of as analogous. Thus, although a dynamic equilibrium that is reproducible in space or time would be desirable, microcosms do not have to be at equilibrium. The results obtained will be greatly determined, however, by the season or point of succession at which trace contaminants are added or experiments are started. Although dynamic equilibrium is not required, microcosms must have had time to establish a number of functional groups that are interacting. The conditions of the system of a nonequilibrium microcosm can be defined as a trajectory path through an  $n$  space determined by the  $n$  structural and functional properties being considered. The impacts of various manipulations on microcosms can be evaluated by observing the effect on trajectories. These trajectories may or may not terminate in equilibrium system states. Because most aquatic or terrestrial systems display at least seasonal successional patterns, studies of nonequilibrium systems may be more useful than studies of equilibrium systems. A field situation may have several equilibriums, all of which are insensitive to perturbation, but the successional process that decides which equilibrium state is ultimately achieved may be greatly affected by perturbation.

One of the major reasons for using microcosms or simplification analogues of ecosystems is to reduce specific variance components and unexplained residual variability. Natural physical and biological assemblages are often variable and undergo seasonal succession. Thus gaining replicability in the behavior of microcosms in space and time results in decreased similarity to natural systems. The magnitude and timing of stochastic events and the within-component variability may be the most salient features in determining the observed structure and function of a community, and reducing this variability may result in artifacts in the microcosms. Population densities, as well as diversity of stream benthic organisms, are greatly controlled by colonization from upstream areas, caused by drift. Thus artificial bounding that restricts this type of variability will drastically influence the results and interpretations of a microcosm of this type. When it is suspected that these events are important in controlling the structure or regulating the function of an ecosystem, microcosms will have low predictability of the behavior of that system.

Besides catastrophic events, microcosms are affected by scaling parameters that may disturb community behavior. Most noticeable among these are ratios of sediment or soil surface to volume and

water surface area to volume in pelagic microcosms. In terrestrial microcosms these effects can be caused by unrealistic light, temperature, and air-circulation regimes. The study of systems including secondary producers becomes difficult because the volume of the microcosm required to support secondary producers would be very large and would negate the usefulness of the microcosm system. Lack of consumers or too large a consumer population density may give biased results (Harte et al., Bowling et al., Gillett and Witt, this volume).

An underlying assumption of all microcosm work is that the experimental system represents either a single function or a complex set of functions expressed by larger uncontrollable field situations regardless of simplifications. Thus all simplifications made must be evaluated to determine the validity of the results obtained.

The greatest value of microcosms is that they enable the study of functioning ecosystems with cybernetic or negative feedback loops in place. If the structure of the microcosm is too specific, however, generality is lost, and, if it is too general, predictability is lost. It is important that microcosms be functionally complete enough so that there is competitive pressure on all major functional groups. If this is not true, erroneous results can be obtained because of compensatory behavior of the various populations. One can state, for example, that the primary interest of an effects study is the periphyton community; however, any study of the effects of a stressor on this component must be conducted in the context of all of the controlling influences, e.g., macroinvertebrate consumers and microbial decomposers. Patrick (1949) found that some pollutional loading could reduce the numbers of "higher" organisms, such as fish, with a concomitant increase in the number of species and density of "lower" organisms. Thus, if one monitors the responses of the lower trophic level, one will make an inaccurate interpretation of ecosystem health. Oftentimes, it will be necessary to impose an artificial cropping on herbivores that are not preyed upon or on predator populations that are not under selective tension. Thus, if the microcosm is to be used in an effects study, the higher trophic levels should be present because of the controlling influence they have on lower trophic levels (see Bowling et al., this volume).

Microcosms are amenable to hierarchical studies because their scale can be readily varied. Processing rates of one component may limit the microcosm carrying capacity of other components, however. One example of this is the large primary and secondary production required to support tertiary consumers, such as fish. Supporting a single fish (e.g., a mosquitofish) at a normal growth rate in a pelagic-type microcosm requires a microcosm of at least  $10^4$

liters (Harte et al., this volume). Gillett and Witt (this volume) reported similar problems with herbivores in terrestrial microcosms. Sufficient size and complexity of microcosms depend on the question to be answered or the hypothesis to be tested. For this reason, creating a generalized microcosm of known complexity is impossible. Two approaches could be taken: (1) A site-specific microcosm could be used to assess localized effects on a very specific area, or (2) a more generalized system with a number of components and pathways general to all ecosystems could be used. Because of the complex interactions in ecosystems, a holistic approach has been advocated with the measurement of integrative system-level parameters. In the second approach, two levels of complexity can be designed. In one system all interactions are well defined; this will be the simpler system where results can be integrated as to mechanisms. A more complex system can be used in an integrative mode where mechanisms are poorly defined but overall community effects are measured. Although the second method allows important interactions to occur, it does not allow description of what may be thought of as independent processes. In many real situations, as the complexity of the system increases, the consequences of effects on one parameter become more ambiguous. It is important that well-designed experiments be conducted to ascertain the degree of sensitivity obtained by this method and to compare it to that required by the question and by community parameters.

Biotic complexity can be restricted by limiting the abiotic structure richness of microcosms. That is to say, a synthetic microcosm constructed with a sand substrate will be structurally and functionally simpler than a microcosm constructed with an organic soil medium or leaf litter, and this will, in turn, be simpler than a microcosm constructed with an intact sediment or soil. The low physical structure richness of the SREL channel microcosms (Bowling et al., this volume) may have been responsible for the relatively low species diversity and few total numbers of invertebrate taxa.

Large-scale microcosms, which allow many interactions, are expensive and time consuming to construct and are not appropriate for use in screening trace contaminants for toxicity and environmental cycling and fates because these tests require that many compounds be examined rapidly and inexpensively (Bowling et al., this volume). Large-scale systems can be used to examine the effects of characteristic trace contaminants, to test hypotheses, and to verify predictive models. It is also suggested that these tests be done critically on elements or compounds for which much is known about chemical and physical behavior in the environment. Toxicity and bioaccumulation and biomagnification information should also be



available. In this way, the effects of interactions that are excluded from single-species toxicity and accumulation studies can be assessed.

Microcosms are probably not appropriate for routine screening of hazardous materials that could potentially be released to the environment. Microcosms have their greatest utility for assessing human health and environmental effects when used in a hierarchical program of investigation (Fig. 1).

Because the effects of a large number of potentially toxic elements and compounds must be tested, the screening tests must be rapid and inexpensive. We feel that microcosms should not be used in routine screening tests but should be used in certain cases where detailed information about an element, a compound, or a class of elements or compounds is necessary. We suggest that the hierarchical design presented in Fig. 1 be followed.

Initially potential human health and environmental effects should be assessed by determining the relative ability of potential environmental contaminants to cause an undesirable effect, as well as the amount of contaminant to be released and the sensitivity of the environment into which it could be potentially released. If the contaminant or its possible transformation products are not toxic, inhibitory, mutagenic, teratogenic, or carcinogenic, or if extremely small quantities relative to their effective concentrations are projected for release, more study is not needed. If a contaminant will be released in high concentrations or is persistent and potentially toxic, however, further study may be indicated. We suggest that simulation models and microcosms can be useful in this process. The best use of microcosms in this scheme would be to examine interactions to evaluate simulation models and simpler tests of toxicity and bioaccumulation.

Some interactions can subsequently be studied by more simply designed factorial or crossed experiments when it is deemed necessary to determine mechanisms. Some ecosystem functions will be so complex that they will be used as integrators of ecosystem function. We envision simple microcosms of reduced complexity containing the essential functional components of natural ecosystems to be adequate for measuring a defined number of rate processes over short periods of time. Complex microcosms, which contain all the major functional groups of natural ecosystems can be useful in identifying chemical accumulation but are insensitive for measuring rates of synergistic and/or competitive transport processes. Synthetic microcosms do not provide estimates of rate constants for identifiable transport processes in specific environments. Thus it must be decided a priori whether studies to be conducted in microcosms are to be fates or effects studies.

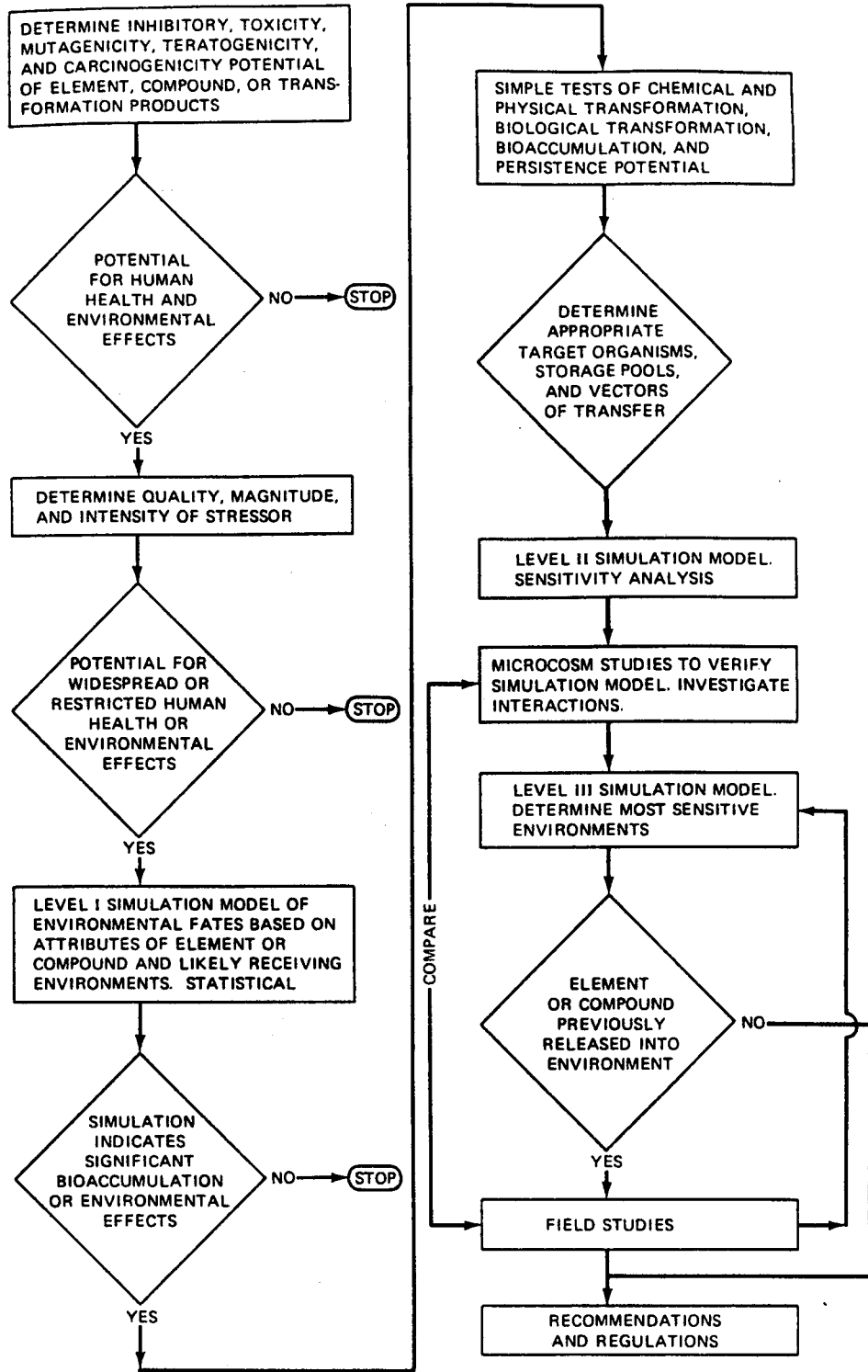


Fig. 1 Flow diagram of a proposed use of microcosms in assessing potential human health and ecological effects.

As a first approximation, it is probably realistic to assume that, in the field, the presence of organisms of one species does not materially affect the average exposure of organisms of a different species. That is, it is unlikely that one species population will alter the behavior of another in a way that causes the latter to be exposed to different levels of chemicals. This is especially true of compounds that are not very toxic but are of interest because they are carcinogenic, mutagenic, or teratogenic. There are exceptions, but these are predominantly cases of competitive displacement (e.g., Connell, 1961) and are likely to be rare for populations (Connell, 1975). Consequently, exposure microcosms need be only complex enough to study the exposure of organisms in single-species tests or in the presence of appropriate food organisms. In fact, the more complex the microcosm, the more difficult it is to determine actual vectors of uptake. Thus it is important to specify vector of assimilation and form of the trace contaminant, which can both be moderated by environmental factors and other organisms. Separability of biotic components generally applies to secondary producers and consumers but often not to populations of microorganisms.

There are environmental processes for which microcosm technology is not appropriate, e.g., predicting and verifying worldwide transport models and determining effects on large ecosystem components, such as forests, including mature trees, and the large vertebrate components of ecosystems, especially ecosystems or systems with very special requirements (e.g., arctic or tropical areas). It can be seen that a small replica of any given real-world situation cannot be achieved. Among the several reasons for this are: (1) scale differences, (2) complexity differences, (3) effect of enclosure, (4) edge effects, (5) source-term effect, and (6) equilibrium considerations.

To date, microcosms have not provided meaningful data on photolytic and chemical transformations of trace contaminants. Present systems cannot adequately deal with photochemical degradation, chemical reactions with other pollutants in the air, wall effects (condensation, adsorption), variable exposure times, and sequential sampling to develop the necessary kinetics for modeling. A number of field conditions that may affect a microcosm's validity to measure rates of decomposition cannot be reproduced. This does not mean, however, that microcosms cannot serve as analogies to some systems.

To be useful research tools, microcosms must minimize unexplained variability without diminishing realism. We realize that complete realism with reduced variability is impossible, and the crux of microcosm research is to simplify and control ecosystem structure and function in such a way as to facilitate the study of structural and

functional components with minimum destruction and loss of important interactions. We submit that microcosms should not be structured to try to mimic natural ecosystems precisely. Expansion to the point that these considerations of scale and edge are not problematical would negate the advantage of the reduced scale of microcosms. The validity of microcosms as simplifications for studying the fates of trace contaminants and effects of perturbations needs to be assessed. We suggest this be done by extensive field-microcosm and microcosm-microcosm comparisons. In conclusion, we reiterate that results of studies conducted in microcosms must be tempered with an understanding of the assumptions made when they are used and that useful information can be gained from the use of microcosms, especially when they are coupled to mathematical models and simpler laboratory studies of mechanisms and rates.

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