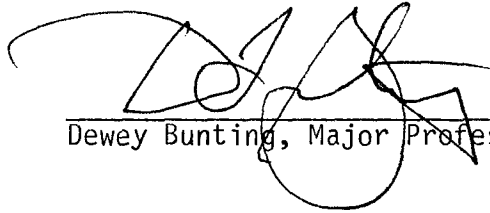


To the Graduate Council:

I am submitting herewith a dissertation written by Joyce Waterhouse entitled "Hierarchical Approaches to the Study of Ecological Process and Pattern." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology.



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Vice Provost
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HIERARCHICAL APPROACHES TO THE STUDY OF ECOLOGICAL
PROCESS AND PATTERN

A Dissertation

Presented for the

Doctor of Philosophy

Degree

The University of Tennessee, Knoxville

Joyce Waterhouse

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ABSTRACT

An approach based on hierarchy theory is applied to three specific problems involving the relationships between levels of analysis in ecology.

The first problem involves "emergence"--the inability to predict the behavior of the whole from its parts. "Relative" emergence is defined to arise from a lack of sufficient information, as opposed to "absolute" emergence, which refers to inherent unpredictability. The observation of relative emergence is nontrivial because it indicates a deficiency of lower level (or reductionist) analyses in certain situations and thus the appropriateness of higher level analyses designed to overcome these deficiencies. To analyze relative emergence, a hierarchical conceptual model is developed, which is then used to clarify several controversies involving emergence and to help assess the benefits and pitfalls of higher level analyses.

If a taxonomic hierarchy can be assumed to reflect a hierarchy of ecological similarity of species, then higher taxonomic levels may be useful in detecting larger scale ecological patterns. Patterns shown by specific and generic level binary similarity coefficients are compared for chironomid species data from a polluted Ohio stream. The ecological similarity of congenics is assessed using the trend in the species:genus ratio along the pollution gradient. No trend toward ecological similarity was found

and it appears that the generic level may best be viewed as resulting in a random loss of species information.

A hierarchical approach assumes that a hierarchy of pattern reflects a hierarchy of process. This means that small-scale "stochastic" factors, such as small differences in larval recruitment, should be manifested as small-scale "noise" added on to the dynamics, while large-scale phenomena, such as large changes in the average predation rate, should affect the pattern on a large scale. This chapter uses simulation models of New England and Australian rocky intertidal communities to show how this assumption may be violated. The model results indicate that three characteristics of the Australian rocky intertidal community may allow small-scale "stochastic" processes to have larger scale effects than in the New England community.

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CHAPTER I

GENERAL INTRODUCTION AND OVERVIEW

The difficulty of simplification of complex phenomena into a form that can be usefully analyzed is a major impediment for advance in most fields of research. A hierarchical approach to systems has become increasingly emphasized in the last 25 years as a means of achieving this simplification (Whyte et al. 1969; Allen and Starr 1982; O'Neill et al., in press). The concept of "scale" refers to the continuous version of a hierarchy and thus differences in scales and differences in hierarchical level will be considered to be analogous concepts.

In general terms, a hierarchy is defined as a partial ordering of a set of elements (Simon 1973), in which there is an asymmetry in the relationship between elements. Several criteria that may be useful in defining this asymmetry include defining higher levels as 1. containing, 2. constraining, 3. providing the context of, 4. behaving at a lower frequency than, and 5. exhibiting less inter-element bond strength (i.e., interaction or connection strength) than, lower levels (Webster 1979).

Since there are a variety of criteria that may be used as a basis for a hierarchy, there are also many different meanings for what constitutes a higher or lower level. Traditionally, a hierarchical view of ecological systems recognizes organisms, populations and communities as successive levels of organization. O'Neill et al. (in press) stress the importance of hierarchies based

on spatio-temporal scales of biogeochemical processes in an ecosystem hierarchy. Organisms can be grouped into taxonomic hierarchies, or classifications based on trophic status (Odum 1971) or functional role (e.g., Cummins 1974; Kaesler et al. 1978). Allen and Starr (1982) discuss approaches that use different data transformations as well as some that vary the scope and resolution of data to identify patterns at different scales (Allen et al. 1977; Kimmerer 1978). For extensive reviews of the variety of concepts and applications see Allen and Starr (1982), O'Neill et al. (in press) and Allen et al. (1984). Different criteria are used for various purposes in this dissertation and will be clarified as they are encountered.

What is needed most from hierarchy "theory" at present is demonstration of its ability to aid in the solution of specific problems of interest in ecology. Therefore each chapter emphasizes the analysis of a specific issue, with a hierarchical approach considered as a tool for analysis, or as a different perspective that may provide insight into the problem. Thus the hierarchical perspective, which is the common thread throughout, may seem subordinate at times to the specific problems being analyzed. This results in a set of studies that may seem somewhat disparate but are unified by their attempts to apply and evaluate a hierarchical perspective. It also results in a situation in which the contribution of each study is not limited to its relevance to a hierarchical perspective and may be of interest entirely in terms of its relation to the specific problem it addresses.

Below are overviews of the relation of each of the chapters to a hierarchical perspective.

A. CHAPTER II

This chapter provides additional introduction and background to hierarchies by taking a theoretical and philosophical approach to their use. This is seen as important because of some major practical impediments to conceptual development arising from misunderstandings at this basic level.

The ability to study or analyze the same phenomena at different hierarchical levels leads to the question of the relation of one level to another. Many people ignore this problem and work in their own fields without concern for how it relates to other fields of research operating at different levels. For instance, research in population genetics can usually proceed without being concerned about the study of mutations on a molecular level. However, some claim that higher level phenomena are reducible to lower level mechanisms and therefore studies of phenomena on lower levels are more valid. The converse of this is the claim that higher level analyses reveal "emergent" behavior--which is defined as unpredictable based on lower level information.

This chapter first explains and develops further the concepts involved in a hierarchical perspective. To achieve this purpose, a hierarchical conceptual model is developed that delineates two hierarchical dimensions simultaneously: temporal and organismal. A discussion of several controversies in ecology and evolution show

how misunderstandings about the relation between hierarchical levels have been pervasive in ecology and have surfaced in the form of controversy over the concept of emergence. The section on benefits and disadvantages of higher level analyses attempts to clarify the implications of a hierarchical approach in more specific problem-oriented contexts.

B. CHAPTER III

An important part of hierarchy theory is the assumption that different types of analyses can detect patterns on different levels or scales (e.g., see Allen and Starr 1982; Maurer 1985). The comparison of analyses of a chironomid community in this chapter involves two types of analysis methods that may allow the detection of higher level patterns. (Portions of this chapter appear in Waterhouse and Farrell 1985.)

1. Aggregate Variables

The grouping of organisms into trophic levels, guilds and functional groups has traditionally been a means to simplify community analysis (e.g., Odum 1971; Cummins 1974). It also allows one to concentrate on some pattern of interest without being concerned with the individual species differences that may be considered to be small-scale details, unimportant to the larger scale pattern. In these cases, the organismal aggregates are derived for the specific purpose of reflecting the large-scale

pattern. Thus the organisms are classified into groups according to criteria that are relevant to the analysis.

Some have suggested that the taxonomic hierarchy may be used to reflect an ecological hierarchy (Green 1979; Vascotto 1976).

According to this proposition, one might expect large-scale ecological differences, such as major habitat boundaries, to be reflected by analyses at higher taxonomic levels, while minor habitat differences would require analysis with more detailed taxonomic resolution. The use of a taxonomic hierarchy of analysis to reflect an ecological hierarchy differs from the examples of guilds and functional groups in that the classification of organisms used in the analyses is based on a criteria (taxonomic similarity) that differs from the ecological criteria corresponding to the pattern of interest. Although ecological similarity is to some extent related to taxonomic similarity, it is certainly not a simple or clear relationship. This chapter approaches this problem by developing a framework for assessing the ecological relevance of generic groupings of aquatic insects of the Chironomidae.

2. Data Transformation

It has also been suggested (Allen and Starr 1982) that the form of data transformation may change the grain of the pattern revealed and thus the hierarchical level observed. For instance, presence/absence data is thought to reflect a coarser pattern than species abundance data (Denslow, unpublished data discussed in Allen

and Starr 1982; Kimmerer 1978). The analyses in Chapter II bring up two points that are relevant to this suggestion.

The first point is that abundance data is not only finer in resolution, but also differs from presence/absence data in that it tends to emphasize only a few dominant species. This may have effects on the analysis that are unrelated to the degree of resolution of the pattern, thus complicating the use of data transformation to identify hierarchical levels.

The second point is that analyses based on presence/absence data need to be further differentiated into those that utilize information on species identity (e.g., similarity coefficients) and those that do not (e.g., species richness indices). Those that do not use species identity may be seen as integrating this more detailed information concerning which species are in which samples. Thus analyses which do not use species identity may allow larger scale patterns in the data to become more apparent, than those which do use information on species identity.

C. CHAPTER IV

This chapter develops simulation models of Australian and New England marine rocky intertidal communities to allow comparison of community structuring mechanisms. Hierarchy and scale are primarily involved in the two ways discussed below.

1. Formulation of the Model

The rocky intertidal system being modeled involves processes occurring on scales ranging from the organismal effects occurring on a local scale of days and centimeters, to oceanographic and climatic factors occurring on scales of weeks and miles. The model therefore must incorporate factors on various scales into its processes and parameters. Model-produced patterns are examined on scales ranging from individual spatial cells, to aggregates of spatial cells to differences between aggregates of spatial cells.

The model was also constructed so that the processes were modeled on a scale appropriate for investigating the patterns of interest. Thus, for instance, individual barnacle growth and thinning was integrated into a term for barnacle cover increase, which was considered adequate for the scales of months and meters being examined.

2. Analysis of the Relation Between Scale of Process and Pattern

The analysis of pattern on a particular scale to detect processes on that scale assumes that small-scale processes have small-scale effects, and large-scale processes have large-scale effects. Whether or not this is true, however, depends on the dynamics involved. In the rocky intertidal zone, the situation may arise in which small-scale differences, such as the exact timing of events, or small differences in abundance, may determine larger scale results, like the dominating organism. At the other extreme,

very large-scale phenomena such as widespread heavy predation may homogenize an area and wipe out any small-scale differences by removing all prey. Thus processes may often have effects on quite different scales than those they originate on. These different types of dynamics are presented in Chapter IV in relation to the degree of stochasticity perceived in different rocky intertidal communities. However, as indicated here, they are also important for assessing the use of a hierarchical approach to community analysis. The ability of the system dynamics to alter the relationship between the scale of process and pattern must be taken into account when using a hierarchical approach to pattern analysis.

CHAPTER II

EMERGENCE AND HIERARCHY

A. INTRODUCTION

A common hierarchical view of ecological systems recognizes different levels of entities (e.g., organisms, populations, communities, ecosystems) and of analyses (e.g., behavior, population dynamics, inter-community comparisons, ecosystem analysis). Disagreement as to the relationship between different levels of entities and analyses has occurred since the early days of ecology when the debate between those favoring holistic, organismal approaches to succession and those favoring reductionistic, individualistic approaches began (see McIntosh 1981). The arguments have often taken the form of the question of emergence; specifically, is the whole more than a mere summation of its parts (Harper 1977; Webster 1979; Innis 1976; Odum 1977; as cited in McIntosh 1981)? And if so, does this mean that the conventional reductionist approach that has been so successful in physics and chemistry in the past, is inadequate in biology? These questions have been discussed by philosophers for over a century in the organicist-reductionist debate (see Hull 1974) without a satisfactory resolution.

As McIntosh (1981) observed, "What is notably lacking in this extended discourse are clear stipulations of what is involved in sum versus whole and reduction or emergence as applied to ecology

(Nagel 1952)." Some recent discussions (Edson et al. 1981; Wimsatt 1980) take the view that ecologists should be content to carry out their research at different hierarchical levels and not be concerned about whether higher level phenomena are "emergent" relative to lower level explanations. However, the continued discussion and controversy over holistic approaches, which stress higher level emergent phenomena, versus individualistic approaches, which stress reductionism, indicates that this tolerance has not been achieved and thus "clearer exposition of hierarchical level, reduction and emergence is required" (McIntosh 1981).

This chapter analyzes the concept of emergence from the standpoint of its use in the ecological literature. Its relation to detailed discussions in the philosophy of science is not examined and no claim is made that this discussion will resolve the issue for philosophers. However, it may be that an examination of the issue in terms of its application to the field of ecology may contribute to its philosophical clarification as well.

Two different concepts of emergence must be distinguished. "Absolute emergence" refers to the unpredictability of higher level phenomena based on unlimited lower level information. This involves inherent unpredictability and therefore is not considered useful or relevant to ecological research (Edson et al. 1981). The term "relative emergence" will be used to refer to the unpredictability of higher level phenomena based on a lower level predictive model that is incomplete due to the failure to include some information needed for prediction. It is this "relative emergence", which is

both observer-dependent and relative to one's model, that will be discussed here.

This relativity of emergence to what is known or included in one's model has led Edson et al. (1981) to conclude that the issue of emergence is irrelevant to the study of ecological phenomena. However this view ignores the methodological, theoretical and philosophical significance of what is included in the lower level model. By claiming emergence, defenders of higher level "holistic" approaches are actually claiming that lower level models arising from reductionist approaches are typically lacking in certain areas and thus are often inadequate for predicting higher level phenomena.

Three types of deficiencies in information that may lead to relative emergence may be identified:

1. failure to include interactions among components;
2. failure to include appropriate constraints;
3. inability to gain sufficient lower level knowledge due to methodological limitations.

This chapter will discuss the three types of deficiencies that lead to relative emergence using a hierarchical conceptual model of a more detailed nature than the simplistic intuitive model that has usually been the basis of the definition (i.e., "summation of parts" and properties of "wholes"). Then the description of these three types of emergence will be applied to several controversies involving the relationship between levels of analysis. The paper will conclude with a discussion of the costs and benefits of the higher level analyses that the presence of emergent properties is

meant to justify. It is hoped this will elucidate the characteristics generating the holist's defense of higher level analyses and the reductionist's mistrust of such analyses.

B. A HIERARCHICAL MODEL OF RESTRAINTS AND DYNAMICS

1. General Approach

In a hierarchical view an entity of a system is seen as both a part of a higher level entity and a whole that can be decomposed into parts itself (e.g., see Simon 1962; Whyte 1969; Allen and Starr 1982; O'Neill et al., in press). In its role as a part, it is affected by its interaction with other parts and by the functioning of the whole. In its role as a whole, it might be viewed as having its own dynamics due to its functioning on a larger scale.

Hierarchical arrangements can be used to organize many types of phenomena or entities into conceptually useful forms. In dynamic systems, the time scale of behavior is often linked to a particular entity as the bases of a dual time scale-entity hierarchy. Possible levels include enzymes with dynamics on scales of fractions of microseconds, to animal behavior on scales of minutes to days, to species evolution occurring on a geologic time scale. A hierarchy of theories, associated with different disciplines (e.g., behavioral ecology, community ecology and paleobiology) also corresponds to this system hierarchy. Other hierarchies can be developed based on other organizational criteria (e.g., spatial relationships, temporal dynamics of nutrient cycling) and may recognize other types of entities (e.g., spatial units, functional groups).

The general hierarchical scheme presented here combines organismal and environmental hierarchies based on their scales of temporal dynamics (Fig. II-1). The result is a pattern of interlocking restraints, influencing and limiting the behavior of ecological units observed on different time scales. Although higher level dynamics are often affected by lower level processes, this scheme emphasizes the higher level restraints to aid in the evaluation of the various interpretations of emergence in ecology. The model is necessarily oversimplified for the purposes of conceptualization and generalization.

2. Detailed Description of Conceptual Model

a. Genetic constraints and organismal dynamics. Throughout Fig. II-1 are placed boxes enclosed by solid lines that signify genetic constraints on organism dynamics. These genetic constraints have been decomposed according to their time scale of effect on the organism, however in reality they are part of an integrated genome. These constraints are effectively static with respect to the organism dynamics (dashed line-enclosed boxes) that they partially determine. On longer time scales, aspects of the genetic system may change, but there are other higher level genetic characteristics that change more slowly and thus constrain them (boxes 3r--i.e., all constraints in row 3, Fig. II-1).

b. Organismal and environmental scales. The horizontal dimension of Fig. II-1 contains a progression of organismal levels

Figure II-1. A hierarchically-based representation of ecological and evolutionary processes. Boxes enclosed by solid lines signify structural constraints while those enclosed by dotted lines refer to dynamics. Box labels consist of a letter signifying the column, a number signifying the row and an "r" for "d" for restraint or dynamics, respectively. Arrows show restraining influences and are labeled as follows: row number (or numbers, if arrow connects two rows) --restraint number. See text for a detailed explanation.

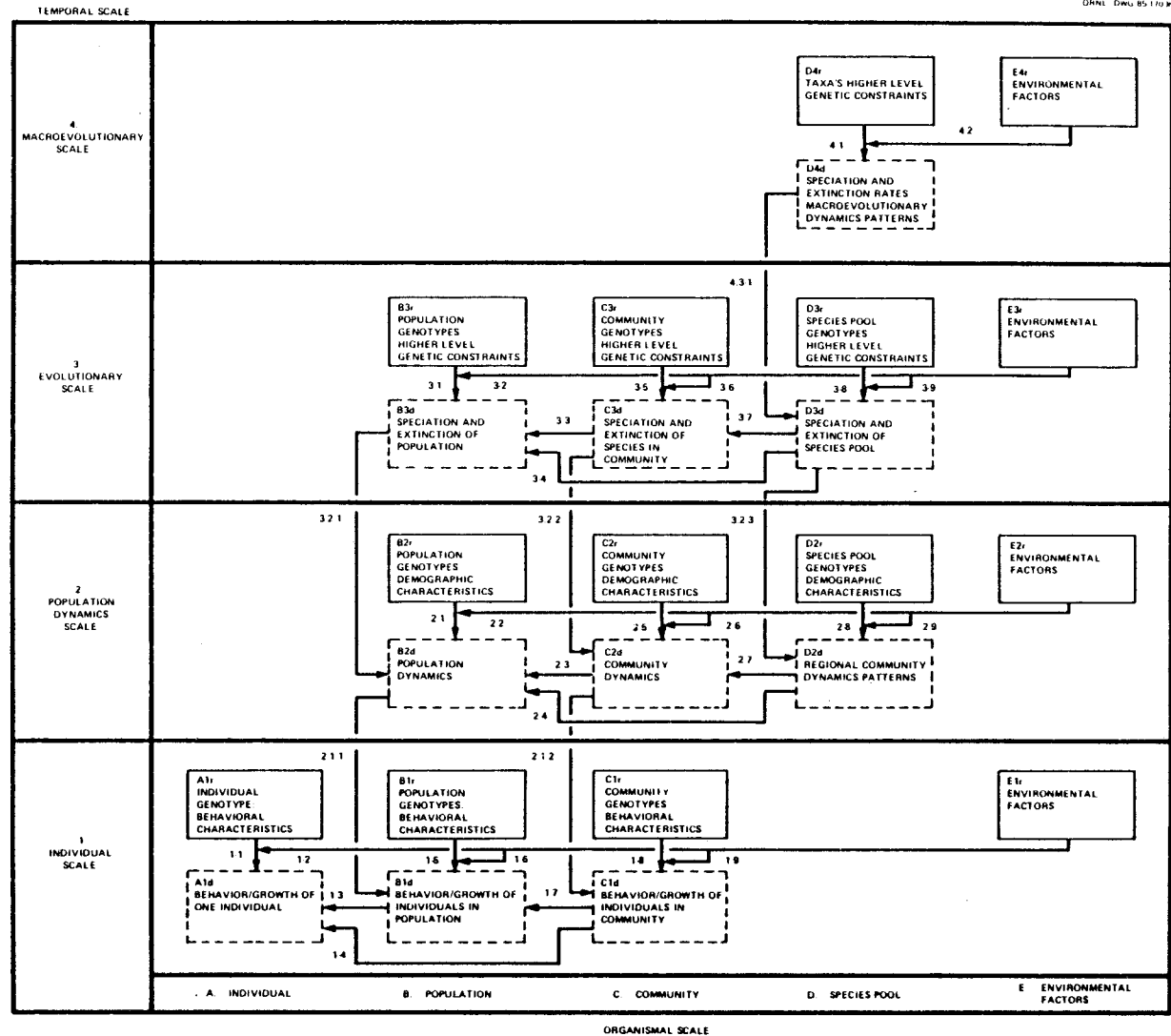


Figure II-1

from left to right that summarizes the restraining interactions among organisms. The term "restraint" is used as a general term that includes interactions between components as well as the slower changing constraints. The relationship between horizontally adjacent dynamical components is one of part to whole, although, since the time scale is the same within a level, the relationship is not really the same as the asymmetrical constraint discussed in Allen and Starr (1982). The environmental hierarchy represented by column E is separate and acts as a restraint on behavior throughout the temporal level. For an example of the interpretation of these relationships, connection 2-2 might be temperature's restraining influence on behavior and growth over a seasonal time scale. Interference competition might be described as the interaction between an individual and the rest of the individuals in the population on a short-term local scale (restraint 1-3).

The environmental hierarchy could be broken down into detailed processes and constraints as well, however this endeavor is more in the domain of physical sciences such as meteorology, physical oceanography or soil science. In this simplified general scheme, environmental effects will be treated as empirical restraints. More detailed models of specific situations would probably need to include reciprocal species effects on the environment and the actual dynamics of physical processes. This would result in two complexly interwoven hierarchies with reciprocal interactions at many levels. For the present purposes, however, it is adequate to consider the environment primarily as an empirical hierarchy with environmental

effects decomposed into levels according to their temporal scale of effect on biological dynamics.

c. Temporal scale. The vertical dimension of Fig. II-1 is a hierarchy of temporal dynamics ranging from the fine resolution of daily organism behavior and growth at the bottom, to the very coarse resolution of events on the geologic time scale at the top of the diagram. The connection between temporal levels is represented by connection numbers such as 2.1-1 and 3.2-2. The temporal dynamics hierarchy is scaled to particular biological phenomena (e.g., individual behavior, generation time, and species evolution) since organisms differ considerably in their activities along an absolute time scale.

Dynamics and restraints for an entity only appear on temporal scales at which they represent the most relevant, characteristic or lasting type of entity. For instance, since individuals are relatively transient, they do not operate on the population time scale as defined here. This is not to say that an individual's behavior is irrelevant to the population scale, but that it is only significant in terms of its role as a part of the higher organismal and temporal levels.

C. RELATIVE EMERGENCE

Three types of relative emergence will now be discussed with reference to the hierarchical conceptual model (Fig. II-1).

1. Failure to Include Interactions Among Components (Type 1)

a. Broad sense. One reason for relative emergence is the failure to include interactions in the lower level predictive model; in other words, the whole is compared to the sum of its isolated parts. Failure to include interactions would be represented by a model that concerns an entity in a particular column (Fig. II-1) without considering the context of other entities with which it interacts. Mating behavior can not be predicted from the observation of isolated individuals, nor can the behavior of a herd be predicted from the behavior of isolated animals, if there are significant intraspecific interactions.

b. Narrow sense. There is another commonly used criterion for emergence due to interactions that is much more restrictive. This criterion requires interactions to be a result of a "coevolution" of parts resulting in their functional interdependence and coordinated dynamics. The entity used as a basis of comparison is the organismal unit, with its high degree of coordination among its parts. The stability and distinctness of the higher level entity over evolutionary time are seen as prerequisites for the development of this restricted type of emergence. Functional integration as a result of evolution is the main concern, regardless of whether discussion centers around the evolutionary process or its ecological outcome.

2. Failure to Include Appropriate Constraints (Type 2)

Failure to specify all the appropriate constraints of a particular level of dynamics in one's model can also result in the appearance of emergent behavior. For example, an explanation of population dynamics (Fig. II-1, box B2d) is not complete if it fails to include environmental constraints (connection 2-2) and inter-level effects (connection 3.2-1). The traditional community equilibrium view may fail to adequately predict a community's dynamics from demographic models due to its failure to include changing environmental constraints.

3. Methodological Limitations (Type 3)

Relative emergence may also arise from practical problems regarding the lower level information needed for predicting certain phenomena. Unpredictability in practice is more likely in situations where the information needed for prediction is methodologically intractable, excessive and detailed. An example from ecology is the prediction of the colonization rate for birds on islands from individual colonization events. The information required is very small-scale (e.g., individual behavior and interactions, weather patterns, and air currents at particular times) and thus would result in practical difficulties in gaining the knowledge for prediction. Thus the colonization rate might, for all practical purposes, be regarded as emergent relative to individual colonization events.

D. AREAS OF CONTROVERSY

The purpose of this section is to discuss three current controversies in evolutionary and ecological theory which involve the issue of the reality, utility and reducibility of higher level phenomena. The consideration of the several meanings of emergence and the hierarchical restraint scheme (Fig. II-1) will aid in clarification of the semantic and theoretical confusion which has impeded the resolution of these controversies.

1. Is Macroevolution Decoupled from Microevolution?

The punctuated equilibrium theory (Gould and Eldredge 1977; Gould 1980) has proposed that species are "irreducible" inputs to macroevolution (Gould 1980) and thus macroevolution is decoupled from microevolution. Speciation and extinction are seen as effectively random with respect to gradual, within-species, microevolutionary change.

Hoffman (1982) has challenged this position with a hypothesis that is designed to account for both gradual and punctuated patterns. He proposes that a high degree of developmental canalization results in punctuated evolution, while gradual change, as predicted by microevolutionary theory, occurs when there is a high degree of developmental plasticity. Thus he states that the different modes of speciation are "mere epiphenomena of the underlying genetic processes which are controlled by a variety of historical, physical, and mechanical factors." What he has done is effectively expand his explanatory system to encompass more

restraints, including the origin of the higher level genetic constraints (e.g., box C3r in Fig. II-1, page 14). Using this explanatory system, he has affirmed the theoretical or absolute reducibility (inherent determinism) of macroevolutionary processes. However demonstration of theoretical reducibility has little effect on the emergent status of speciation and extinction relative to certain predictive models, which Gould (1980) and others imply. Adequate lower level information is not readily obtainable (Type 3 emergence) and higher level constraints prevent the use of a mere extrapolation of microevolutionary theory operating at small scales (Type 2 emergence). It is, in fact, these higher level constraints which are producing many of the macroevolutionary patterns. Information can be integrated over groups of taxa and periods of geologic time and speciation and extinction rates compared to each other and to simulation model results to allow detection of these patterns (see Stanley 1979). Admittedly, lower level factors may bias higher level patterns (see Arnold and Fristrup 1982, for means of including this effect). Nevertheless, in general, this type of analysis is appropriate for studying the effects of large-scale patterns and restraints in macroevolution.

2. The Controversy Over Higher Levels of Selection

As Arnold and Fristrup (1982) state, there is a "tendency among evolutionary theorists to account for biological observations without recourse to higher levels of analysis whenever possible." Though this may be true, the validity and utility of group, species,

and community selection concepts is still far from settled, as shown by current discussions (Maynard Smith 1976; Hull 1980; Gould and Eldredge 1977; Stanley 1979; Arnold and Fristrup 1982; Vrba 1983). In this section, an attempt will be made to clarify the relationships between several views of higher level selection.

In this section, broad and narrow views of group selection and species selection will be discussed. The broad views assert the validity of higher level selection due to relative emergence resulting from interactions and constraints. The narrower views identify additional criteria for higher level selection.

a. Group selection.

(i) Narrow interpretations.

(a) Irreducibility of the mechanism. Some discussions focus on the necessity for the mechanism of selection to be entirely due to selective propagation and extinction of groups (see Maynard Smith 1976). This emphasis on the mechanism probably occurs because group selection theory has stressed traits that are disadvantageous on the individual level, thus requiring the mechanism of selection to occur on the group level. In order for this type of group selection mechanism to operate, groups must be relatively stable and discrete, thus limiting the situations where higher level effects are considered valid.

(b) Irreducibility of effect--group adaptation. Some discuss the need for adaptive organization of the group in order for a particular level to serve as a valid higher level of selection

(Williams 1966; Hull 1980). Higher level selection is required to act in the same way as organismal selection and result in functional interdependence and specialization of the parts. This criterion requires stable and distinct entities as well, and also requires the capacity for specialization of the parts.

(ii) Broad interpretation.

In a broad sense, the only requirement for a group selection effect is that individual fitness be affected by the context of other individuals present. This might be termed "group context selection" to avoid confusion with the narrower meanings. The processes and patterns do require consideration of the group level (Arnold and Fristrup 1982) and thus exhibit relative emergence due to interactions (Type 1). However, the mechanism may still involve selection between individuals and the effect may be individual adaptation not group adaptation (sensu Hull 1980). A large degree of stability and distinctness of groups strengthens the group effect but is not essential for the theoretical validity of this group context effect (called a group "treatment" effect by Arnold and Fristrup 1982). The effect occurs as long as the individuals are in contact long enough for the context to affect the organisms chances for survival and reproduction. In a hierarchical model of selection (Arnold and Fristrup 1982; Gould 1982), the group effect is only one level of selective constraint that may be affecting a trait.

b. Species selection.

(i) Narrow interpretation.

(a) Species must be discrete, stable entities. Although many would consider species as sufficiently stable and discrete (particularly those favoring the punctuated equilibrium model of evolution), others might claim that species do not satisfy this criterion and hence are not valid higher level entities. Even if the species change, however, the lineages could show selective extinction. There seems to be no valid reason why forces affecting gradual evolution of a species may not occur concomitantly with the larger scale forces affecting the differential extinctions of these lineages.

(b) Species adaptations must be more than simply additional organism adaptations. Vrba (1983) stresses that species selection must be limited to cases where the above statement is true. The nature and context of the statement implies that this requirement is viewed as necessary in order to establish the irreducibility of speciation and hence species selection.

(ii) Broad interpretation.

Apart from these restrictive criteria for emergence, it is proposed here that the tendency for selective species extinction to occur as a result of relatively large-scale geologic changes is enough to consider species selection as a relatively emergent phenomenon. This might be called "macroevolutionary context selection".

From this section, it should be clear that there are several different ideas of what characteristics are necessary in order to establish higher level selection. Which criteria are most appropriate depends on the problem being investigated. The main point is that there is a broad sense of emergence involving higher level contexts or restraints, which is applicable to many phenomena regardless of whether any of the more restrictive criteria apply.

A possible way to summarize these contexts is presented in Fig. II-2. So far, group and macroevolutionary contexts have been discussed (Fig. II-2, 2a and 1b). The community context will be discussed in the next section.

3. The Community Integration vs Species Individualism Controversy

Recent discussions of emergence in community ecology have involved the importance of interspecific interactions in ecological and evolutionary time. Odum (1977) and Salt (1979) describe emergence as resulting from higher levels being more than the sum of their isolated parts.¹ Both infer that this type of emergence is due to coevolution of communities resulting from the evolutionary effect of species interactions.

¹ Salt's (1979) discussion is misleading, however, because he is not consistent in his requirements that the summed parts be isolated. For instance, if one sums productivities of individual species present in the community, the effects of interspecific interactions are already included in the individual productivity values. This is true of other measures he mentions that by definition must be summed, but since the individual values already include the effect of interspecific interactions, they are not in reality isolated parts.

		Temporal Context (Constraints, Type 2 Emergence)	
		a. Microevolutionary	b. Macroevolutionary
Organismal Context (Interactions, Type 3 Emergence)	1. Individual genetic constraints	1a. Microevolution of organism	1b. Macroevolutionary context selection
	2. Deme or group	2a. Group context selection	2b. Macroevolutionary context selection affected by group context
	3. Community	3a. Community coevolution	3b. Macroevolutionary context selection affected by community context

Figure II-2. Various types of higher level selection classified according to their organismal and temporal contexts.

Controversy in community ecology has thus centered around the importance of interspecific interactions and the role of coevolution in the development of these interactions. Some ecologists (e.g., Odum 1977; Levins and Lewontin 1980) emphasize the importance of interactions and coevolution, while others (e.g., Simberloff 1980) contend that species "act as individuals" and that there is little reason to suppose that coevolution plays a significant role. Those emphasizing individualism describe higher level phenomena as "mere epiphenomena" of individualistic species responses rather than "emergent properties" (Simberloff 1980).

In order to clarify these issues, three views of the community will be characterized based on several factors that relate to emergence (Fig. II-3). The two extreme views (alternatives 1 and 3) are the most controversial and are often strongly associated with particular ideas of emergence. The first view (Fig. II-3, alternative 1) is that communities are not distinct or stable, and that interactions are therefore insignificant. Species are independent of one another in their dynamics on both evolutionary and ecological time scales and thus neither interactions nor higher level organizational principles contribute to the relative emergence of community or evolutionary dynamics.

The other extreme view (Fig. II-3, alternative 3) is that communities are stable and distinct, interactions are of general importance, and they result in coevolution and community selection (Type 1 emergence--narrow sense). Species are thus considered highly interdependent and a substantial degree of community

<u>Stability and Distinctness of the Community</u>	<u>Importance of Interspecific Interactions</u>	<u>Ecological and Evolutionary Scale Effects</u>	<u>Relative Emergence</u>
1. Community unstable and indistinct	Interaction insignificant	Ecological: species do not affect each others abundances. Evolutionary: evolution occurs independently of other species.	Ecological: no emergence due to interactions. Evolutionary: no higher level organizational principles.
2. Community generally unstable and indistinct: an open, nonequilibrium system	The importance of interspecific interactions varies with time and species considered	Ecological: certain species affect each others distri- butions and abundances at certain times. Species "editing" may result in a sort of community organization. Evolutionary: coevolution is possible for certain species. Species affect each other's distributions and result in range shrinkage and an increase in extinction rate producing a species selection effect.	Ecological: interactions may produce relative emergence regardless of evolutionary effects. Species "editing" may also contribute to relative emergence by producing higher level patterns and principles. Evolutionary: particular cases of coevolution may produce some functional interdepend- ence. Species selection may be affected by interactions and produce large-scale patterns and principles that appear emergent.
3. Community stable and distinct	Interactions are of general importance	Ecological: species distri- butions are strongly dependent on the abundances of other species. Patterns are largely a result of coevolution. Evolutionary: coevolution is important and results in a functionally integrated community.	Ecological: emergence due to interactions. Evolutionary: higher level principles of organization and functional interdepend- ence contribute to the perception of emergence.

Figure II-3. Three alternative views of communities on ecological and evolutionary time scales.

organization is present. Although interspecific competition is viewed as generally reduced, various types of interactions still occur and thus there is relative emergence due to interactions (Type 1--broad sense). As a result of community-level interactions operating over evolutionary time, higher level principles of organization and functional interdependence may be observed.

It appears that the controversy has become prolonged because of confusion resulting from the common, intuitive feeling that stability or equilibria, the importance of interactions on ecological and evolutionary time scales, and the emergence of phenomena at higher levels are strictly related. The following discussion of the intermediate alternative (Fig. II-3) will show that the strictness of the above set of associations is more apparent than real.

According to the second alternative, ecological communities are rarely stable or discrete. This corresponds to a nonequilibrium view in which communities are open systems (Caswell 1978) and migration and colonization on various scales are important. Although species interactions in ecological time may occur, their effects do not translate directly into evolutionary effects as is expected in a closed, equilibrium system (Fig. II-3, alternative 3). These ecological-scale interactions result in the potential for relative emergence (Type 1--broad sense) regardless of evolutionary effects, since species in isolation generally have different dynamics than species in the context of particular communities. In addition, interactions may result in the exclusion

of particular species under certain conditions that results in a sort of community organization. This species "editing" by a community on an ecological time scale (Fowler and MacMahon 1982) also may contribute to the relative emergence of higher level principles without the assumption of coevolutionary effects.

Varied degrees of interaction and constancy of co-occurrence will result in the possibility of some specific coevolutionary relationships developing over evolutionary time (e.g., pollinator-plant coevolution). According to this view, traditional coevolution of competitors is possible under certain circumstances but is not widespread. However the ability of a community context to sometimes exert a species "editing" effect on an ecological time scale, may contribute to species selection by influencing species abundances and distributions and hence their extinction rates (Fowler and MacMahon 1982). This type of species selection effect (Fig. II-3, 3b) may also be reflected in patterns and principles of community organization.

The ecological and evolutionary properties of species "editing" have an important implication for viewing "nonequilibrium strategy" species. Paine (1981) has opposed the characterization (Stanley and Newman 1980; Newman and Stanley 1981) of the chthamaloid barnacles as the evolutionary losers to balanoid barnacles, by countering that the chthamaloid's competitively-inferior nonequilibrium strategy has its own advantages. Paine's point is well-taken, but the presence of balanoids has nevertheless reduced the abundance and distribution of chthamaloid species, which has probably increased balanoid

extinction rates (Newman and Stanley 1981). Perfectly good "nonequilibrium strategies" for particular species in ecological time are not in contradiction to larger scale patterns of evolutionary decline in species richness due to the long-term effects of competitors.

With this description of the three views of communities in Fig. II-3, no associations between present ecologists and the extreme views are intended. Rather the purpose is to point out certain unnecessary associations and needed distinctions. It is apparent from current literature that most ecologists have views somewhere in the range of possibilities presented in the intermediate alternative (Fig. II-3). Naturally, there is a large amount of research needed to determine the importance, mechanisms and effects of various processes discussed under this alternative. But it is hoped that this discussion may help clarify some issues so that further effort will not be expended attacking extreme views that are rarely defended or misinterpreting more moderate ones.

In concluding this discussion of the integration versus individualism controversy, three main points should be stressed:

1. One form of relative emergence--that due to a failure to include interactions--does not require coevolution of any kind.
2. Unstable and indistinct communities may still contain important interactions and some form of community organization resulting from processes on an ecological time scale.

3. Consistent co-occurrence and stability are not necessary for a sort of coevolution on the level of species selection. Thus the "ghost of competition past," which Connell (1980) attempted to dispel in the form of traditional coevolution, makes a reappearance in the form of species selection's effect on community structure (Fowler and MacMahon 1982).

E. AN ASSESSMENT OF HIGHER LEVELS OF ANALYSIS

The emergence issue is relevant for the practice of ecology primarily due to its relation to the question of the validity and necessity of higher levels of investigation and analysis for understanding the ecology and evolution of organisms. It turns out that what causes relative emergence are the restraints (Types 1 and 2) and methodological limitations (Type 3) that higher levels of analysis are designed to take into account, thus compensating for the limitations of a purely reductionist approach. In fact, this suggests a fairly direct correspondence between situations that appear to require higher level analyses and those that may appear emergent. The following section will discuss the benefits and pitfalls of higher levels of analysis through further examples and discussion.

1. Benefits of Higher Level Analyses

a. Higher level analyses can include interactions and constraints that might be undetectable at a lower level of analysis.

(i) Interactions. The community level of analysis--which studies populations and their natural context of potentially interacting species--may be able to predict phenomena and explain patterns that studies of only one species or isolated species are unable to do. The previous discussion of the community ecology controversy illustrates this view. Naturally, the significance and effect of interaction is quite variable and requires further study.

(ii) Constraints. Constraints operate on a wide range of spatial and temporal scales and care must be taken that the chosen level of analysis will be able to detect the environmental factor or biotic process of interest. Considerations such as these have been common for some time in the form of discussions of data aggregation, sample size and scope of the study and various principles of experimental design (Greig-Smith 1964; Goodall 1974; Gauch 1982; Green 1979; also see Allen and Starr 1982). Other illustrations of the importance of the scale of the study include the observation that correlation results may differ depending on universe size (Gauch 1982; Webb, unpublished study described in Allen and Starr 1982) and the tendency for diversity trends to depend on the scale of the study (e.g., the distinctions among alpha, beta and gamma diversity as pointed out by Whittaker 1972).

The scope of the study (size of sampling universe) must be large enough to include evidence of significant changes in the constraint of interest. The resolution (amount of detail) should be fine enough to detect relevant changes, but not so fine as to bury the larger scale pattern in small-scale or effectively random information. Average values or rates are often used to integrate this small-scale variation.

Acknowledgment of the importance of scale has been particularly important for work on ecological systems with many important scales far from the typical observer scale (e.g., forest dynamics: Shugart 1984; Delcourt et al. 1983; and microscopic algal ecology: Allen 1977; Allen and Starr 1982; Harris 1979). However the study of any ecological system could benefit from investigations and analysis on multiple levels. It is becoming increasingly apparent that certain controversies, such as the problem of community continua versus discreteness (Allen and Starr 1982; O'Neill et al., in press) and the equilibrium versus nonequilibrium debate (O'Neill et al., in press), may stem from differences in the scale of the observations.

b. Higher level analyses simplify data collection and theoretical development.

The principle of parsimony is often used as a reason to do away with higher level concepts if they are theoretically reducible to lower levels. However, what is most parsimonious in terms of the processes basic to all of science is certainly not most parsimonious to those who practice science at some higher level of organization.

An example so obvious as to almost be trivial is that of the organism level. One might possibly argue that the organism is a superfluous higher level entity since it is reducible in theory to physical and chemical processes. Yet obviously biologists must ignore this sort of parsimony argument and continue to treat the organism as a "real" entity in order to advance biological knowledge. The organism level is a theoretically and practically necessary higher level entity because of its clearly emergent status relative to approaches in physics and chemistry. By the same reasoning, for the practicing macroevolutionist, species selection is the most parsimonious construct, just as the organism is a parsimonious description of reality for the biologist.

2. Pitfalls of Higher Level Analyses

a. Failure to include important lower-level inputs. Higher level analyses often operate on the assumption that many effects referred to as "chance" or small-scale processes will either have little effect on the higher level pattern or at least tend to average out. In reality, this will not always be true. If the problem is recognized, it can be overcome by taking more or larger samples, by restricting one's study to samples where the problem is minimized, or by removing extraneous variability through analytical techniques such as analysis of covariance. A more serious problem occurs when the presence of these confounding effects is not even known. Utilization of knowledge of lower level mechanisms and their influence on higher level patterns is recommended to avoid this

problem. An example of this is found in palynology, where the manner in which local climatic and topographical factors affect the accumulation of pollen, is studied so that the large-scale patterns may be adjusted for these smaller scale biases (Tauber 1965, 1977; Bonny and Allen 1984).

b. Use of inappropriate higher level entities. If a higher level entity is being studied, it is often assumed to have certain characteristics that are relevant to the process being studied. If this assumption is incorrect, false conclusions may be drawn. For instance, if one is interested in the coevolution of a particular set of species one must be certain that the "community" has existed for a sufficient time for the coevolution to have occurred. It should be stressed that the appropriateness of the higher level entity depends on the process being studied. While a particular "community" might not be a suitable higher level entity for certain evolutionary-scale processes, it might be well-suited to the study of processes occurring in ecological time.

c. Need for complex interpretations of higher level indices. A good example of this problem is found in the interpretation of species diversity patterns (e.g., Pianka 1978; Hurlbert 1971). Diversity indices have the ability to integrate the effects of a wide array of processes occurring on many scales. But for these same reasons, they have the disadvantage of often requiring complex multi-factor explanations. This does not necessarily mean that

diversity indices should be abandoned; however one should not expect them to be amenable to simplistic types of analysis and theory.

d. May promote neglect of underlying mechanisms. An example of this type of problem may be found in the use of certain "holistic" community parameters (Levins 1968; Levins and Lewontin 1980; Lane 1975; Lane et al. 1975). These measures, which include average niche breadth, carrying capacity and species diversity, are described as:

1. remaining more constant than lower level measures such as species abundances;
2. showing meaningful covariation with certain large-scale environmental changes.

Although they may be useful as such in some circumstance, knowledge of the processes accounting for their supposed constancy and meaningful variation would greatly increase their explanatory value. Simberloff (1980) makes the point that the properties of Levins' "holistic" community measures observed in Lane et al. (1975), may result from a statistical property of any random assemblage of species under certain reasonable constraints.¹ It also seems possible that their properties might result from energetic constraints or species interactions in ecological time. The explanation that some "holists" might prefer--coevolution to maximize some community parameter or stability--may not be the

¹It is not clear whether Simberloff means that the "random assemblage" includes ecological time scale interactions.

appropriate one. These criticisms are not meant to imply that a complete reduction to lower levels is necessary. Instead, they are meant to illustrate the view that "holistic parameters" are probably more useful and certainly more intellectually accessible if there is at least some knowledge of the mechanisms they are actually reflecting. Indeed, more knowledge of the mechanisms involved should also help deal with the other three dangers that have been discussed.

The conclusion of this section is that higher level analyses greatly facilitate the elucidation of important system patterns; patterns that often can be observed in no other way. There are pitfalls, but they can usually be avoided through careful analyses based on a knowledge of important processes--including lower level mechanisms.

F. CONCLUSIONS

The main theme of this chapter is the interpretation of higher level entities, principles and analyses--in other words, the implications of a hierarchical view of the ecology and evolution of organisms. The term emergence has been central to the discussion because it is used to express the often intuitive view of the relation between levels in a hierarchy of processes and patterns. That the discussion is based on the emergence issue does not imply support for general use of the term when there is a specific description that is more to the point. Indeed, it would be preferable for disagreements as to the choice of levels of analysis

to focus on specific issues, such as the advantages and disadvantages of higher levels of analysis, some of which are presented here. Disagreements over the occurrence of emergence in particular situations should also be replaced by more specific discussions such as:

1. assessments as to whether particular higher level interactions or constraints can be safely left out of a predictive model due to their lack of significant effect;
2. analyses to determine whether details of lower level information may have larger scale effects or may be averaged for the purposes of prediction at a higher level.

Another primary issue, which frequently becomes involved in discussions of hierarchy and has pervaded much of the present analysis, is the question of whether higher level selection is necessary for the validity of a hierarchical approach. Although higher level selection has interesting implications for hierarchies in nature (e.g., see Allen and Starr 1982; O'Neill et al., in press), the present analysis indicates it is not necessary for emergence or the validity and utility of a hierarchical approach.

CHAPTER III

IDENTIFYING POLLUTION RELATED CHANGES IN CHIRONOMID COMMUNITIES
AS A FUNCTION OF TAXONOMIC RANK

A. INTRODUCTION

One of the most recurrent problems faced by ecologists is the difficulty of replacing subjective comparisons of species lists with objective numeric values summarizing the similarity among the communities. Many analytical techniques have been suggested to evaluate species check lists. However, many of the qualitative methods based on binary data have been ignored by ecologists because species abundance data are thought to be superior to species presence/absence data for comparing ecological communities (Greig-Smith 1964; Clifford and Stephenson 1975). Recent studies using binary data have been successful in detecting patterns of change in ecological communities (Green 1979; Peterson 1976; Polovino et al. 1982; Allen 1971). Results of these studies indicate that qualitative data are not inferior to quantitative data but rather answer questions at a different level of resolution.

When samples are to be compared on the basis of the organisms present in each, it is usually assumed that species-level identification is necessary for adequate evaluations. However, for some organisms, such as immature aquatic invertebrates, species identification may be difficult, unreliable, or impossible. Because this taxonomic confusion is frequently the case, species distribution

patterns often must be derived from generic or mixed species/generic data. This is generally regarded as a handicap; however, some research has proposed that the use of higher taxonomic levels may actually allow the detection of pattern on a larger scale (Green 1979; Vascotto 1976). The objective of this study is to investigate the relation between specific and generic-level analyses by assessing the ecological relevance of generic groupings.

B. METHODS

To approach this problem, specific and generic-level binary similarity coefficients are calculated from the distribution of chironomids along a heavy-metal pollution gradient in a small Ohio stream. The patterns shown by the specific and generic-level coefficients are compared. Theoretical framework based on the species:genus ratio is then developed and used to examine the ecological relevance of the generic groupings.

The data on chironomid communities were obtained from Elam's run, a second-order limestone stream in southwestern Ohio that receives a complex heavy-metal effluent from a metal-plating industry. A detailed description of the study area and sampling methods has been published previously (Winner et al. 1980). Briefly, samples were taken from five shallow riffle areas at varying distances from the source of effluent. Occurrence of 57 chironomid (midge) species was determined at each station using both box and emergence samplers. All species identifications were based on adults, either from field specimens or from larvae reared

in the laboratory. Species abundances were obtained for adults collected in emergence traps. Copper, zinc, and chromium concentrations were monitored to assess chemical pollution gradients.

Eighteen binary similarity coefficients were chosen from the literature (Clifford and Stephenson 1975; Boesch 1977; Sokal and Sneath 1963; Lamont and Grant 1979) and calculated for each two-way comparison of species lists for specific and generic-level data. Values used to calculate binary similarity coefficients are as follows:

A = conjoint presences;

B = species present in first station but not second station;

C = species present in second station but not first station;

D = species absent in both stations being compared but present at one of the other three sampling stations.

Correlations between specific and generic-level binary similarity coefficients were calculated, and plots of the data were used to compare the patterns shown by specific and generic-level values.

The rarefaction technique was used to calculate the number of genera (G) expected for a random sample of S species from a species pool consisting of all species sampled at the five stations.

Formulas for the expected number of genera and its variance have been previously published (Hurlbert 1971, Simberloff 1978) as has been a Fortran program that provides the necessary results (Simberloff 1978). Differences between actual and expected numbers of genera at each of the five stations were tested using the z statistic corresponding to a normal distribution. The finite

population correction term was included in the calculation of the variance because of the large sample size relative to the species pool. The normal distribution was assumed to be an adequate approximation within the range of sample sizes used.

C. RESULTS AND DISCUSSION

1. Trends Along the Heavy-Metal Gradient

Heavy-metal concentrations showed a downstream decline with increased distance from the heavy-metal source. Copper, for instance, had mean levels of 336, 237, 221, 87, and 74 $\mu\text{g/L}$ for stations 1 through 5, respectively. Although the concentration differences were not statistically significant because of extreme variability, there were clear downstream changes in the percentages of caddisflies and chironomids as well as changes in the chironomid species list (see Winner et al. 1980). The number of species per station increased with increasing distance below the point of metal introduction (Table III-1). An exception to this trend is station 2, which is closer to the pollution source than station 3, but has more species (Table III-2). Species relative abundance data also indicate this reversal in the expected ordering (see section on abundance data, below). This reversal may be due to a 40% decrease in average current velocity from station 2 to 3, which may result in pulses of heavy-metals persisting for longer intervals at station 3 than at station 2 (R. W. Winner, pers. comm.). I have altered the station ordering in the presentation of results to coincide with what appears to be the more biologically relevant gradient. Other

Table III-1. Chironomid species list for Elam's run listed by genera in order of decreasing number of species per genus.¹

Species	Station				
	1	2	3	4	5
<u>Pentaneura currani</u>				+ ²	
<u>Pentaneura bifasciata</u>		+		+	
<u>Pentaneura fimbriata</u>				+	
<u>Pentaneura flavifrons</u>		+		+	+
<u>Pentaneura melanops</u>	+	+	+	+	+
<u>Pentaneura pilosella</u>				+	
<u>Pentaneura sinuosa</u>	+	+	+	+	+
<u>Pentaneura cornuticaudata</u>					+
<u>Cricotopus trifasciatus</u>		+	+	+	
<u>Cricotopus bicinctus</u>	+	+	+	+	+
<u>Cricotopus exilis</u>	+			+	+
<u>Cricotopus infuscatus</u>	+	+	+	+	+
<u>Cricotopus slossonae</u>			+	+	
<u>Cricotopus varipes</u>		+	+	+	+
<u>Metriocnemus aequalis</u>					+
<u>Metriocnemus atratulus</u>					+
<u>Metriocnemus exagitans</u>					+
<u>Metriocnemus lundbeckii</u>	+		+	+	+
<u>Orchocladius dubitatus</u>	+	+		+	+
<u>Orchocladius obumbratus</u>		+	+	+	+
<u>Orchocladius stamfordi</u>					+
<u>Orchocladius johannseni</u>			+	+	
<u>Tanytarsus dissimilis</u>				+	+
<u>Tanytarsus exiguus</u>			+	+	
<u>Tanytarsus neoflavellus</u>		+	+	+	+
<u>Tanytarsus viridiventris</u>					+
<u>Polypedilum convictum</u>	+	+	+	+	+
<u>Polypedilum halterale</u>					+
<u>Polypedilum scalaenum</u>					+
<u>Chironomus attenuatus</u>	+		+	+	+
<u>Chironomus riparius</u>	+			+	
<u>Cryptochironomus digitatus</u>		+			+
<u>Cryptochironomus fulvus</u>		+	+	+	+

Table III-1 (Continued)

Species	Station				
	1	2	3	4	5
<u>Dicrotendipes fumidus</u>			+		+
<u>Dicrotendipes neomodestus</u>		+			
<u>Eukiefferiella brevinervis</u>		+	+	+	+
<u>Eukiefferiella sordens</u>		+	+	+	+
<u>Larsia decolorata</u>		+	+	+	
<u>Larsia planensis</u>		+			
<u>Micropsectra deflecta</u>		+	+	+	+
<u>Micropsectra dives</u>					+
<u>Phaenopsectra flavipes</u>		+			+
<u>Phaenopsectra obediens</u>				+	
<u>Ablabesmyia monilis</u>					+
<u>Corynoneura scutellata</u>	+	+		+	+
<u>Cryptotendipes pseudotener</u>				+	
<u>Diamesa nivoriunda</u>					+
<u>Diplocladius cultriger</u>		+		+	
<u>Microtendipes pallidus</u>				+	
<u>Natarsia baltimoreus</u>	+	+	+	+	+
<u>Parachironomus tenuicaudatus</u>			+		
<u>Paratendipes albimanus</u>	+				+
<u>Procladius culciformis</u>	+	+	+	+	+
<u>Psectrotanypus dyari</u>	+	+	+	+	
<u>Stictochironomus flavicingula</u>		+		+	+
<u>Thienemanniella similis</u>		+		+	+
<u>Trichocladius nitidus</u>				+	+

¹Data were obtained from Winner et al. (1980).

²Presence at a station is indicated by a "+".

Table III-2. The actual and expected values for the numbers of genera and the species:genus ratio.

Station Number	Number of Species	Species:genus Ratio		Number of Genera				<u>z</u> ¹
		Actual	Expected	Actual	Expected	Variance of Expected Number of Genera		
1	15	1.36	1.31	11	11.45	1.17	-0.38 (n.s. ²)	
3	24	1.50	1.50	16	16.04	1.24	-0.03 (n.s.)	
2	28	1.56	1.57	18	17.78	1.18	0.19 (n.s.)	
4	39	1.77	1.78	22	21.86	0.86	-0.99 (n.s.)	
5	39	1.86	1.78	21	21.86	0.86	0.17 (n.s.)	

¹Statistic corresponding to the normal distribution used to test for the difference between actual and expected number of genera.

²Not significant at $\alpha = .05$.

interpretations of these data are possible and further study would be necessary to determine all the factors producing the species distributions, hence the apparent station orderings. Since the purpose was to compare species and genus-level similarity analyses, I do not deal further with the problem of precisely determining the "correct" pollution ordering. The basic conclusions hold regardless of the ordering of stations 2 and 3.

2. Comparison of Specific- and Generic-Level Coefficients

Comparing patterns shown by species and genus level data for values A, B, C, and D and the 18 binary similarity coefficients plotted against the 10 station comparisons (Fig. III-1) shows that most of the similarity patterns are in good agreement for specific and generic-level data because the peaks and depressions generally coincide.

This agreement in overall patterns conflicts with the results of correlations between specific and generic values for some of the coefficients (Fig. III-1). This conflict is probably due to correlation analysis reflecting differences in specific and generic-level coefficients that do not disrupt the overall pattern seen in these graphs. Generally, lower correlations were found for binary similarity measures that either use D in the numerator or do not use all three presence values (A, B, and C).

One might expect to find good agreement in the pattern shown by specific and generic-level coefficients because the values of A, B, C, and D from which the coefficients were calculated also show

Figure III-1. Binary similarity coefficients for specific- and generic-level data plotted against station comparison. The correlation coefficient for the relationship between specific-level values (dotted lines) and generic-level values (solid lines) is presented (* $p < 0.05$; ** $p < 0.01$). Part (a) contains coefficients that lack D in the numerator and include all three presence values (A, B, and C). The coefficients in Part (b) either have D in the numerator or do not include A, B, and C.

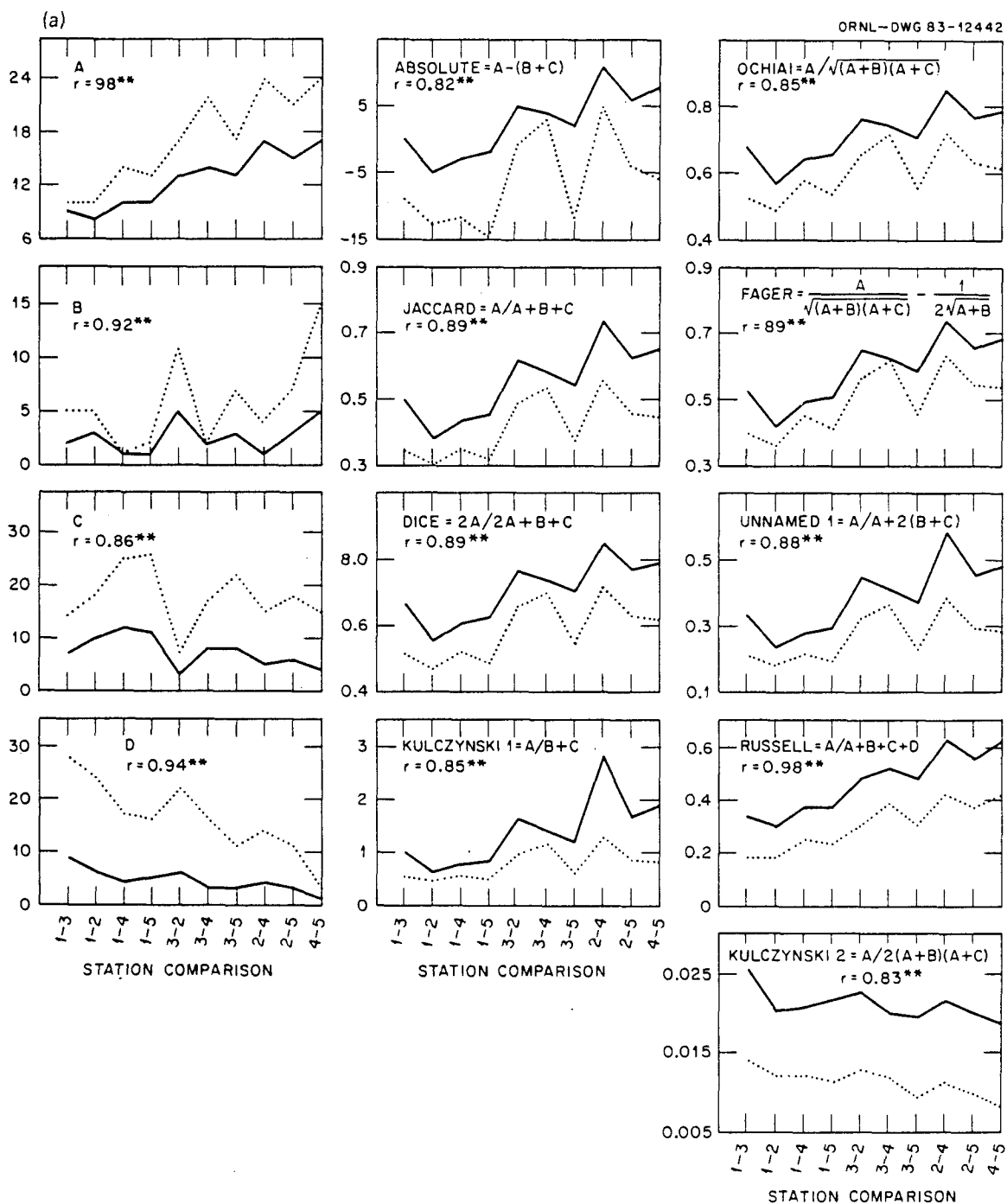


Figure III-1

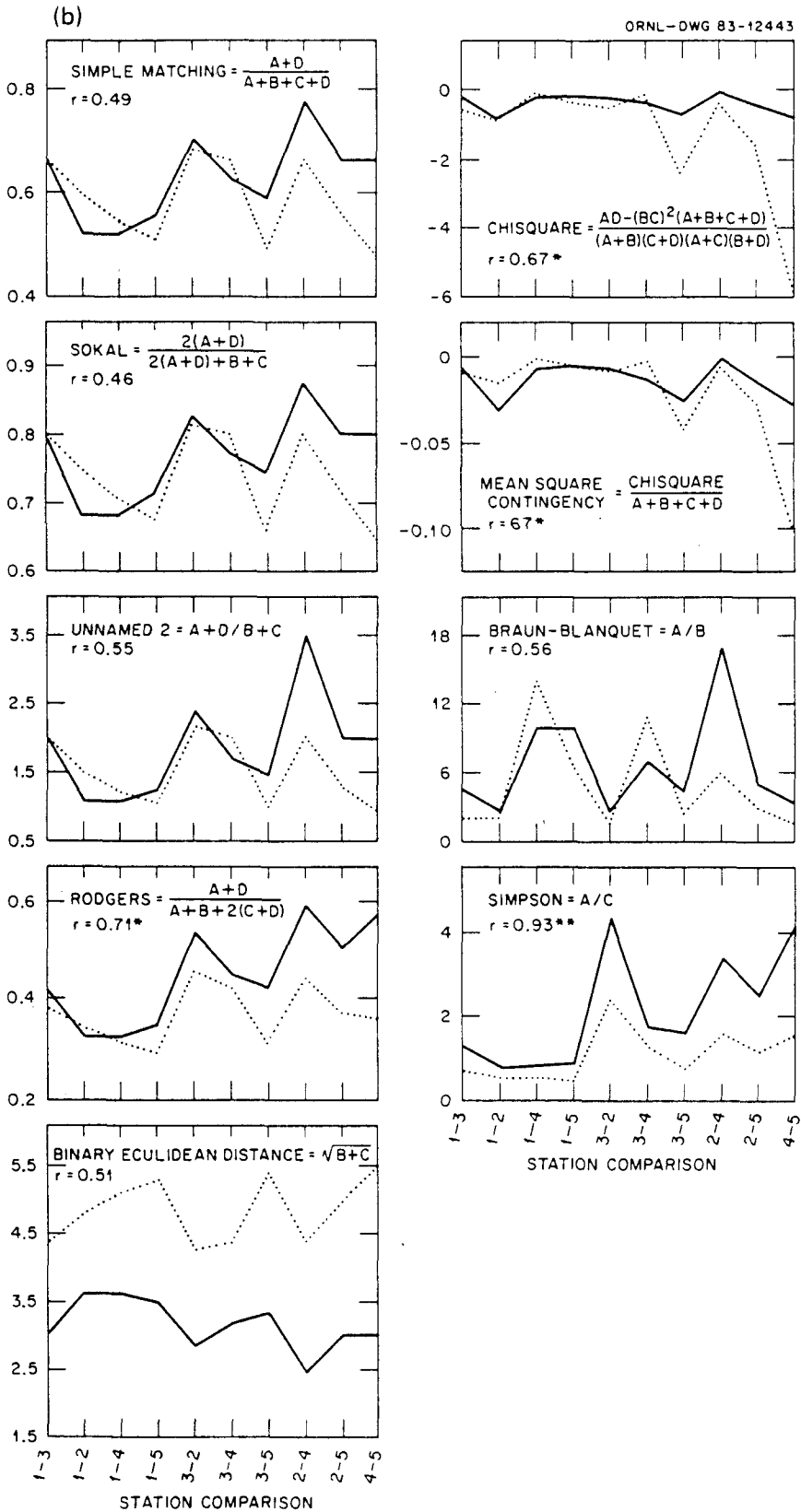


Figure III-1

similar patterns at the two levels. Furthermore, coefficients that showed lower correlations might be considered less appropriate for ecological data. In general, these coefficients either included conjoint absences (D) in the numerator or did not include all three presence values--A, B, and C (Fig. III-1b). These findings concur with theoretical considerations that recommend omitting conjoint absences (D) from calculations of station similarity (Goodall 1973; Clifford and Stephenson 1975).

Despite the overall similarity in pattern, it should be cautioned that differences between specific and generic-level patterns are probably sufficient to generate different station orderings if sensitive ordination techniques are used. However, with known inherent variability and the higher sampling error involved with detecting the presence of very rare species, it seems unlikely that these small differences in the patterns of the binary similarity coefficients are biologically or statistically significant. Therefore, discussions of binary similarity coefficient patterns in high variability situations such as this should not treat small changes in coefficient values as biologically meaningful. An alternative approach, which appears to reduce this problem, is the ordering of stations by the number of taxa. Such a richness index is less susceptible to chance variation because it more effectively integrates small-scale information specifying which species were found at a station and thus allows the detection of the larger scale pattern. This approach is most appropriate in

situations such as this, where the relevant ecological change is successive deletions of taxa.

3. Assessing the Ecological Relevance of Generic Groups

To examine more closely the effect of using generic groupings, the number of species per genus at each station was calculated. An increase in the species:genus ratio with decreasing pollution effects was observed. The significance tests show, however, that the actual number of genera is not significantly different from that expected for a random sample of S species (Table III-2).

These results are relevant to a consideration of the ecological significance of generic groupings. The acceptance of the null hypothesis shows that it is not necessary to attribute ecological significance to generic groupings of chironomid species to explain trends in the species:genus ratios along the heavy-metal gradient (Table III-2). Two alternative hypotheses that imply similarity of congenetics may be considered (Table III-3). One hypothesis predicts more species/genus at the more polluted stations, suggesting that many of the pollution-tolerant species belong to a few "pollution-tolerant genera." The results presented here do not support this hypothesis because congeneric chironomid species do not appear to be similar in their tolerance to heavy-metal concentrations (Tables III-1 and III-2). Resh and Unzicker (1975) also found little congeneric similarity in pollution tolerance for 61 aquatic macroinvertebrate genera. Other studies (Green 1979; Vascotto 1976) have suggested that congeneric species are similar on

Table III-3. Ecological relevance of generic grouping and consequence on binary similarity coefficients associated with three possible trends in the mean number of species per genus.

Hypothesis	Ecological Relevance of Generic Grouping	Effect of Using Generic Level on Coefficient Pattern
H_0 : S/G ¹ is similar to number expected by chance.	None--or mixture of opposing effects (i.e., H_1 & H_2) with neither effect predominating.	Some loss of information but adequate if S/G not too high.
Two Alternatives		
H_1 : S/G at more polluted stations greater than expected by chance.	Indicates similarity among congeners in pollution response (i.e., "pollution-tolerant genera").	Generic level similar to species level or may show a larger scale pattern if generic similarity is on a grosser scale.
H_2 : S/G at more polluted stations less than that expected by chance.	Competition between ecologically similar congeners reduces their ability to coexist in polluted areas.	Generic level should be less effective in showing station differences.

¹S/G = mean number of species per genus at a station.

relatively large-scale habitat characteristics, with species differences occurring on a microhabitat scale. This would mean that the taxonomic hierarchy would correspond to a hierarchy based on ecological similarity. Although this type of pattern was not observed at the scale of our study, it is possible that a study of larger scope might show that generic distributions reflect larger scale environmental features.

The other alternative hypothesis (Table III-3) suggests that fewer species per genus should be found at the polluted stations (e.g., more monotypic genera). Reduced numbers of species per genus could result from reduced coexistence of similar competing congeners in polluted areas. This is analogous to the interpretation of lower species:genus ratios on islands (Grant 1966; William 1964). The lack of this trend in the chironomid data does not preclude the possibility that competitive exclusion of chironomid species may increase with an increase in heavy-metal pollution. It may just be that in general, congeners are not particularly similar ecologically and hence the basis for using changes in the species:genus ratio as an indication of competition no longer exists.

Each of the three possibilities for the ecological relevance of generic groupings (Table III-3) is associated with an effect on the similarity indexes calculated at the generic-level. If congeners are similar in pollution response (Table III-3, first alternative hypothesis), the generic-level analyses should be acceptable because

only redundant information is lost. The second alternative hypothesis suggests a tendency for stations to have similar genera, with any differences attributable to polluted stations having fewer coexisting congeneric species. This situation would result in a decreased ability for generic-level analyses to differentiate between stations.

The acceptance of the null hypothesis indicates that the actual effect on the binary similarity coefficients is a random loss of species information with the collapse to the generic-level of taxonomic identification. Suggestions that a taxonomic hierarchy might correspond to an ecological hierarchy are not supported at the scale of this study (Green 1979; Vascotto 1976). Thus, further consideration of the utility of generic-level in gradient detection will focus on patterns of information loss.

The amount of information lost appears to be related to the number of species in each genus. Chironomid genera containing many species contribute little to the ability of the generic-level coefficients to differentiate between stations because at least one species is usually present at every station. In this study, 2 genera with 6 and 8 species showed this effect. However 13 of the 27 genera had only 1 species and 7 had only 2 species. Obviously, monotypic genera do not lose information when collapsed to the generic-level, and genera with two species generally lost little information. In addition, many chironomid taxonomists would have split many of the genera in this study, resulting in more

genera with fewer species per genus (M. W. Boesel, pers. comm.). These changes would result in less information loss and even closer agreement between specific and generic-level data.

Mixed specific and generic identifications should result in less information loss than generic-level data. However, patterns detected using binary data may be biased toward the patterns shown by taxa identified to species because they will contribute relatively more information to the analysis. Similar biases may occur when more than one person does the identifications, since taxa identified by "splitters" will also contribute more information to the analysis. Naturally, identification to only the family or order level, results in greater potential for loss of species distribution information. Examination of the amount and pattern of information loss along environmental gradients could be undertaken in other data sets in a manner analogous to that used here (e.g., using species:family or species:order ratios) to determine what effect higher level analyses will have on pattern detection.

Kaesler et al. (1978) used hierarchical diversity indexes (which calculate components of the total diversity attributable to different taxonomic levels) to show that the amount of information lost by using higher taxonomic levels may not be sufficient to necessitate species level identification. The approach used here indicates that not only the amount, but also the pattern of information loss along a gradient may be important for gradient detection. This pattern of information loss (species:genus ratio

trend) is determined by the similarity of congenetics in their response to a particular environmental gradient. Thus both the type of organism and the environmental gradient considered may have an effect on the pattern of information loss and hence the utility of higher taxonomic levels in gradient detection.

It should also be stressed that the robustness of the pattern to be detected is an important consideration for the determination of the appropriate level of identification. A very fine-scale gradient may require specific-level analyses while relatively coarse gradients may be detectable at the generic, family and even order level of classification. However, this does not reflect the correspondence between a taxonomic and ecological hierarchy, but merely the ability to withstand information loss, which is greater for robust patterns.

4. Use of Abundance Data

Caution should be used in extrapolating these results to other types of coefficients or evaluations. For example, conclusions as to the effect of using generic-level taxonomic identification appear to be different when abundance data are used. When the three most abundant species are plotted along the heavy-metal gradient (Fig. III-2), the stations can be easily differentiated. However, when the generic-level is used, two of the dominant species are combined so that their changing abundances cancel out, and the analysis no longer differentiates among stations 1 through 4. Therefore, for approaches that rely heavily on the abundances of a

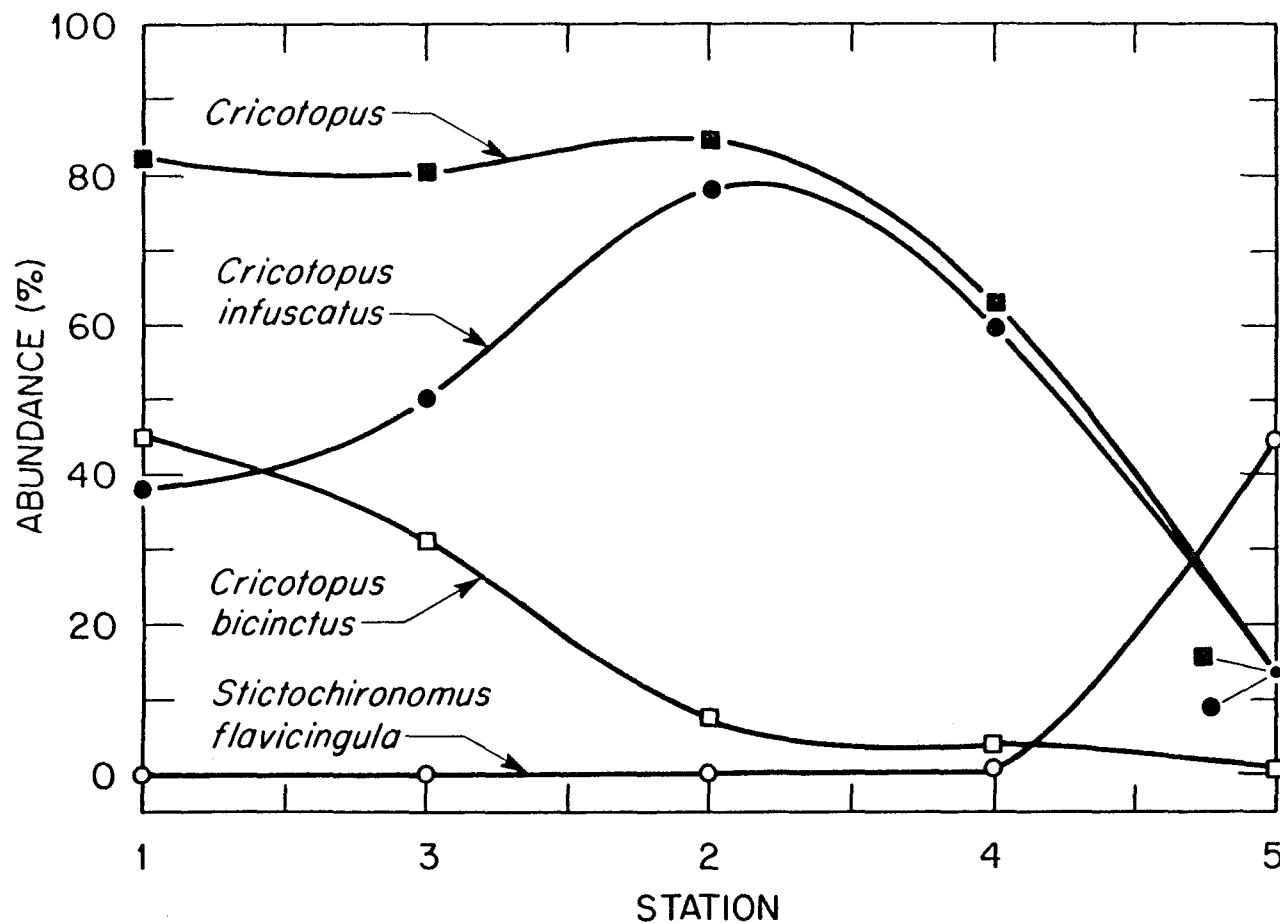


Figure III-2. Proportional abundances of the three dominant chironomid species plotted along a heavy-metal gradient. (See text for comment on station ordering.) Cricotopus refers to the combined abundances of C. infuscatus and C. bicinctus. Data were obtained from Winner et al. (1980).

few dominant species (i.e., evenness indexes, quantitative coefficients, and indicator-species approaches), it appears that the use of the generic-level could lead to serious biases. These approaches do not have the advantage of using many species that on the average may retain the general similarity pattern even after information is lost at random through the collapse to the generic-level. Because quantitative indexes are generally sensitive to a few dominant species, they require similar pollution tolerance characteristics of congeners to adequately represent species distribution patterns. These assumptions, at least for the response of congeneric chironomid species to heavy-metal pollution, are not supported.

The difference in conclusions for abundance and qualitative data may partially resolve the apparent disagreement in the literature regarding the adequacy of higher taxonomic levels. Studies using diversity indexes (Kaesler et al. 1978; Hellowell 1978) have indicated that the generic or family level may often be adequate while studies emphasizing indicator species, bioassay procedures and rare species detection (Resh and Unzicker 1975; Resh 1979) stress the need for species identification. Although diversity indexes may be influenced by dominant species, they also include the effect of numerous other species through the richness component, and thus may be better able to withstand information loss. As Resh (1979) notes, the use of higher taxonomic levels will probably result in an underestimation of species diversity; however,

this is unlikely to be a problem for studies which compare diversities with the same level of taxonomic resolution.

CHAPTER IV

PROCESS, PATTERN AND SCALE IN ROCKY INTERTIDAL COMMUNITIES:

A SIMULATION MODELING APPROACH

A. INTRODUCTION

Research in marine rocky intertidal habitats has led to a number of generalizations and conceptual models regarding community structuring mechanisms such as disturbance, competition and predation (e.g., Paine 1966, 1977; Connell 1972, 1975; Menge and Sutherland 1976; Lubchenco and Gaines 1981a). Recently, a number of these generalizations have been challenged by alternative hypotheses that emphasize, among other things, the importance of environmental stochasticity in structuring communities (e.g., Underwood and Denley 1984; Dayton 1979). Comparison of work in Australian and New England rocky intertidal communities provides an example of these different views of community structure. Studies in New England (Menge 1976; Lubchenco and Menge 1978) have had a deterministic emphasis, generally viewing stochastic variation as "noise," affecting the details but not altering the large-scale determination of pattern. Studies in Australia (Underwood et al. 1983; Underwood and Denley 1984) have emphasized recruitment variation, and other "stochastic" effects, indicating that these "details" may have long-term effects and create large-scale patterns resembling those resulting from factors such as competition and predation.

In this study, simulation models of Australian and New England communities are developed to supplement the field work and conceptual models pertaining to these views of community structure. Marine benthic models developed up to the present have included the patch dynamics model of Paine and Levin (1981), and barnacle population models by Roughgarden et al. (1984) and Wethey (1985). Some more general models, which are applicable to the sessile adults and highly dispersive propagules of many intertidal organisms, include those of Vance (1980), Yodzis (1978; in press) and Chesson and Warner (1981). These models have been excellent tools for providing hypotheses and exploring aspects of community dynamics, but have not been specific enough or included enough species and environmental variation to address the present questions.

The simulation models presented here are designed to investigate community structuring mechanisms in these two specific communities. The models are first tested against available anecdotal, experimental and descriptive information. Three factors are then investigated to determine their ability to account for the difference in importance of stochasticity perceived in the two communities:

1. differences in means and variances of predation and recruitment;
2. the existence of a size refuge from predation in Australia, but not New England;

3. the different mechanisms of competition exhibited by the primary barnacle competitors, large limpets in Australia and mussels in New England.

These factors are considered in the framework of a conceptual model of stochasticity as it relates to scale. Unexplained variation, seen as synonymous with stochasticity, is related to the nature of the system and its response to variation on different scales. This differs from other views of "stochastic" versus "deterministic" communities as simply a matter of abiotic versus biotic control (Sale 1977; 1984; Grossman 1982; Grossman et al. 1982).

B. COMMUNITY DESCRIPTIONS

Rocky intertidal communities are generally characterized by the dominant sessile species that occupy the rock substrata. The dominant species usually vary with vertical height on the shore, which is determined by submersion time. Differences in wave exposure, determined by geographic features and the orientation of the shore line, provide an important ecological gradient. Predator activity and abundance tend to decline with increasing wave exposure, thus adding another factor to the gradient. Space for attachment is the major limiting resource for sessile species such as barnacles and mussels. Algae are most abundant in the low zone and places protected from the waves. Slow moving consumers are important throughout the community and may include predatory and grazing snails, limpets and starfish.

This study will consider mid-intertidal zone (1.8 to 0.6 m above mean low water) barnacle communities in New South Wales, Australia, and Maine and Massachusetts in New England, U.S.A. The community in New England is relatively species-poor, possibly due to the harsh climatic conditions (Menge and Sutherland 1976). The primary species in the mid-intertidal zone areas of moderate to high wave exposure being modeled are the barnacle, Balanus balanoides, the mussel Mytilus edulis, and the predatory snail Thais lapillus. Mussels are able to overgrow barnacles and *Thais* consumes both mussels and barnacles. Furoid algae is important in protected areas and its effects are included in one of the model tests.

The Australian community is in New South Wales, in a warm temperate climate, and includes considerably more species than the New England community (Underwood et al. 1983). There are several species of barnacles and numerous grazing snails and limpets. Once again, only the three species considered most important for determining the distribution of barnacles will be included. Barnacles, in this model, may be viewed as a guild of barnacle species, since the barnacle species' interactions with limpets and predators are generally similar. The primary barnacle species is considered to be Tessieropora rosea and the primary predator is the gastropod Morula marginalba. High densities of the large limpet Cellana tramoserica result in the accidental crushing or dislodging of newly settled barnacles, known as "bulldozing". Established barnacles prevent Cellana grazing, thus making preemption mutual. Other interactions complicate the situation in both communities and

may contribute to the different views of community structure but model investigations of these will be reserved for later model experiments.

C. MODEL DESCRIPTIONS

A simulation model, named RITS for Rocky Intertidal Simulation, was developed for use in this study. For the New England version of the model, NE is appended to the acronym, to form RITSNE, while for the Australian community AT is added to form RITSAT. The models use sets of difference equations to which random variation and seasonal patterns are added. They are designed to portray patterns resulting from many stochastic and deterministic biotic and abiotic constraints, including only as much mechanistic detail as is considered necessary for dynamics at the scales of interest.

The models are designed to incorporate effects operating on very different scales. The basic modeling units are individual spatial cells on the order of a square meter. The processes affecting organism abundances on a local level such as this, range from the immediate conditions of current abundances and local topography, to large-scale oceanographic conditions determining such things as wave exposure and the abundance of propagules. This model divides the effects on each spatial cell into components determined by local abundance, and effects caused by external, larger scale factors. Local influences include the dependence of growth on the current barnacle or mussel cover, and the influence of the availability of free space on various processes. Large-scale

influences include barnacle and mussel recruitment rates, which are unaffected by local abundances due to high dispersal. The effects of mobile organisms, such as predators and limpets are also primarily determined by factors occurring over areas much larger than the basic spatial unit.

The patterns stemming from these processes may also be examined on several scales. The local level of an individual spatial cell has already been mentioned. An intermediate level may be generated that is represented by the mean and variance of an aggregate of spatial cells. Thus the manner in which variability in processes is translated into variability in pattern can be investigated. On a large scale, different aggregates representing different sites can be compared to look at large-scale differences.

1. The New England Model (RITSNE)

The species modeled were chosen specifically for their importance in the community and their direct relation to the community structuring mechanisms to be investigated. The equations used for this model are presented in Table IV-1. Processes are considered in terms of their effect on barnacle abundance. Therefore, the core of the model is the equation for the increase in barnacle cover (equation 1). For studying the scales of interest, it was not considered necessary to keep track of individual barnacles and the growth and thinning process. Thus all variables are expressed in terms of percent cover. The increment in barnacle cover from one time step to the next is the sum of barnacle

Table IV-1. Model equations for New England version (RITSNE).

Process	Equations	Parameter definitions
Barnacle recruitment and growth	$(1) \quad B(i,j)^1 = B(i,j-1) + F_B(i,j) \cdot [R_B(i,j) + G_B \{B(i,j-1) - B_A(i,j-1)\}] - P(i,j) - C_m(i,j)$ $(2)' \quad B_A(i,j) = B(i-1,m), \text{ when } j = 1$ $B_A(i,j) = B_A(i,j-1) - P(i,j)[B_A(i,j)/B(i,j)], \text{ when } j > 1$	i = years, 1...n j = seasons, 1...m $B(i,j)$ = barnacle percent cover $B_A(i,j)$ = adult barnacle percent cover $F_B(i,j)$ = proportion of space free of mussels and barnacles $R_B(i,j)$ = barnacle recruitment increment G_B = barnacle growth rate $P(i,j)$ = predation loss $C_M(i,j)$ = loss due to mussel competition
Mussel recruitment, growth and competitive effect	$(3) \quad M(i,j)^1 = M(i,j-1) + F_M(i,j-1) \cdot [R_M(i,j) + G_M M(i,j-1)] - P(i,j)$ $(4) \quad C_M(i,j) = [M(i,j) - M(i,j-1)] \cdot [B(i,j)/100 F_M]$	$M(i,j)$ = mussel percent cover $F_M(i,j)$ = proportion of space free of mussels $R_M(i,j)$ = mussel recruitment increment G_M = mussel growth rate
Free space dynamics	$(5) \quad F_B(i,j) = [100 - M(i,j) - B(i,j)]/100$ $(6) \quad F_M(i,j) = [100 - M(i,j)]/100$	
Seasonal and stochastic effects on recruitment and predation	$(7) \quad R_B(i,j) = r_B S_B(j) + \epsilon_1$ $(8) \quad R_M(i,j) = r_M S_M(j) + \epsilon_2$ $(9) \quad P(i,j) = p S_p(j) + \epsilon_3$	r_B = barnacle recruitment rate r_M = mussel recruitment rate p = predation rate $S_B(j)$ = barnacle recruitment seasonal pattern $S_M(j)$ = mussel recruitment seasonal pattern $S_p(j)$ = predation loss seasonal pattern $P(i,j)$ = net predation loss $\epsilon_1, \epsilon_2, \epsilon_3$ = random components, chosen from a normal distribution with variance S^2
Wave disturbance	$(10) \quad \text{If } U < W(j) \text{ then } M(i,j) = 0 \text{ and } B(i,j) = 0, \text{ superceding other equations}$	$W(j)$ = probability of wave disturbance U = number chosen from random uniform distribution

¹When $j = 1$, $B(i,j) = B(i-1,m)$, and $M(i,j) = M(i-1,m)$

recruitment and growth, multiplied by the proportion of free space available. Predation and competition losses are also subtracted at each iteration.

Adult barnacles are those assumed to have approached their maximum size and thus these must be subtracted from the total barnacle cover used in the growth increment. Adult barnacle cover at the beginning of a year equals the total barnacle cover present at the end of the previous year's growing season (equation 2). This adult barnacle cover value is then decremented during the course of the year by predation losses.

The mussel equation is similar in form to the barnacle equation, with a few differences (equation 3). Because barnacles do not retard the growth and settlement of mussels, barnacle-occupied space is included in the free space term (equation 6). In fact, barnacles facilitate mussel attachment; a minimum of 10% barnacle and/or mussel cover is assumed to be a prerequisite for mussel settlement. Since this mussel species (Mytilus edulis) continues to grow for at least 8 to 10 years (though it rarely lives that long in this environment), there is no growth adjustment based on age. Mussels are unaffected by interspecific competition, thus no competition term is included. The magnitude of the barnacle loss due to mussel competition is simply the amount of the mussel increment, adjusted for the proportion of the space occupied by barnacles (equation 4).

The parameters in the model that respond to large-scale factors (barnacle and mussel recruitment and predation loss--equations 7-9)

may be decomposed into three components: a constant rate, a seasonal component and a stochastic component chosen from a random normal distribution with variance s^2 . In some model runs, the random components are set to zero and the model becomes completely deterministic (except for wave disturbance). In other runs, there is random variation between time steps and spatial cells. In one experiment, a between-year component is added to the random variation, by choosing yearly means from a random normal distribution.

A seasonal pattern of wave disturbance probabilities is also assigned to a model run. A random number generator is used to generate random uniform numbers that determine whether a wave disturbance has occurred (equation 10). A wave disturbance event is simulated by setting barnacle and mussel cover values to 0%, superceding all other calculations at this iteration.

2. The Australian Model (RITSAT)

The barnacle equation in the Australian model (Table IV-2) is basically the same as in the New England model. The primary difference is that barnacles in the Australian version are affected by preemptive competition by limpet "bulldozing" rather than by mussel overgrowth, as in New England. Thus, in Australia, the competition loss occurs as a subtraction of a proportion of the incoming recruits crushed or dislodged by limpets rather than a subtraction from the total cover of adults and juveniles.

Table IV-2. Model equations for Australian version (RITSAT).

Process	Equations	Parameter definitions ¹
Barnacle recruitment and growth	(11) $B(i,j)^2 = B(i,j-1) + F_B(i,j-1) \cdot [R_B(i,j) - C_L R_B(i,j) + G_B(B(i,j-1) - B_A(i,j-1))] - P(i,j)$ (12) $B_A(i,j) = B(i-1,m)$, when $j = 1$ $B_A(i,j) = B_A(i,j-1)$, when $j > 1$	$C_L(i,j)$ = proportional loss due to limpet competition $F_B(i,j)$ = proportion of space free of barnacles
Limpet dynamics and competitive effect	(13) $N(i,j) = L(i,j) \cdot [\lambda_0 + \lambda_1 B(i,j)]$, $0.0 \leq N(i,j) \leq 11$ (14) $Y(i,j) = \alpha_0 + \alpha_1 R_B(i,j) F_B(i,j)$ (15) $C_L = [1/Y(i,j)] \cdot N(i,j) F_B(i,j)$, $0.0 \leq C_L \leq 1.0$ (16) $L(i,j) = L + \epsilon_4$	$N(i,j)$ = effective number of limpets $L(i,j)$ = limpet population level $Y(i,j)$ = barnacle recruitment rate adjustment L = limpet population level effect $\lambda_0 = 11$ $\lambda_1 = -0.18$ $\alpha_0 = 1.0$ $\alpha_1 = 0.5$
Free space dynamics	(17) $F_B(i,j) = [100 - B(i,j)]/100$	
Size refuge from predation (additional restriction)	(18) $P(i,j) \leq B(i,j) - B_A(i,j)$	

¹All variables not defined here are the same as defined in Table IV-1.²When $j=1$, $B(i,j)=(i-1,m)$

If a size refuge from predation is included, the cover of adult barnacles is also calculated as before, except that there is no predation loss, since adults are considered to be too large to be preyed upon (equations 12). In addition, the predation loss from the total barnacle cover is constrained so that it does not exceed the cover of juvenile barnacles (equation 18). Little has been published on what sizes must be achieved, or whether the refuge is independent of predation density and other details that would add realism to the model. The assumption used here--immunity from predation after one year--would probably be equivalent to the maximum effect of a size refuge. The requirement that barnacles attain a minimum size before being preyed on (see Denley and Underwood 1979) is not included since its effect is likely to be transient.

The major difference between the Australian and New England communities is the importance of the limpet-barnacle interaction in the Australia community. The interaction is presented in terms of three features of the interaction. These three features will become particularly important for the model experiments to be presented later.

a. Asymmetrical reciprocal preemption. Because the large limpet Cellana requires free space for grazing, the potential number of limpets for each cell is negatively related to barnacle cover (equation 13). This potential number is multiplied by $L(i,j)$, the population level of limpets on a larger, regional scale. Limpets

are mobile enough that the number of limpets in a cell is not considered dependent on the numbers present at the previous time step.

Limpets also have a preemptive effect on incoming barnacle recruits. This competitive effect is directly related to limpet density (equation 15). The barnacle-limpet competitive interaction is asymmetrical because limpets only affect the rate of successful recruitment of barnacles, and not the increase in cover due to the growth of established barnacles. Barnacles, however, affect all adult limpets.

b. Limpet-barnacle spatial positive feedback. The relation between limpet numbers and barnacle cover (equation 13) is related to the limpet's requirement for adequate contiguous free space. Underwood et al. (1983) noted that the scale of barnacle heterogeneity was important in determining how much space limpets could keep clear. If the available free space was dispersed into many small gaps, limpet movement and ability to graze was greatly hampered. Our model does not explicitly consider different barnacle dispersion patterns, however an assumption of moderate patchiness and its influence on effective limpet numbers is included in equation 13. This effect is included by choosing a slope (λ_1) of -0.18 that results in the effective number of limpets reaching 0 at approximately 67% barnacle cover. The actual number of limpets would probably be greater than 0, but their ability to graze a significant portion of the free space would be negligible because of

the obstructions created by established barnacles. It is the number of limpets effectively "bulldozing" that are of interest, rather than the actual number in the area. The present model uses an index to reflect this effective limpet number until it can be better quantified. A positive feedback results because increases in barnacle cover reduce the effective limpet number (equation 13), which then increases the rate of successful barnacle recruitment even further by reducing the competitive effect (equation 15).

c. Threshold in limpet effect. This threshold occurs when the limpets reach a density at which their competitive effect on barnacles reaches 1.0 and thus limpets succeed in removing all settling barnacles (equation 13). An alternative would be a curve that only approaches 1.0 asymptotically. However, for relatively small areas, limpets can reach levels at which no barnacles survive, making the threshold model appropriate (B. A. Menge, Oregon State University, Corvallis, Oregon, pers. comm.). The point at which the threshold occurs also depends on the slope of the competitive effect equation $[1/Y(i,j)]$, which is a function of barnacle recruitment (equation 14). As the barnacle recruitment rate, and thus $Y(i,j)$, increases, the proportion of barnacles removed by limpets decreases.

Model parameters such as the regression coefficients in the limpet equations, and the seasonal predation and recruitment patterns were given rough estimates that were consistent with empirical work. Considering the high variability these values are likely to show in the field, the paucity of the type of data needed,

and the general nature of the trends of interest here, this is probably justifiable. Future work will include more extensive parameter estimation and sensitivity analyses.

D. MODEL TESTING

1. New England

Data were obtained for the mid-intertidal at 6 locations along a wave exposure gradient (see Menge 1976 for detailed descriptions of sites and field methods). Three sites, an exposed, intermediate, and protected site, were used to test the model. In each case, model results for individual cells were tested for consistency with results of field experiments. Data from the field experiments were then used to obtain means and variances of parameters for a multi-cell model run that was compared to field transect means. This latter test is on a larger scale and involves data that are independent of the data used to construct the model.

a. Wave-exposed site. The model was first tested against experimental and transect data for Pemaquid Point, a site with relatively high exposure to wave disturbance. Storms, occurring primarily in the winter, remove patches of barnacles and mussels. Field experiments showed that predation has little effect in this area (Menge 1976).

The model results were first compared to a 100 cm^2 field experiment control (Fig. IV-1). The barnacle and mussel settlement parameters were estimated from the increase in cover in the

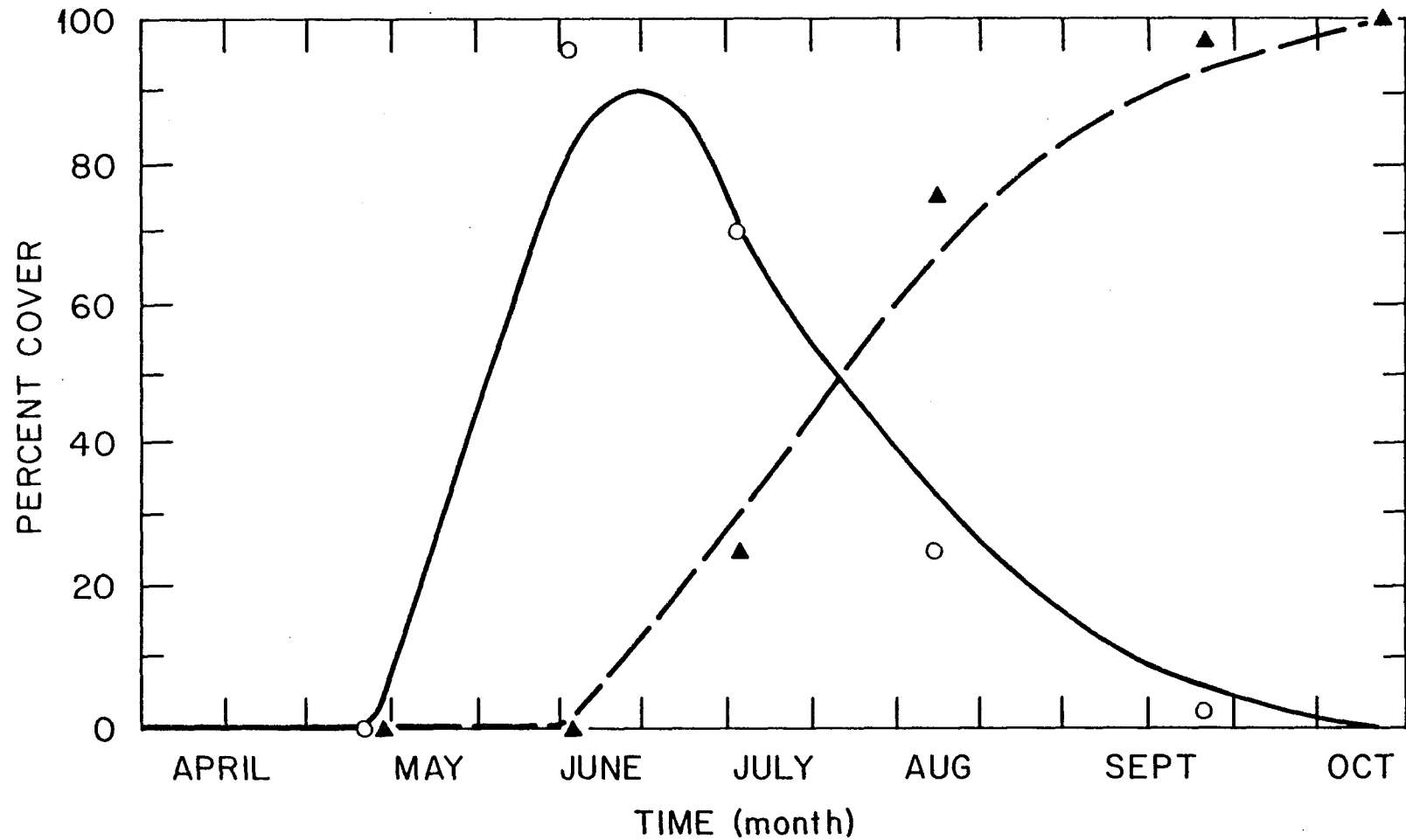


Figure IV-1. New England model results compared to data from field experimental control at Pemaquid Point, Maine. The data are from Menge (1976). (Solid line = model results for barnacles; dashed line = model results for mussels; o = field data for barnacles; ▲ = field data for mussels.)

experimental plot during the first two weeks of settlement. The model was able to reproduce the dynamics to reasonable approximation during the rest of the year, based on the initial estimates.

The model was tested on a larger scale against an independent estimate of mussel and barnacle density from transects taken in the experimental area. The mean and variance of the barnacle and mussel settlement rates were calculated from their initial increases in appropriate exclusion experiments. The cells in this multi-cell model run were initialized at barnacle and mussel covers of 10% and 75%, respectively, since mussels took a few years to "equilibrate". The wave disturbance probability was assumed to be equal to the wave exposure index calculated by Menge (1976). These values were calculated from the numbers of experimental cages removed in storms. The extent of agreement of model results based on these values, with the field transect data, will test the assumption that cage loss probabilities adequately estimate the probability of sessile organism removal.

The model and field results were compared over a four year period (Fig. IV-2). Percent cover data were transformed using the arcsin transformation (Draper and Smith 1981) and the means and confidence intervals were plotted. The field data are linked by dashed lines and each data point represents a different transect in the same area; thus temporal differences include spatial variation as well. The dashed line merely connects the data points and it should not be interpreted as representing the dynamics during these periods. It should also be noted that the model results for

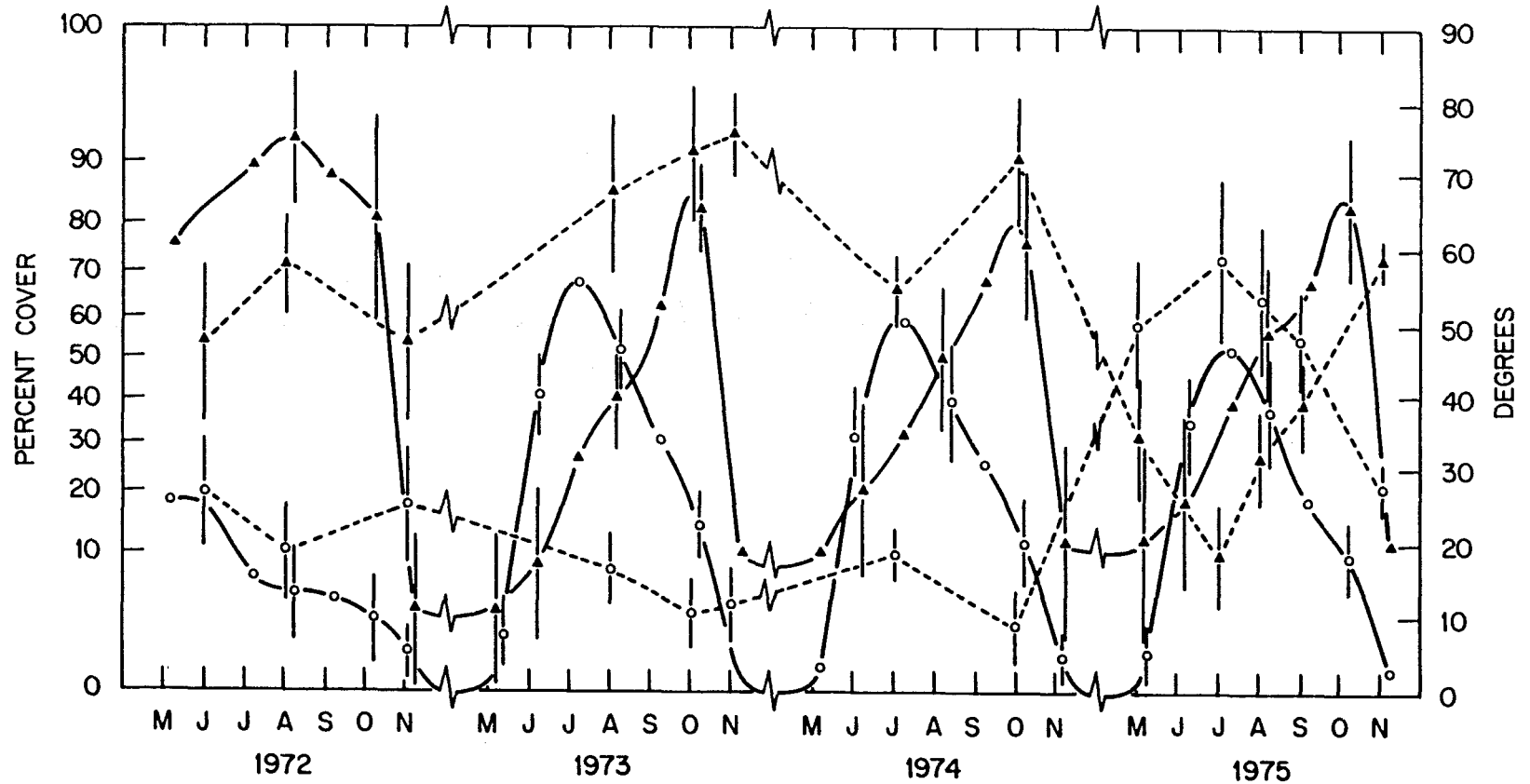


Figure IV-2. Means and confidence intervals for model results and field transect data for Pemaquid Point, Maine, for wave disturbance probabilities based on cage loss rates. Confidence intervals are based on transformed data (arcsin transformation) and values are shown plotted against percent cover and degrees (units of transformed data). The data are from Menge (1976). (Solid lines = model results; dashed lines = field transect data; ▲ = mussels, o = barnacles.)

November actually represent the winter low in cover value due to wave disturbance.

When the wave disturbance level was set to equal the cage loss rate, the simulated mussel and barnacle levels exhibited lower overall mussel levels and greater seasonality than the field data for the first three years, but showed reasonably good agreement during the fourth year (Fig. IV-2). A reduced wave disturbance probability level ($0.25 \times$ cage loss rate) produces closer agreement with the data over the first three years, but diverges during the fourth year (Fig. IV-3). The degree of model fit, measured by the proportion of field data points for which field and model confidence intervals overlap, shows a similar pattern (Table IV-3). The better fit of the reduced disturbance rate model for 3 of 4 years suggests that on the average, cage loss probabilities overestimate organism removal rates. The year-to-year variation in the field data indicates that the additional pattern of year-to-year variation in disturbance rate is required in order for the model to successfully produce large-scale barnacle and mussel patterns based on experimental data.

b. Intermediate wave exposure site. The area used to represent intermediate wave exposure is Little Brewster Cove. In this area, predation is frequently found to be an important influence (Menge 1976).

Model results were first compared to the results of a predator exclusion experiment, using barnacle and mussel settlement rates

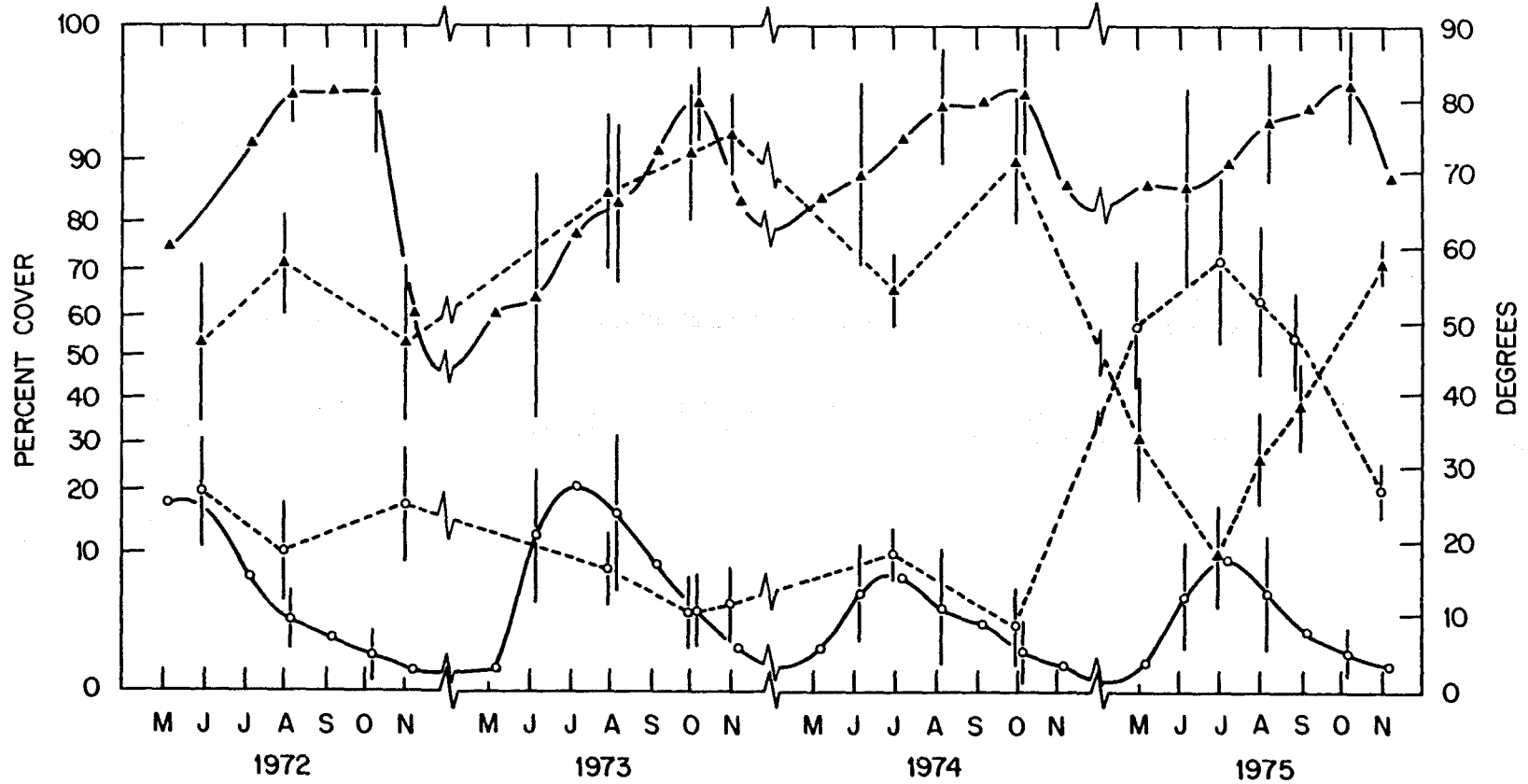


Figure IV-3. Means and confidence intervals for model results and field transect data for Pemaquid Point, Maine, for wave disturbance probabilities based on $0.25 \times$ cage loss rates. Confidence intervals are based on transformed data (arcsin transformation) and values are shown plotted against percent cover and degrees (units of transformed data). The data are from Menge (1976). (Solid lines = model results; dashed lines = field transect data; ▲ = mussels, o = barnacles.)

Table IV-3. Degree of agreement between model results and field transect data.¹

	Wave-exposed Site (Pemaquid Point ²)		Intermediate Wave Exposure Site (Little Brewster Cove)		Wave-protected Site (Nahant)			
	High Disturbance Simulation 1972-1974	Low Disturbance Simulation 1975	Low Disturbance Simulation 1972-1974	1975	1973-1974	1975	Simulation Without Furoid algae 1973-1974	Simulation With Furoid Algae 1973-1974
Barnacles	0.38	0.40	0.88	0.0	0.67	0.0	0.13	0.63
Mussels	0.50	0.80	0.63	0.0	0.33	0.0	0.63	0.50
Barnacles and Mussels	0.44	0.60	0.75	0.0	0.50	0.0	0.38	0.56

¹Proportion of field transect data points for which confidence intervals overlap the confidence intervals of the simulation results.

²See Menge (1976) for site descriptions.

based on their initial increase, as before. The model showed reasonably good agreement with the data for the predator exclusion experiment (Fig. IV-4). The model results were then compared to the results of the field experiment control plot, to which predators had access. Predation was added to the model to determine what level of predation, if any, could account for the difference between results for the predator exclusion and control. A loss rate of 14% cover was found to produce good agreement (Fig. IV-5).

A similar procedure was used in three other cases to obtain estimates of predation loss in the area. In two of these cases, mussels were overestimated by the model at all levels of predation. This may be due to an underestimation of mussel predation by the model, which considers barnacle and mussel predation loss as equal. Another possibility is an underestimation of the density-dependent component of mussel increase as a result of growth and/or a settlement aggregation effect. If the majority of mussel cover increase is due to a density-dependent component, then the increase rate will be low at very low covers, and may be more easily controlled by predation. Since mussel settlement begins after predators have become active, they may not have a chance to establish enough cover for the density-dependent effects to become important.

The ability of the model to simulate empirical data in some cases and not others may indicate the existence of spatial variability in the parameters and/or processes. Rather than adjust the model to fit these divergent results, the present simulations

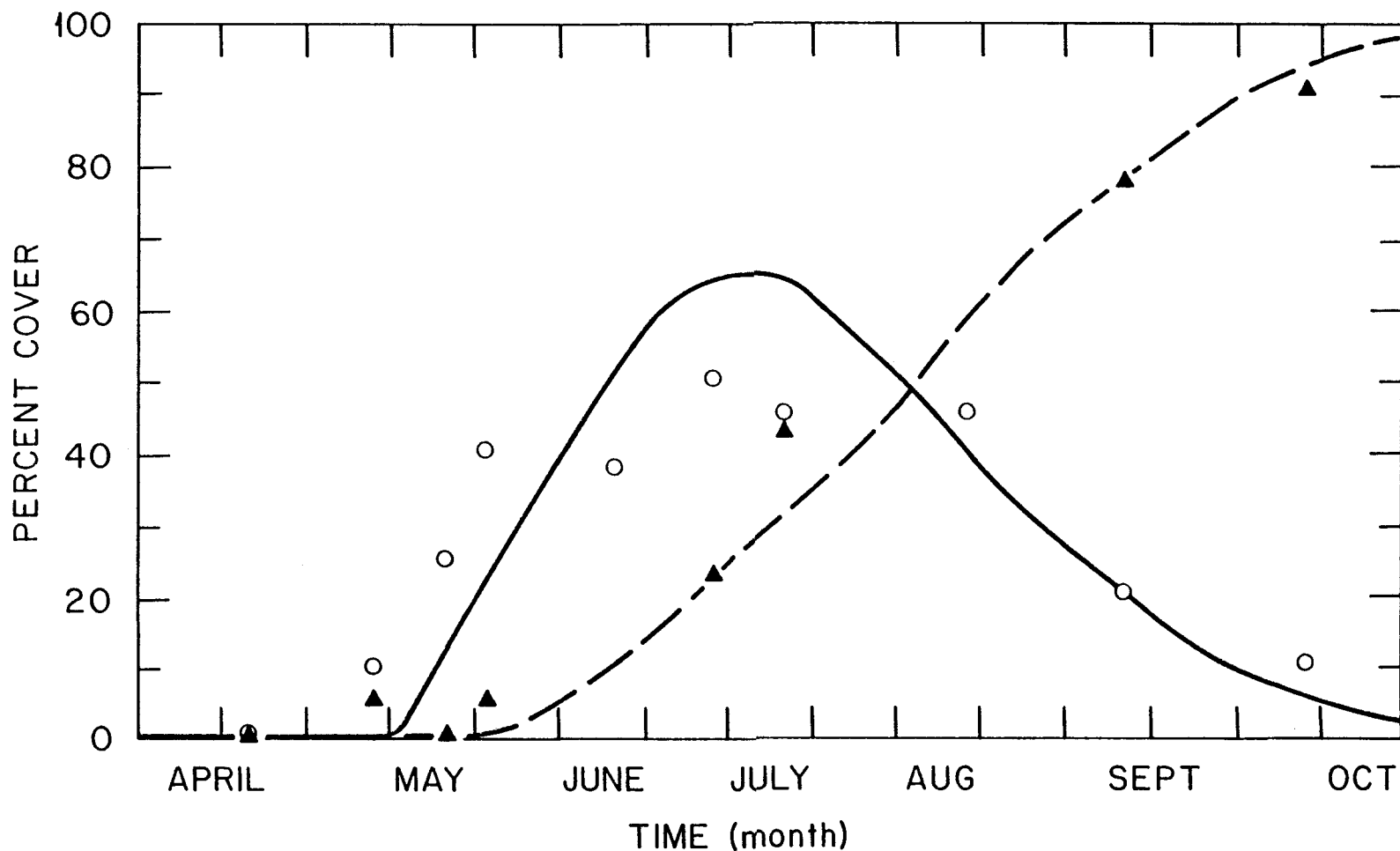


Figure IV-4. New England model results compared to data from predator exclusion field experiment at Little Brewster Cove, Massachusetts. The data are from Menge (1976). (Solid line = model results for barnacles; dashed line = model results for mussels; o = field data for barnacles; ▲ = field data for mussels.)

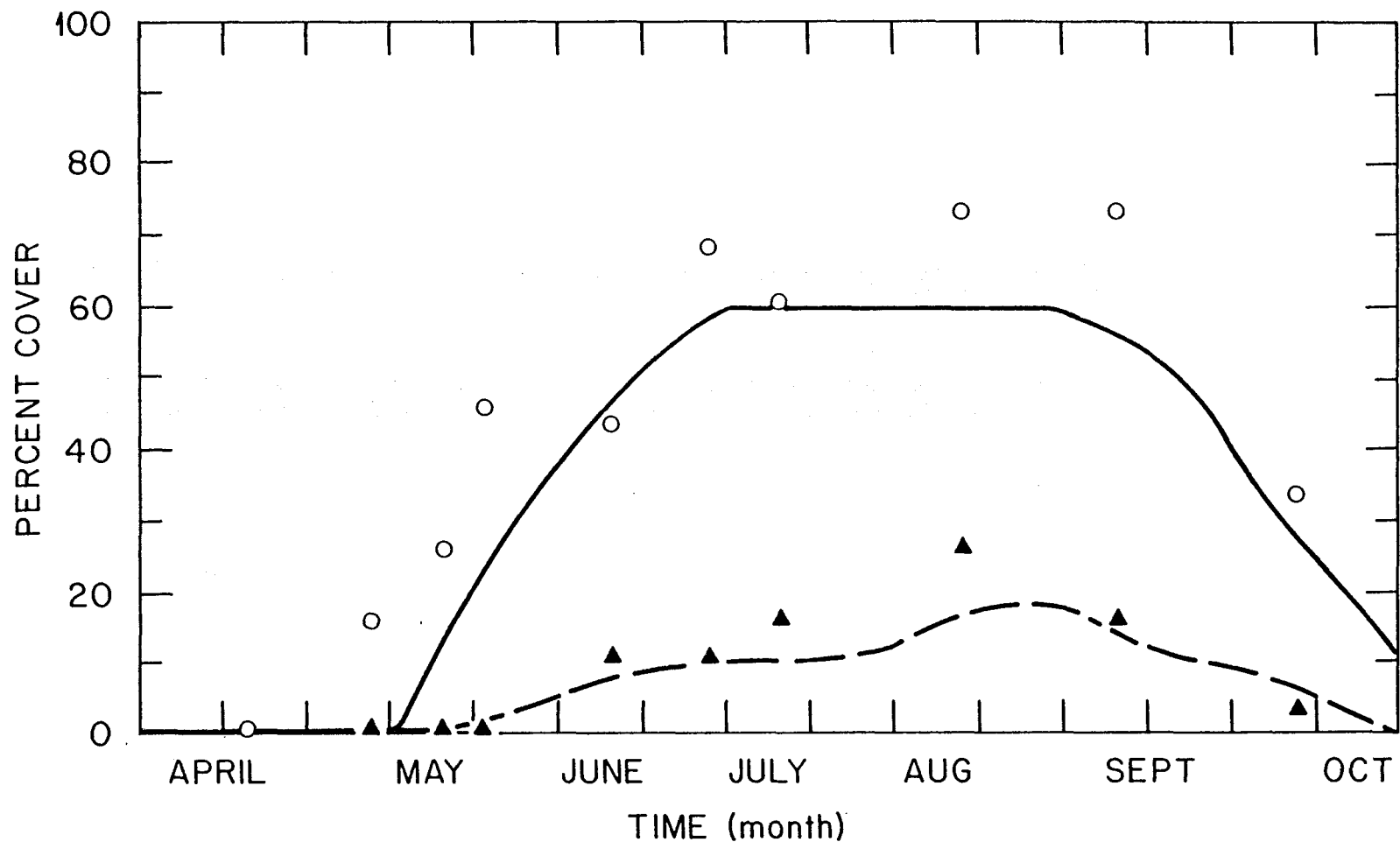


Figure IV-5. New England model results compared to data from field experiment control at Little Brewster Cove, Massachusetts. The data are from Menge (1976). (Solid line = model results for barnacles; dashed line = model results for mussels; o = field data for barnacles; Δ = field data for mussels.)

disregard mussels in order to obtain barnacle predation rates from these three field experiments.

The model was then run with the parameter means and variances derived from the field experiments. Barnacle and mussel rates were obtained from the appropriate exclusion experiments, and predation rates were obtained from the procedure just discussed. The simulated barnacle and mussel means of 25 spatial cells were in a similar range as the field transect means in the first two years (Fig. IV-6). The model results showed a gradual increase in mussel cover, which resulted in an overestimation of mussel levels by the model in later years. This indicates that the underestimation of the effect of predation on mussels by the model was not limited to the three field experiments described above, but extended to the larger scale. Some of the divergence between model and field results may also be accounted for by the use of predation levels based on experiments from 1973, for which predation losses were unusually low (Menge 1976). This would account for the better model fit in 1973 (Table IV-3).

c. Wave-protected site. Canoe Beach Cove is used as a representative of a site protected from heavy wave exposure. Predation has been observed to be an important influence in this area (Menge 1976).

The model results for this area were first compared to the predator exclusion experiment results and found to give a reasonably good fit (Fig. IV-7). A predation level of 20% cover was found to

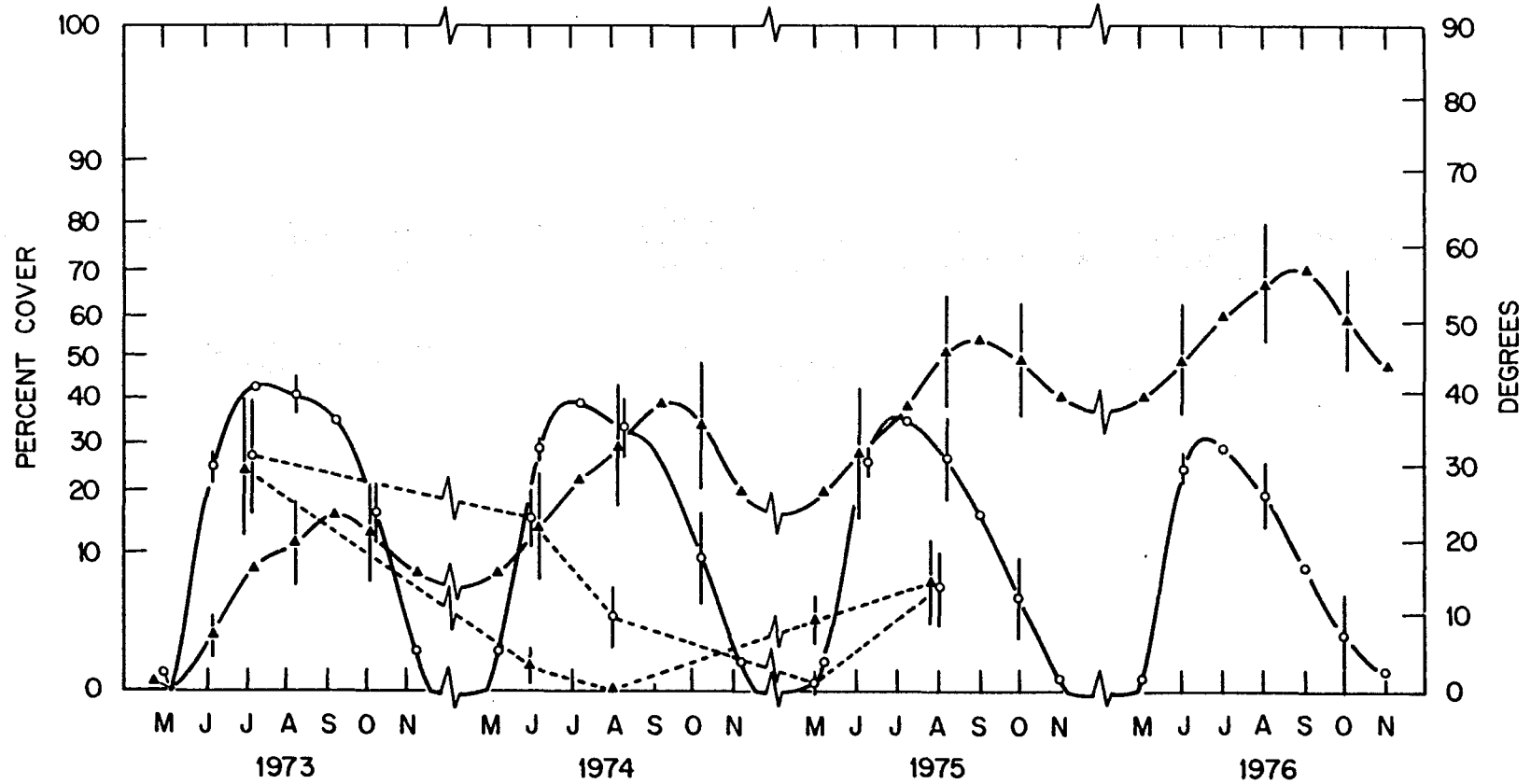


Figure IV-6. Means and confidence intervals for model results and field transect data for Little Brewster Cove, Massachusetts. Confidence intervals are based on transformed data (arcsin transformation) and values are shown plotted against percent cover and degrees (units of transformed data). The data are from Menge (1976). (Solid lines = model results; dashed lines = field transect data; ▲ = mussels, o = barnacles.)

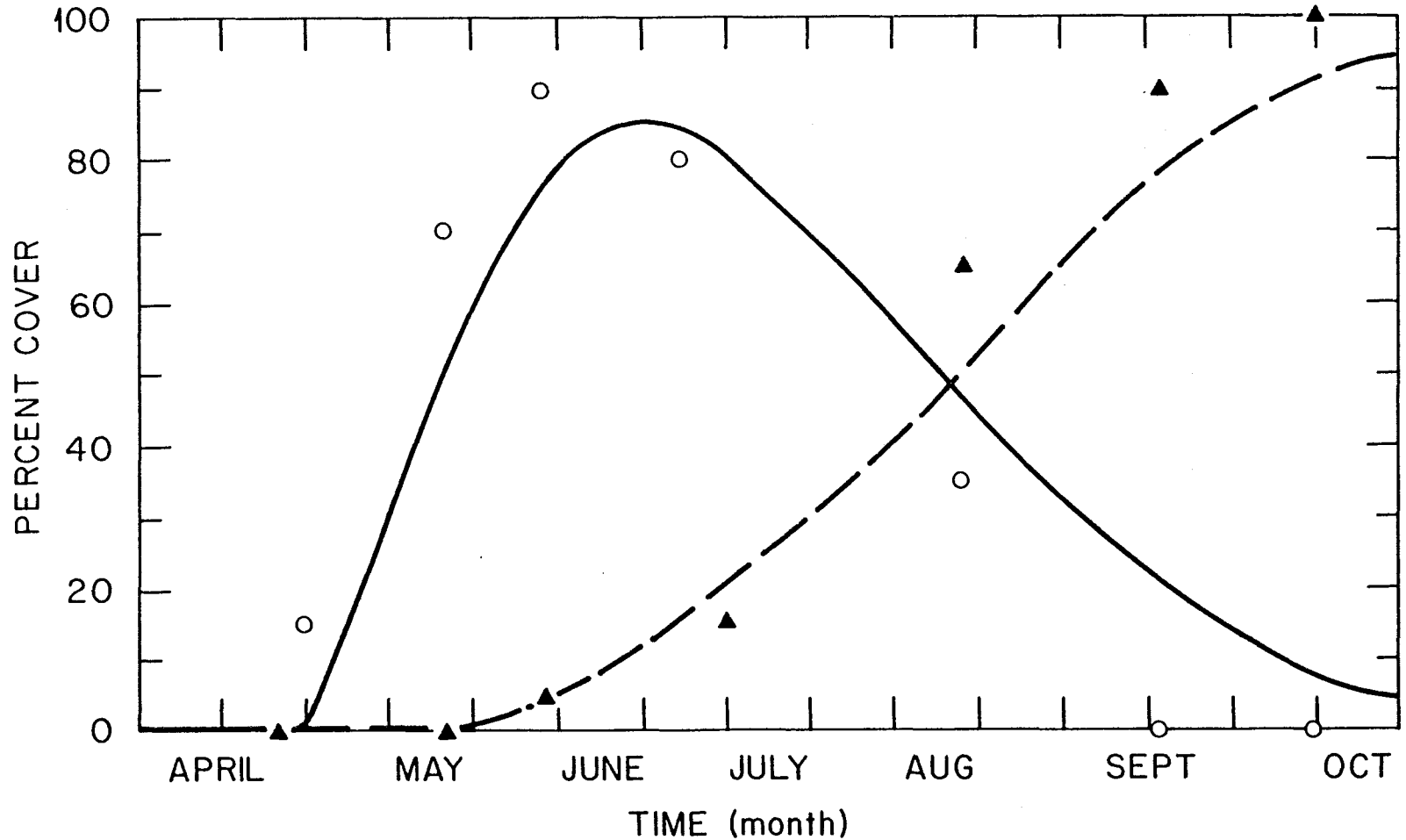


Figure IV-7. New England model results compared to data from predator exclusion field experiment at Canoe Beach Cove, Nahant, Massachusetts. The data are from Menge (1976). (Solid line = model results for barnacles; dashed line = model results for mussels; o = field data for barnacles; ▲ = field data for mussels.)

adequately model the pattern in the control (Fig. IV-8). Similar procedures were used to obtain predation levels in three other cases. As before, these values were used as rough estimates of predation means and standard deviations for the multi-cell model runs, along with the barnacle means and standard deviations calculated from the field experimental results.

The multi-cell model results showed greater seasonal barnacle increases than were exhibited by the data (Fig. IV-9). The lower seasonality observed in the field may be accounted for by the dense canopy of furoid algae that becomes increasingly abundant as wave exposure declines. Furoid algae tend to reduce the ability of juvenile barnacles to survive, through the "whiplash" effect of their fronds sweeping the rock surface. Furoid algae reduce the effective barnacle recruitment rate and thus the seasonal variation. To illustrate the effect of the algal canopy, the model was run using barnacle recruitment rates calculated from experiments affected by furoid algae. Mussel and predation rates could not be obtained from the experiments and were set at what were considered to be reasonable values. Overlap between model and field confidence limits is improved by a closer fit to barnacle dynamics (Table IV-3); however, barnacles still show more seasonal variation in the model output (Fig. IV-10).

It should be noted that predation levels at the different sites are not strictly comparable because different seasonal patterns were used. Whether predation is heaviest early or late in the year may affect the average cover as well as the seasonal pattern.

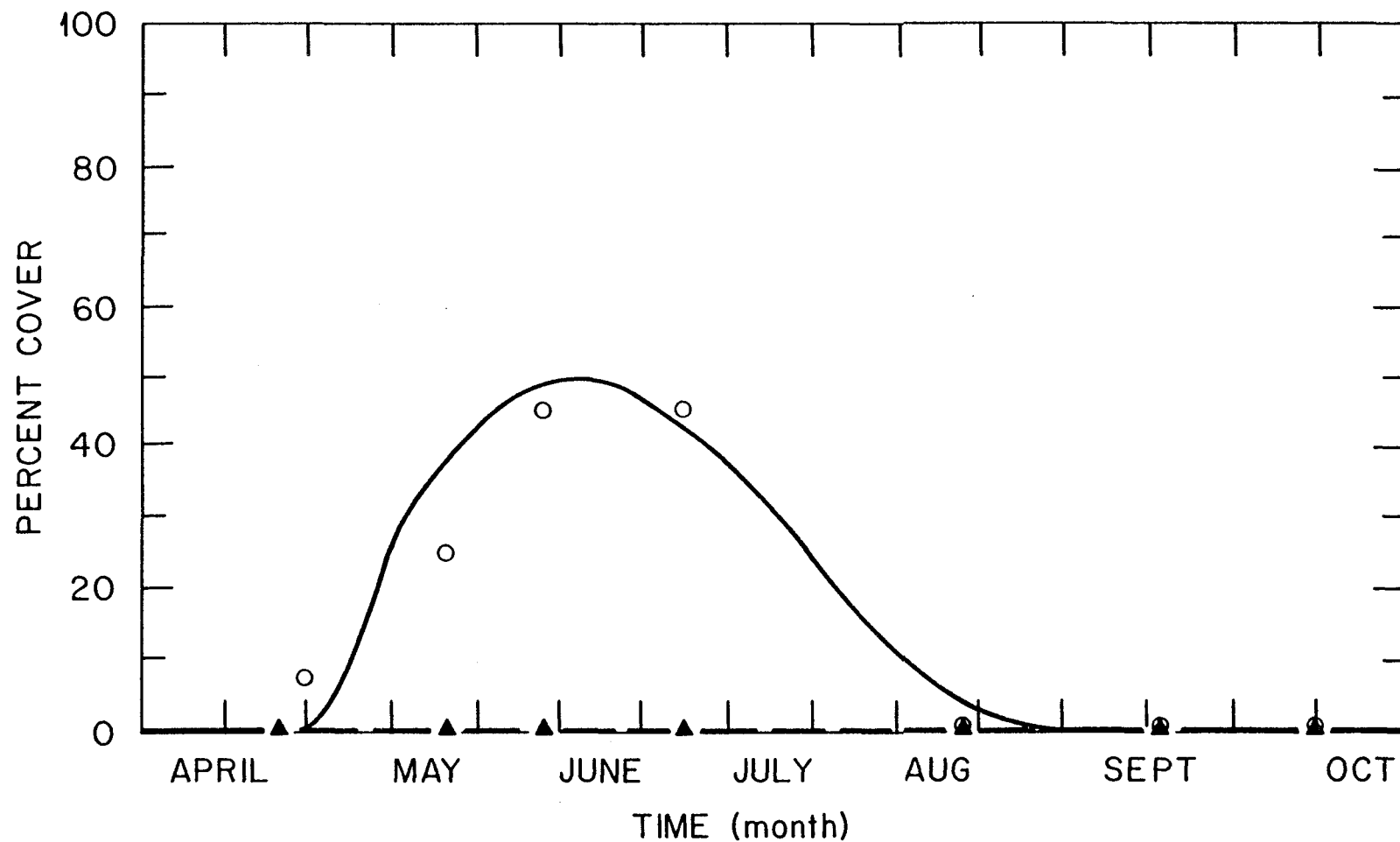


Figure IV-8. New England model results compared to data from field experiment control at Canoe Beach Cove, Nahant, Massachusetts. The data are from Menge (1976). (Solid line = model results for barnacles; dashed line = model results for mussels; o = field data for barnacles; ▲ = field data for mussels.)

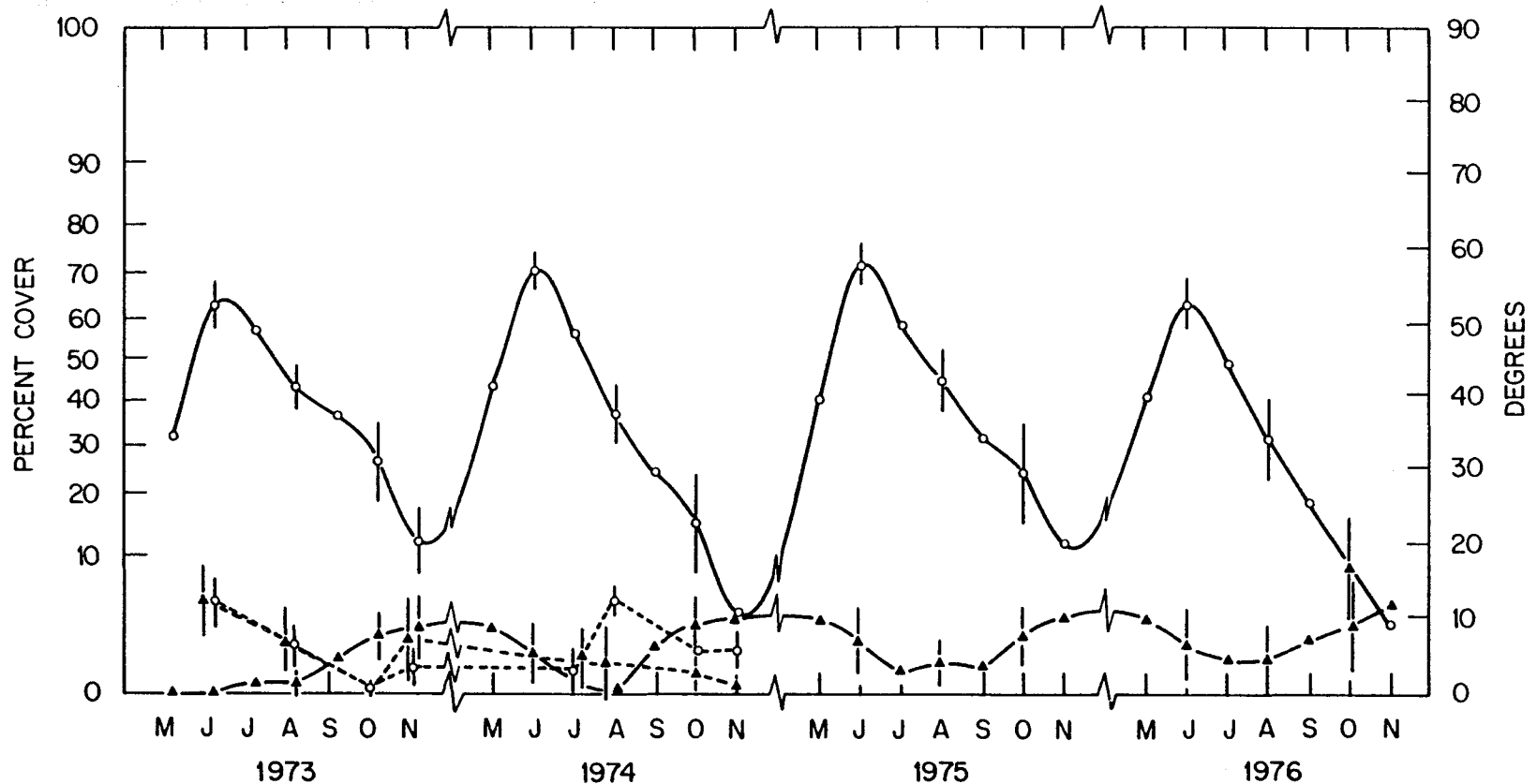


Figure IV-9. Means and confidence intervals for model results and field transect data for Canoe Beach Cove, Nahant, Massachusetts. Confidence intervals are based on transformed data (arcsin transformation) and values are shown plotted against percent cover and degrees (units of transformation). The data are from Menge (1976). (Solid lines = model results; dashed lines = field transect data; $\blacktriangle$ = mussels, $\circ$ = barnacles.)

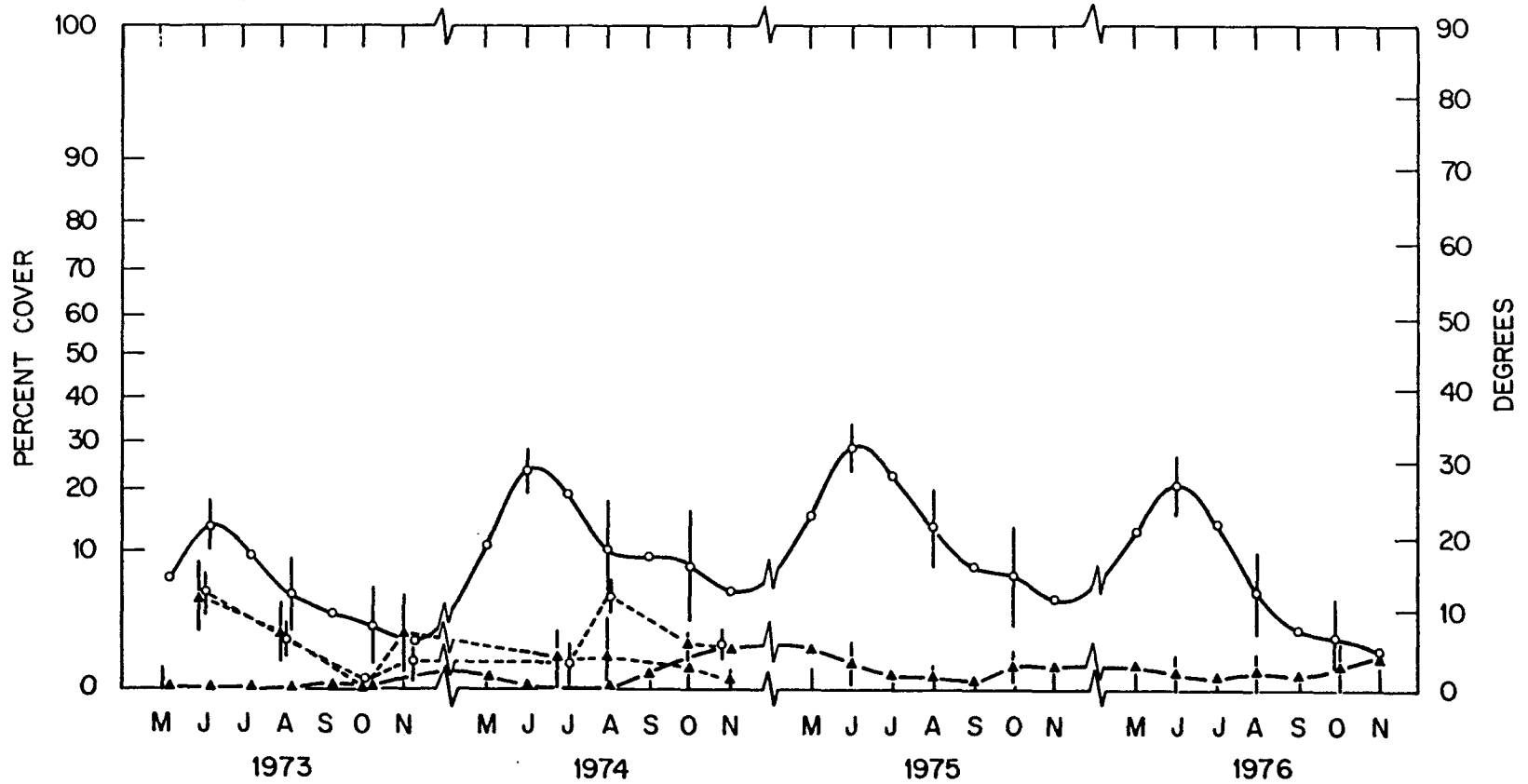


Figure IV-10. Means and confidence intervals for model results and field transect data for Canoe Beach Cove, Nahant, Massachusetts with the effects of furoid algae included. Confidence intervals are based on transformed data (arcsin transformation) and values are shown plotted against percent cover and degrees (units of transformed data). The data are from Menge (1976). (Solid lines = model results; dashed lines = field transect data; $\blacktriangle$ = mussels, $\circ$ = barnacles.)

Parameter estimates, particularly for mussels and predators at the two less exposed sites, are based on very small sample sizes. Hence they can only be considered as very rough estimates that require further refinement. Thus some of the departures from the field data might be corrected by better parameter estimation. In addition, the multi-cell model runs use random variation, rather than a sequence of values designed to correspond to particular years, which vary considerably. Despite these difficulties, the ability of the model to produce the dynamics and average levels at different sites along the wave exposure/predation gradient is viewed to be reasonably good. Departures from agreement with the field data are instructive and indicate areas for further investigation.

2. Australia

Most of the published data on Australian community dynamics monitors numbers of individual barnacles, making comparison with the percent cover output of the model problematic. Therefore, the Australian version will be evaluated by giving examples of model results and relating them to reported qualitative patterns.

The Australian version differs in seasonality from that in New England. The season of growth and activity in Australia is practically year round, so, whereas the 16 iterations used in New England correspond to two week intervals from April to October, in Australia, the 16 iterations are considered to span the entire year, with approximately 3 week time steps. The barnacle settlement period is much longer in Australia, lasting several months, rather

than 6-8 weeks, as in New England (Denley and Underwood 1979). For the present, no wave disturbance is included, since a quantification of the effect of wave disturbance has not been published for these areas. The size refuge effect is not included in these simulations because of the lack of data on the extent of its occurrence. For short-term simulations such as these, the effect of a size refuge would be small.

Underwood et al. (1983) describe a pattern in community structure occurring in New South Wales along a wave exposure gradient. At wave-exposed sites, predation is reported to be low and limpets rare, with barnacles dominating the area. At protected sites, predation is high and limpets are dominant. At sites of intermediate exposure, predation and limpet levels are intermediate and variable, and a patchy barnacle-limpet mixture occurs. The model was run for 2 years and 9 spatial cells for a variety of predation and limpet levels, including stochasticity in predation, limpets and barnacle recruitment (Table IV-4).

Barnacle domination occurred when predation and limpets were low. An example of the dynamics over two years for one of the spatial cells is given in Fig. IV-11. Intermediate barnacle densities could be achieved by moderate limpet levels and low predation, or by low limpet levels and moderate to high predation (Table IV-4). Random variation in parameter values produced changes in the dominant organism in the model results from one year to the next (Figs. IV-12 and IV-13). This agrees with reports of changes in dominance in the field reported by Underwood et al. (1983) for

Table IV-4. Model parameter values producing different degrees of barnacle and limpet domination in the Australian community.¹

Barnacle Domination (>80% Barnacles)	Barnacles and Limpets (20-80% Barnacles)	Limpet Domination (<20% Barnacles)
L=0.0, P=0.0	L=0.3, P=0.0	L=0.5, P=4.0
L=0.1, P=0.0	L=0.5, P=0.0	L=0.3, P=8.0
	L=0.0, P=4.0	L=0.5, P=8.0
	L=0.1, P=4.0	
	L=0.3, P=4.0	
	L=0.0, P=8.0	
	L=0.1, P=8.0	

¹Values are based on the average cover of 9 spatial cells at the end of 2 years. (L = limpet population level mean; P = predation loss mean.)

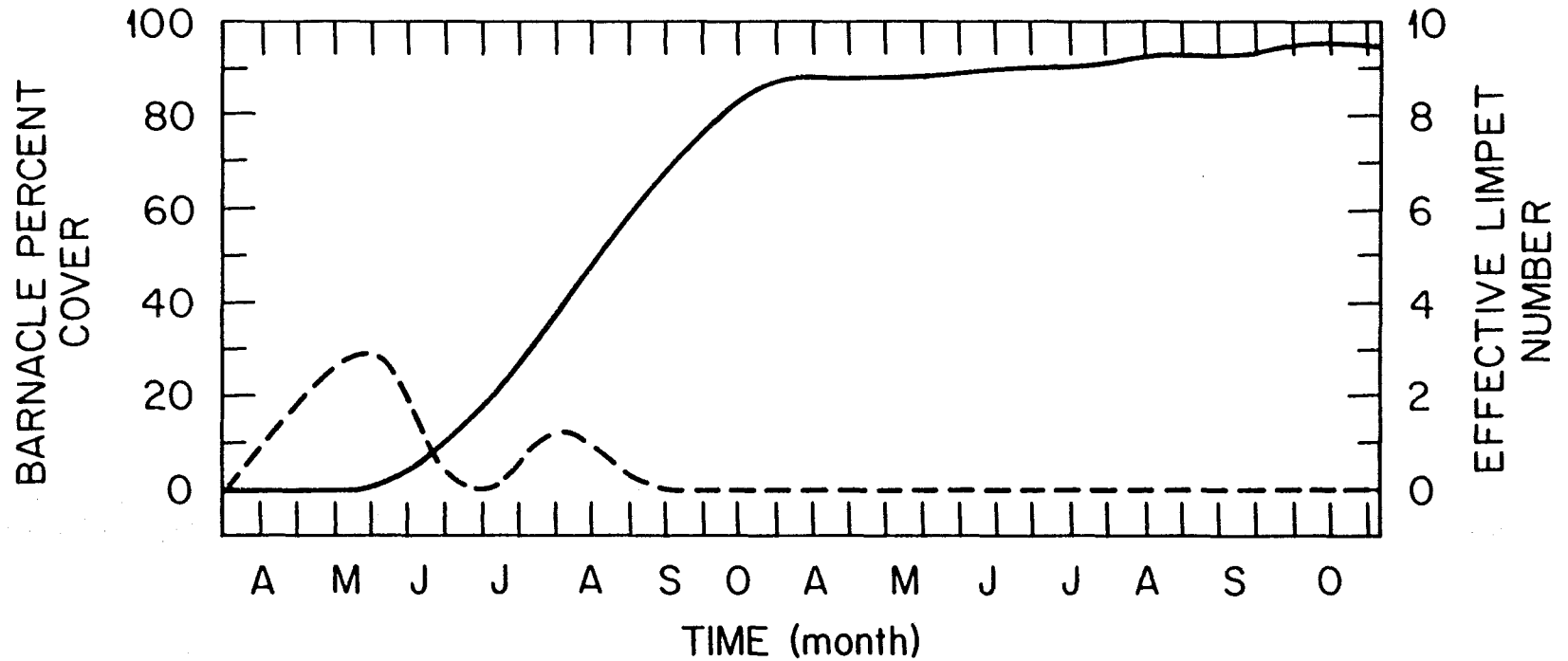


Figure IV-11. An example of model results for a single spatial cell representing a wave-exposed site in New South Wales, Australia. (Solid line = barnacles; dashed line = limpets.)

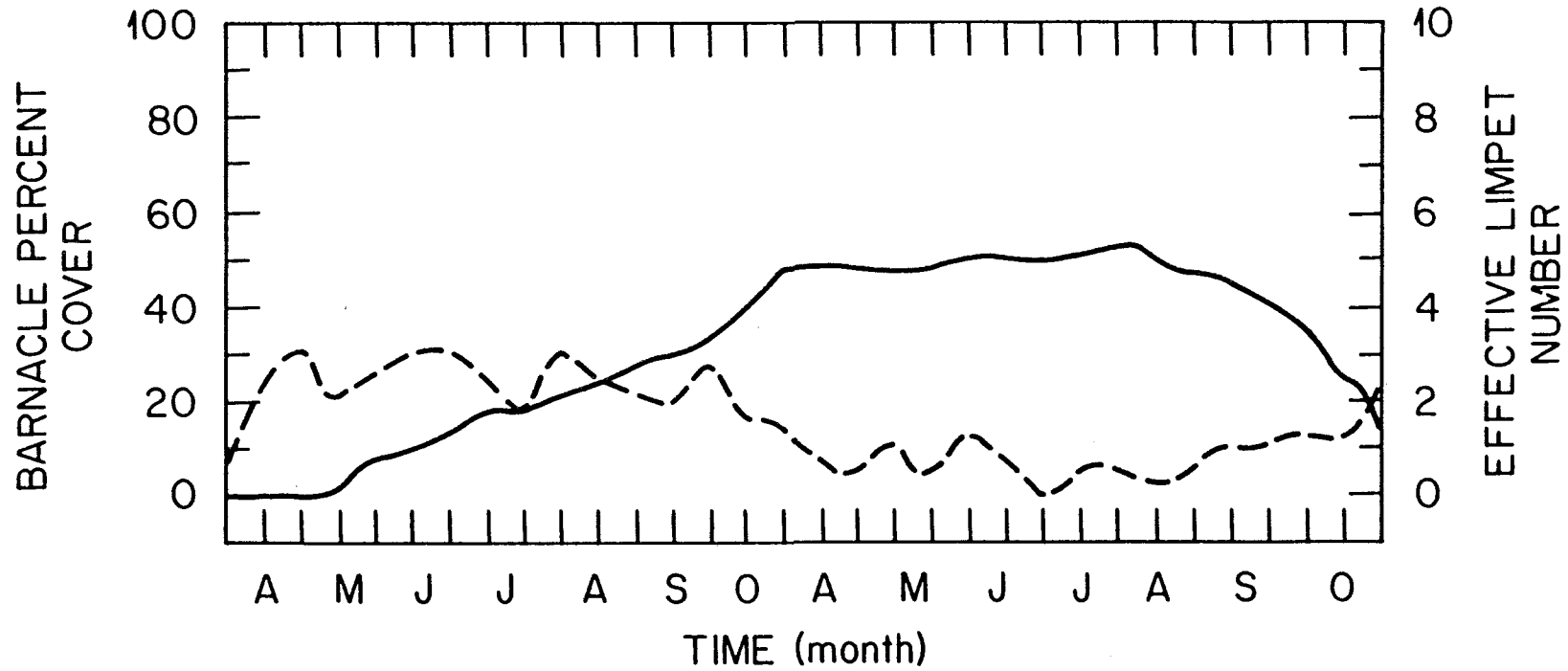


Figure IV-12. An example of model results for a single spatial cell representing a site with intermediate wave exposure in New South Wales, Australia. Solid line = barnacles; dashed line = limpets.

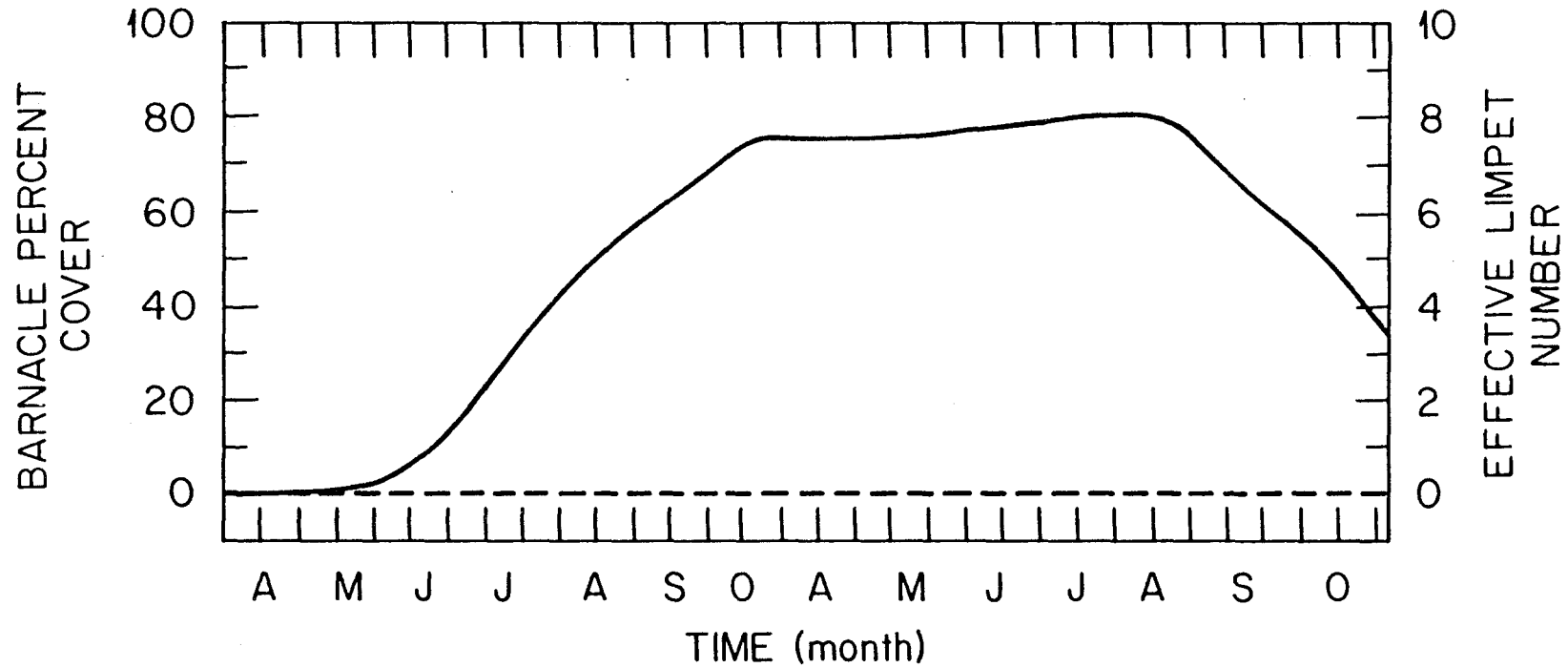


Figure IV-13. A second example of model results for a single spatial cell representing a site with intermediate wave exposure in New South Wales, Australia. (Solid line = barnacles; dashed line = limpets.)

mixed barnacle-limpet areas. It should be noted, however, that the decline of barnacles from predation in the second year would not occur if the maximum size refuge effect modeled here, were included.

Several combinations of parameters produced results similar to the wave-protected areas where barnacles are scarce and limpets and predators are relatively abundant (Table IV-4). An example of model results for the dynamics of one cell is given in Fig. IV-14. Limpet levels on these graphs should not be interpreted as actual levels being predicted, but only as indications of the trends in the effective limpet numbers (see model description).

E. MODEL EXPERIMENTS

1. A Conceptual Model of Stochasticity and Scale

Now that the model has been shown to be reasonably consistent with the available data, attention will be returned to investigating possible reasons for the greater emphasis on stochasticity as an explanation for pattern in Australia than in New England. A conceptual model of stochasticity and scale, based on the following three assertions, is developed as a framework for the model experiments.

The first assertion is that stochasticity is related to the ability to obtain sufficient information for accurate prediction. Even the most apparently random effects may be predicted if unlimited information is available. This differs from some current uses that equate stochasticity with environmental effects or

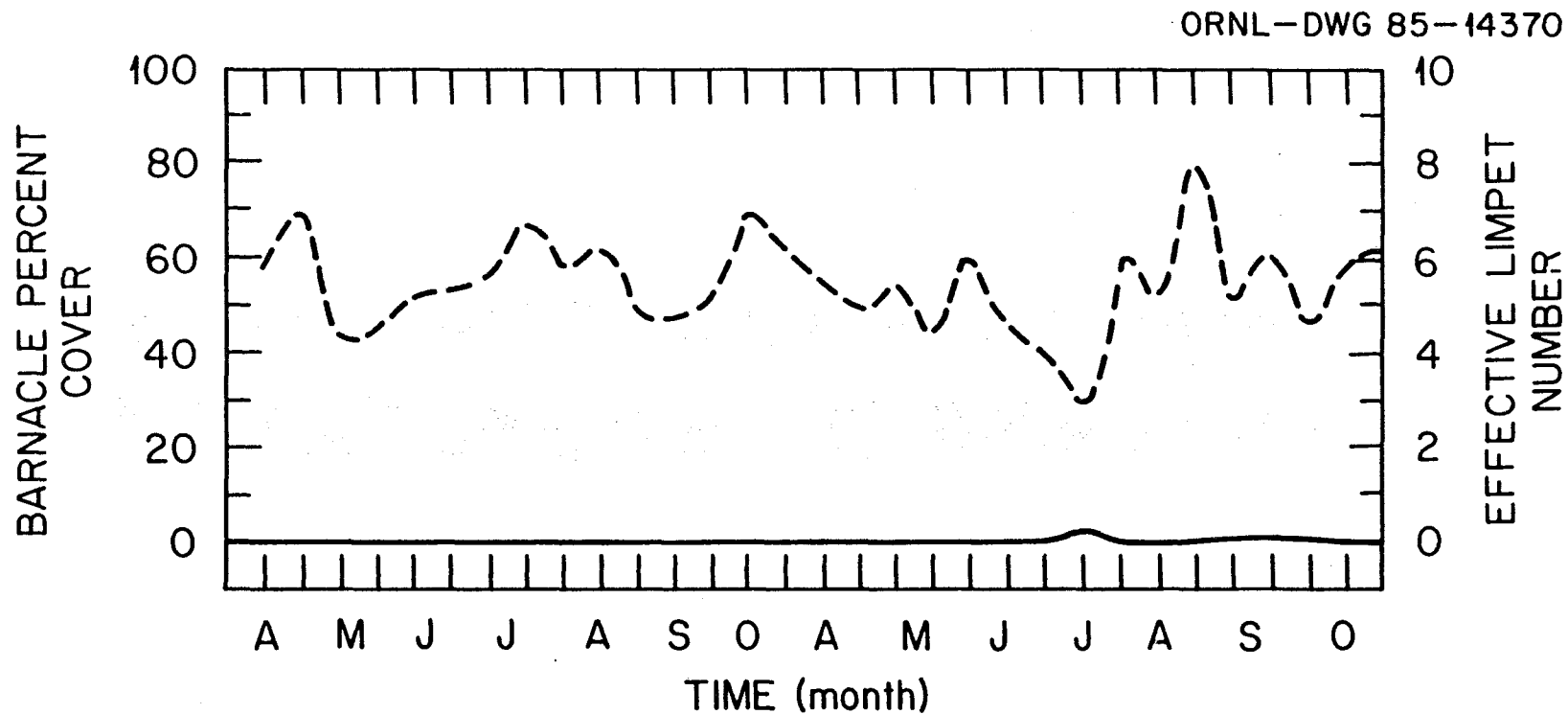


Figure IV-14. An example of model results for a single spatial cell representing a site with low wave exposure in New South Wales, Australia. (Solid line = barnacles; dashed line = limpets.)

"nonequilibrium" communities (Underwood et al. 1983; Grossman 1982; Grossman et al. 1982).

The second assertion is that small-scale information is harder to obtain and thus is associated with greater stochasticity. Small-scale information refers to detailed information with fine resolution in space or time, or involving precise quantitative measurement. This view has precedent in demographic theory, which may make relatively accurate predictions about large aggregates, but must regard individual events such as individual births and deaths, as stochastic.

In the cases discussed here, large-scale information is derived from scales closer to the observer scale, thus generally making the information easier to obtain than small-scale information. However, it should be noted that patterns occurring on scales much larger than the observer (e.g., climatic and oceanographic patterns) may appear as stochastic as those on very small-scales because of limitations on our ability to obtain sufficient information at such distant scales.

Finally, it is asserted that systems can be ordered based on their tendency to magnify or suppress small-scale variation and this ordering is related to the stochasticity of the system.

The conceptual model divides systems into three categories (Fig. IV-15); however in reality, variations in the degree of stochasticity should be considered as continuous. Each category will be discussed, with general examples, to be followed by

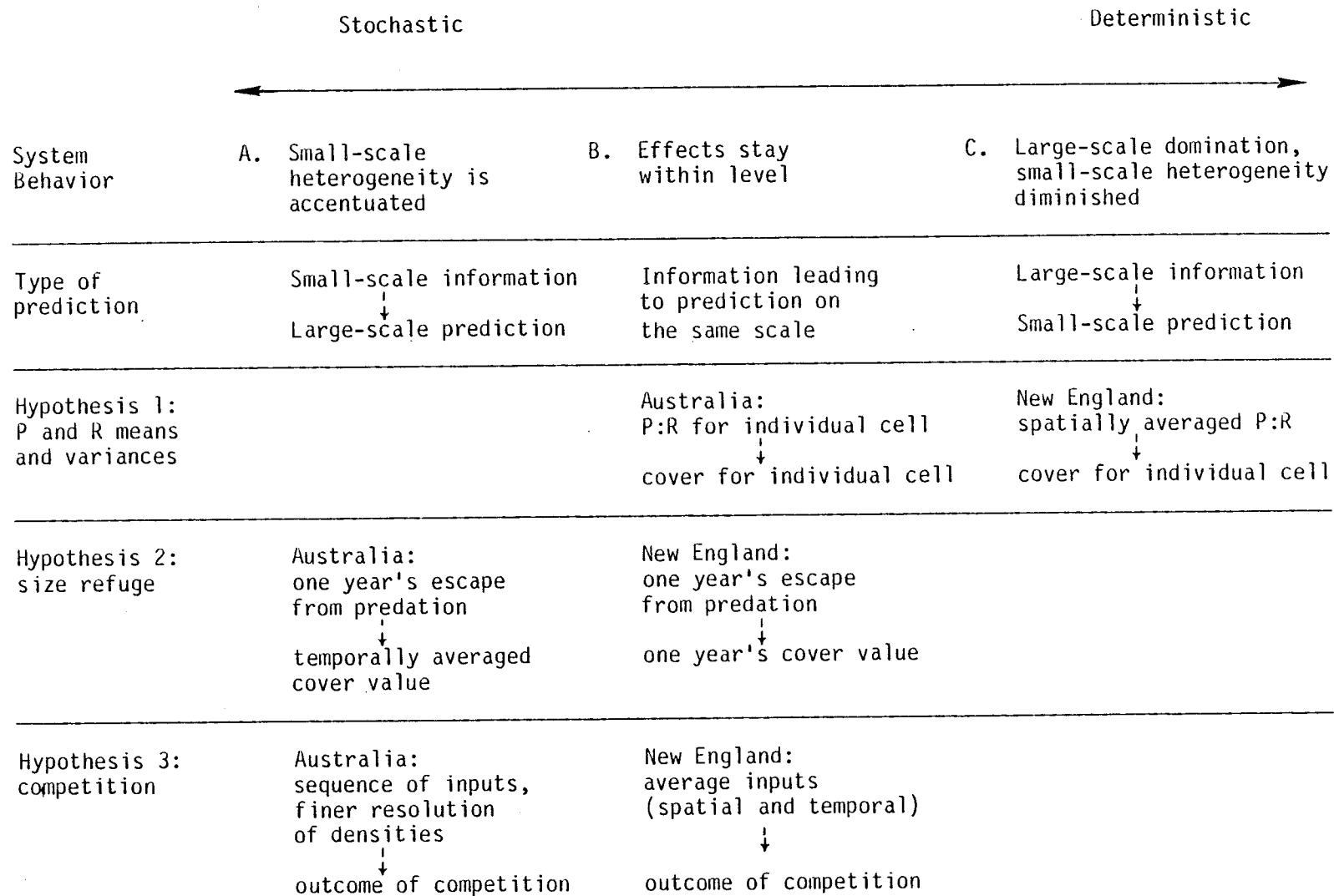


Figure IV-15. A conceptual model of stochasticity and scale. [P = predation rate; R = barnacle recruitment rate; ($\rightarrow$) should read "is adequate for prediction of."].

discussions of the three specific hypotheses (last three rows of Fig. IV-15) when the model experiments are presented.

In the most stochastic type of system, represented by column A, small-scale heterogeneity in time or space is accentuated. Systems of this type may often exhibit positive feedbacks through which small changes may be magnified. Multiple stable state models often have important positive feedbacks resulting in small differences leading to different equilibria or basins of attraction (Holling 1973). In general, cases in which historical effects are important would be placed in this category. In this type of system, small-scale information is needed to arrive at large-scale predictions.

At the other end of the gradient, represented by column C, is the case in which some factor, which varies on a larger scale, is able to dominate any small-scale variation that exists. For example, certain disturbances, like a substantial temperature change over a large region, might destroy the vegetation, thus wiping out any small-scale spatial variation. For this type of situation, large-scale information is sufficient to make even small-scale predictions.

The intermediate position on the gradient (Fig. IV-15) is for cases in which the effects of changes tend to stay within a level. A change in average temperature might affect the average values for vegetation without significantly changing small-scale heterogeneity. Small-scale changes produce small-scale effects and large-scale changes produce large-scale effects. This is the view

most compatible with the use of a hierarchical mode of analysis where patterns on a particular scale are seen as reflecting processes on that scale (Allen and Starr 1982).

The view of stochasticity presented here should be differentiated from the view of community variability or stochasticity (e.g., equilibrium or nonequilibrium status) as dependent on the scale at which the system is observed (Paine and Levin 1981; Shugart 1984; O'Neill et al., in press). The present model stresses differences in the nature of the system that will tend to make it often appear stochastic. The two ideas of stochasticity are somewhat related, however, since a highly stochastic system, as defined here, will allow small-scale variation to affect larger scales, thus making the system appear stochastic on more observational scales.

The next section discusses model experiments that investigate the hypothesis that stochastic effects play a greater role in the Australian intertidal community than in New England.

2. Model Experiment Results and Discussion

Three factors are suggested here as potentially contributing to the greater role of stochasticity reported in the Australian community. These three hypotheses are not considered to be mutually exclusive; indeed they may all aid the expression of variability. The simulation results allow exploration of their potential roles;

however testing of the hypotheses requires additional empirical investigations.

a. Relative recruitment and predation levels. One possible cause of differences in the importance of stochasticity in the two communities is differences in the recruitment level relative to predation. The following model experiments allow a quantitative examination of this hypothesis.

The version of the model used for the following experiments includes only barnacle recruitment and the removal of barnacles by predatory snails, in order to isolate this one factor from the others. It might be considered a general case, in that it includes nothing that is unique to New England or Australia. The seasonal patterns used are also intermediate between the two communities. The model was run for 49 spatial cells or replicates for one year for various combinations of recruitment and predation intensities and variabilities.

The model experiments can be viewed on two scales that can be related to the conceptual model of scale and stochasticity (Fig. IV-15). For this hypothesis, relatively small-scale information refers to the individual recruitment and predation levels for each cell. Large-scale information refers to the spatially-averaged recruitment and predation levels.

It is hypothesized that certain predation and recruitment levels lead to situations in which the larger scale average value is adequate to predict cover values for individual cells (Fig. IV-15,

column C). If the New England community exhibits this behavior, it might be considered to be relatively deterministic. Under other conditions, possibly occurring in Australia, the actual predation and recruitment levels for individual cells might be necessary to predict the cover for individual cells. In this case, system effects and prediction stay within a level, resulting in greater stochasticity (Fig. IV-15, column B).

Model results that indicate the conditions under which these two situations occur will now be discussed.

Table IV-5 shows means and variances for final barnacle cover for different levels of predation relative to recruitment. The values are given in percent cover, and, after an arcsin transformation, in degrees (Draper and Smith 1981). When predation is low relative to recruitment, most replicates are near 100% cover. The standard deviation is very low and thus the final covers for each replicate cell is relatively predictable based solely on the average levels. At the other extreme, when the predation rate is high relative to barnacle recruitment, the final barnacle mean is 0%. This result is also highly predictable based on the average levels as indicated by the standard deviation of 0%. When the rate of recruitment is intermediate relative to the predation rate, the resulting cover values tended to have higher standard deviations. Therefore, at these intermediate levels, average predation and recruitment rates are not as effective at predicting individual cell cover values. Although the transformed data results in somewhat

Table IV-5. Model results showing the effect of barnacle recruitment and predation levels on end-of-year barnacle percent cover.

Recruitment Mean	Recruitment Standard Deviation	Predation Mean	Predation Standard Deviation	Mean	Mean (Transformed ¹)	Standard Deviation	Standard Deviation (Transformed)
10	6	0	0	96.2	79.1	2.1	3.0
10	6	5	6	71.4	58.1	11.6	7.5
10	6	10	6	48.5	43.9	16.6	10.1
10	6	15	6	15.2	17.6	16.3	16.1
10	6	20	6	0.7	1.4	3.5	4.9
10	6	25	6	0.0	0.0	0.0	0.0

¹Arcsin transformation used (0-90°, see text).

higher standard deviations for extreme values, the overall pattern is similar to that of the untransformed percent cover data.

According to the model results, Australia might be considered to be more stochastic if the predation:recruitment ratio is in the intermediate range. B. A. Menge (unpublished MS and pers. comm.) has observed that recruitment rates are considerably lower in Australia than in New England; however, more information on predation rates is necessary to complete the comparison.

In New England, emphasis has been placed on variation along the predation gradient resulting from variation in wave exposure (Menge 1976; Menge and Sutherland 1976; Menge and Farrell, in press). Recruitment rates seem to be generally quite high, but the predation gradient causes the predation:recruitment ratio to go from one extreme to the other, along the gradient, presumably passing through intermediate ratios, where stochasticity should become more important. It may be that this intermediate ratio zone is less extensive in New England and this is why stochasticity is given less emphasis. Or it may just be the tendency to emphasize the larger scale, more deterministic patterns in the New England community, which accounts for the different perception of the importance of stochasticity in the two communities.

The present discussion emphasizes the importance of the rate of recruitment relative to predation. However, preliminary model investigations indicate that other factors, such as absolute recruitment levels, recruitment and predation variances, and seasonal patterns are also important. Some investigators have

emphasized the importance of absolute recruitment rates (Connell, in press; Roughgarden et al. 1984) in determining community structure, with recruitment variation being most important when average recruitment rates are low. B. A. Menge (unpublished MS and pers. comm.) stresses the importance of considering predation and competition as well, stating that the effects of recruitment variation should be most important when predation and competition are low, or relatively constant.

b. Barnacle size refuge from predation. Another feature that may distinguish Australian and New England communities is the refuge in size from predation reported for barnacles in Australia (Underwood and Denley 1984). Underwood and Denley (1984) give an example of an area where one year class from three years back made up the majority of barnacles in a region. This is interpreted as being due to especially high recruitment during that year, resulting in many barnacles escaping predation and subsequently being immune to predation because of their large size. The relation between predation intensity and prey size allows barnacle cover for one year, a temporally small-scale phenomenon, to influence the average cover over several years, a temporally large-scale phenomenon (Fig. IV-15, column A, page 100). Thus a relatively small-scale event has effects on a larger scale than would be expected in situations like New England, where a size refuge is lacking (Fig. IV-15, column B, page 100).

The size refuge effect was modeled by assuming that any barnacles present at the end of one year were adults and, therefore, too large to be preyed upon. Little has been published on what sizes must be achieved, or whether the refuge is independent of predation density and other details that would add realism to the model. In the absence of such detailed information, this simple case will be investigated, which is considered adequate for the general type of effect of interest.

The barnacle cover values for the end of each year are shown in Table IV-6 for 4 years and 9 replicates for the case where no size refuge exists and a between-year component of barnacle recruitment and predation variability is included. Without a size refuge, barnacles that escape predation for one year, and thus have cover values greater than 0%, are likely to be consumed the next year. Any increase in barnacle escapes, as in the first year, will affect the average cover only via one year's effect. On the other hand, when a size refuge exists, barnacles that escape predation the first year are safe from predation because they become too large to be consumed. An increase in escapes in a given year may now influence the average cover for several years (Table IV-7). The existence of adult barnacles that are immune from predation has the additional effect of making escapes from predation in later years unlikely (Table IV-7). This is because there is room for fewer barnacle recruits, and those that do settle, are preyed upon more heavily. This acts to further increase the role of a single year's escape.

Table IV-6. Effect of variable predation and recruitment on barnacle percent cover at the end of the year: no predation size refuge.¹

Replicate	Year			
	1	2	3	4
1	33.0	0.0	17.6	0.0
2	24.5	0.0	7.3	12.9
3	40.2	0.0	26.2	0.0
4	9.7	0.0	12.9	0.0
5	0.0	0.0	14.6	0.0
6	6.6	0.0	12.0	0.0
7	4.5	0.0	13.0	0.0
8	10.3	0.0	14.7	0.0
9	21.1	0.0	14.7	0.0

¹Average end-of-year barnacle cover over all 4 years = 8.2.

Table IV-7. Effect of variable predation and recruitment on barnacle percent cover at the end of the year: size refuge from predation after one year.¹

Replicate	Year			
	1	2	3	4
1	33.0	33.0	33.0	33.0
2	24.5	24.5	24.5	24.5
3	40.2	40.2	40.2	40.2
4	9.7	9.7	9.7	9.7
5	0.0	0.0	14.6	14.6
6	6.6	6.6	6.6	6.6
7	4.5	4.5	4.5	4.5
8	10.3	10.3	10.3	10.3
9	21.1	21.1	21.1	21.1

¹Average end-of-year barnacle cover over all 4 years = 17.6.

c. Competition. Another difference between the two communities is in the primary type of spatial competitor that barnacles are faced with in the mid-intertidal zone. In Australia, the large limpet Cellana tramoserica is the primary competitor, while in New England, it is the mussel Mytilus edulis. Three main features of the limpet-barnacle competitive interaction seem likely to magnify small-scale variability. These features were discussed in detail previously, but briefly are as follows:

1. reciprocal preemption, which results in the importance of the temporal sequence for predicting the outcome of competition;
2. spatial positive feedback, resulting in a magnification of small differences;
3. a threshold in the limpet effect, promoting an all-or-none effect that magnifies small differences.

These features of the barnacle-limpet interaction are hypothesized to make the Australian community more stochastic than the New England community, in which the competitive interaction is one of simple overgrowth (Fig. IV-15, page 100).

The effect of mussel competition was investigated by calculating the mean and standard deviation of barnacle cover at the end of the year for two years, at several mussel recruitment rates (Table IV-8). The results of the model runs show that without competition, most barnacle cells reach covers near 100%, as indicated by the high mean and reduced standard deviation by the end of the second year. By the end of the second year, most cells are entirely dominated by mussels, as indicated by barnacle means at or

Table IV-8. Model results on the effect of mussel competition on end-of-year barnacle percent cover.

Mussel ¹ Recruitment Mean	First Year				Second Year			
	Mean		Standard Deviation	Standard Deviation (Transformed)	Mean		Standard Deviation	Standard Deviation (Transformed)
	Mean	(Transformed ²)			Mean	(Transformed)		
0	96.9	80.5	1.8	3.6	99.6	86.5	0.3	1.4
3	10.4	16.8	13.6	10.5	0.03	0.5	0.2	1.0
6	5.8	12.6	6.6	6.4	0.0	0.0	0.0	0.0
9	2.2	7.7	2.2	3.7	0.0	0.0	0.0	0.0
12	0.8	4.6	1.0	2.4	0.0	0.0	0.0	0.0

¹Other model parameters: barnacle recruitment mean = 10; barnacle standard deviation = 4; mussel standard deviation = 10.

²Arcsin transformation used (0-90°, see text).

near 0%. The eventual domination of the cells by mussels is thus fairly deterministic.

The limpet competitive effect shows a somewhat different pattern (Table IV-9). Mean barnacle cover still decreases with higher limpet levels; however, barnacle cover increases with time. On the whole, variability remains at higher levels than for the case of mussel competition for both transformed and untransformed data. This supports the hypothesis that limpet competition may produce greater stochasticity in the outcome of competition as a result of the different nature of the competitive effect.

F. GENERAL DISCUSSION

Environmental variability or stochasticity has been characterized in various ways in ecology, ranging from a destabilizing force (May 1973; Hanson and Tuckwell 1978), to a diversity-maintaining influence (Huston 1979; Connell 1978), to a resource (Levins 1979). Its role in some communities has been described as producing "stochastic" communities as opposed to biotically controlled "deterministic" communities (Grossman 1982; Grossman et al. 1982). Debate on the role of environmental stochasticity has been persistent in ecology and is still leading researchers to claim that environmental variability has been ignored in favor of equilibrium approaches (Wiens 1977, 1984; Dayton 1979; Underwood and Denley 1984; Sale 1984). It is suggested here, that differences in the effect of variability in different communities

Table IV-9. Model results on the effect of limpet competition on end-of-year barnacle percent cover.

Limpet ¹ Population Mean	First Year				Second Year			
	Mean	Mean (Transformed ²)	Standard Deviation	Standard Deviation (Transformed)	Mean	Mean (Transformed)	Standard Deviation	Standard Deviation (Transformed)
0.0	96.9	80.5	1.8	3.6	99.6	86.5	0.3	1.4
0.2	92.4	74.3	3.3	3.3	98.9	84.1	0.6	1.4
0.4	73.8	59.9	13.8	9.0	95.8	78.6	2.2	3.1
0.6	37.0	35.7	22.7	16.1	81.2	65.9	18.0	12.5
0.8	2.0	3.3	5.5	7.7	15.1	16.7	20.2	18.2

¹Other model parameters: barnacle recruitment mean = 10; barnacle standard deviation = 4; limpet standard deviation = 0.3.

²Arcsin transformation used (0-90°, see text).

may not be entirely due to differences in observed levels of environmental variability or biases of researchers, but may be related to the manner in which small-scale, unpredictable effects are translated by the system into pattern. Systems that are observed to be more stochastic may appear this way because they are affected by or may even magnify the effects of small-scale variability, while for other systems or parameter values, the effects may be reduced. Thus the nature of the system determines the relation between the scale of the process and the scale of the pattern it produces. This study has identified several types of system characteristics that have been seen to be important in this respect.

The first factor investigated was the rate of predation relative to barnacle recruitment. Model results showed that varying the predation level influenced the variability of final barnacle cover. At intermediate levels, variability was high, resulting in less predictable cover values, while at the extremes, the constraints of 0% and 100% cover forced the variation to decline. This pattern of variability can be related to the intermediate disturbance hypothesis (Connell 1978; Huston 1979). Intermediate disturbance rates relative to the population's rate of increase allow the highest species diversity. At the extremes, the constraints of physical stress at high disturbance rates, or competitive exclusion at low disturbance rates, limit diversity. High variability or diversity in zones that are intermediate or transitional between community types, known as ecotones, may result

from a related mechanism. Higher variability in space and time has been observed in several rocky intertidal communities in areas of intermediate wave exposure and predation (e.g., Menge 1976; Underwood et al. 1983; Hawkins and Hartnoll 1983).

For this hypothesis, the model predicts that intermediate values of predation relative to recruitment should result in higher variability. More percent cover data on predation and recruitment is needed, particularly for Australia, to determine whether the communities studied there fall in the intermediate range. The role of absolute predation and recruitment levels and the degree of seasonality needs to be further investigated with model and field studies, since some preliminary model results suggest they are important as well.

The model results used in evaluating the second hypothesis indicate that the barnacle size escape from predation reported in Australia may increase the effect of variability. This effect is related to what has been termed "historical effects." The size escape from predation achieved by barnacles may allow one year's effect to influence the cover values over later years. Thus a large component of the barnacle cover reflects the predation or recruitment level at some time in the past rather than any current conditions. This effect has been observed for another barnacle, Balanus cariosus (Dayton 1971), and for some types of algae (Lubchenco and Gaines 1981b) as well as other organisms (see Connell 1975). Examples of historical effects complicating interpretation

of current patterns may be found in forests (Shugart and Noble 1981) and fisheries (Aggus 1979; Adams and DeAngelis, in press).

In order to assess the actual role of size escapes in increasing stochasticity, further field data are needed on the frequency of occurrence of size escapes. The model also predicts that there will be fewer barnacles escaping predation in areas where escapes have occurred in the past and large barnacles are present. This is because the same predation losses are concentrated on fewer small, predation-susceptible barnacles. This could be tested in the field by comparing the numbers of recruits escaping predation in areas where large barnacles are abundant and areas where they are rare.

Preemptive competitive interactions such as the barnacle-limpet interaction, result in another type of historical effect, in which the order of settlement determines the outcome. Yodzis (1978) modeled this preemptive effect using Lotka-Volterra competition equations. In this formulation, when the competition coefficients are large, the identity of the competitive dominant is contingent upon the initial conditions, i.e., the initial numbers of settlers of each species. The majority of examples of preemptive competition have come from subtidal benthic communities (Sutherland 1974; Sutherland et al. 1977; Woodin 1976; Peterson 1980), where the need to know the order of settlement certainly contributes to stochasticity in those communities.

For the third hypothesis, the model results indicated that positive feedback and threshold effects in the limpet-barnacle

interaction could also contribute to the greater variability in the Australian community. Positive feedback has been receiving greater attention in ecology in recent years (e.g., see DeAngelis et al., in press). There are a number of examples of dramatic changes in ecosystems that have been described as occurring after a threshold is passed and positive feedbacks exceed the stabilizing homeostatic forces. In some examples, like the spruce-budworm system, species are hypothesized to alternate between two different densities (see Holling 1973). In other systems, the capacity to absorb the effects of anthropogenic influences may be surpassed at some threshold, and community composition may change drastically through species extinctions and invasions (Smith 1968 and Glendening 1952, as discussed in Holling 1973). These dramatic examples are in contrast to the more subtle role of positive feedbacks and thresholds occurring here. Initial variability between spatial cells, which might otherwise produce a continuum of species abundances, may result in an increase in inter-cell variability. The role of positive feedback in the creation of spatial heterogeneity has also been shown in diffusion models (Levin 1974; Okubo 1980; DeAngelis et al., in press). However, the mechanism, as modeled here, differs in that it does not include inter-cell movement.

The model predictions for the third hypothesis could be tested in the field by measuring limpet densities and variation in Australia, and mussel recruitment levels and variation in New England, and comparing barnacle cover variation over time for replicate spatial cells. More field and model investigations are

also needed to determine the relative importance of each of the features of the limpet-barnacle interaction.

Future model experiments will investigate other species and environmental factors that may contribute to differences in community structure and the degree of stochasticity (Underwood et al. 1983). The larger number of species with significant interactions reported for Australia (Underwood et al. 1983) may increase the apparent level of stochasticity. This effect on stochasticity provides an interesting contrast to situations in which greater diversity may result in more constant and intense interactions, thus making the outcome more deterministic (e.g., the effects of predator diversity on prey distributions; Menge and Sutherland 1976). Model experiments involving combinations of factors is also needed. For instance, predation may reduce the level of limpets needed to produce high variability, since limpets and predators have complementary effects on barnacle cover.

Comparison of processes affecting community structure in different communities will certainly be a long process due to the diversity of factors potentially affecting organism abundance and pattern. It is hoped that the type of model experimentation approach presented here will facilitate this process by quantifying current conceptual models and generating new hypotheses for evaluation in the field.

CHAPTER V

CONCLUDING REMARKS ON THE USE OF A HIERARCHICAL APPROACH

This research has applied and evaluated a hierarchical approach to ecological problems ranging from the theoretical problem of emergence to community comparisons and methodological issues. It is appropriate at this point to assess the usefulness of this approach for gaining insight into these problems and to summarize what has been learned about hierarchies in the process.

Perhaps one of the most significant advantages of the use of a hierarchical approach is the explicit recognition of the different levels of analysis, offering different perspectives for viewing the same processes and patterns. Although the use of multiple descriptions can be a powerful tool for increasing understanding of a system (Bateson 1979), it also can create difficulties and apparent contradictions. As seen in Chapter II, these have often taken the form of controversies over the concept of emergence. The difficulty of relating different levels of analysis in the emergence controversy has been increased by overly simplified representations of hierarchies, which use generally undefined terms such as "summation" of parts and "properties of wholes." A more detailed hierarchical conceptual model was developed to help clarify the issue of emergence. The analysis showed that neither inherent indeterminism nor coevolution are necessary for the appearance of emergence. Instead emergence should be thought of as being relative to one's lower level predictive model and arising from the failure

to include interactions or constraints, or from methodological limitations on the availability of sufficient lower level information. Further work on the relation between levels needs to be pursued; however, as Chapter IV indicates, the relation between levels may be system-dependent and require analyses specific to particular systems.

A hierarchical perspective offers a way to relate different analyses of the same data by viewing the analyses as occurring at different scales. Although conceptually attractive in its unifying ability, this presents the danger of naive application, in which the intricacies of the relation between analysis technique and ecological processes are ignored. In particular, one must consider the nature of the supposed higher level analysis techniques and their relation to the ecological patterns of interest. In Chapter III, a taxonomic hierarchy of specific- and generic-level analyses was considered in relation to a pollution gradient. Genera were seen as providing species groups that may or may not indicate similarity in pollution response. The nature of these species groups determines whether genera may constitute a higher level of analysis of pollution patterns. Analysis in term of hierarchies allowed the question to go beyond that of whether genera can reflect species' patterns, to consider the alternatives for the significance of congeneric groupings and their effect on generic-level analyses. Analysis of the species:genus ratio trend indicated that congeneric chironomid species were not generally similar in pollution response, but could nevertheless be adequate to represent species patterns

under certain circumstances. The primary insights into the use of a hierarchical approach to analyses gained from this chapter are:

1. that the significance of higher level organismal groups must be considered in terms of the ecological pattern of interest to determine their utility for higher level analyses;

2. additional factors affecting the significance of analysis techniques may affect their ability to show higher level patterns (i.e., similarity coefficients vs species richness measures and abundance vs presence/absence data, as discussed in Chapters I and III).

These factors may have different importance depending on the system and purpose of the analyses.

The assumption that processes on a particular scale generally lead to patterns on a similar scale is important for the use of hierarchies because it increases the integrity or autonomy of different levels of analysis. This does not mean that this assumption is essential to the applicability of a hierarchical approach; only that it affects the way in which it may be applied. The model comparisons of rocky intertidal communities in Chapter IV show that differences in system dynamics can result in processes at one scale affecting patterns on different scales. These differences in system dynamics were shown to relate to the apparent degree of stochasticity indicated by studies of New England and Australian intertidal systems (Menge 1976; Underwood et al. 1983). It should be noted that the gradient of stochasticity, as defined here, depends on the nature of the system and how it suppresses or

magnifies small-scale variation and not on the level of analysis or the amount of external variability.

The hierarchical structure apparent in many systems and the dependence of many phenomena on the level of analysis suggests that approaches based on scale and hierarchy have the potential to provide new insights, hypotheses, and generalizations that may stimulate ecological research. It is probably more important at this point to use applications of hierarchy "theory" to learn more about how or when to apply it, than to look for situations in which one may demonstrate its strengths. Balanced assessments and investigations of its strengths and weaknesses as well as delineation of different types of hierarchies and situations for which they are useful will promote the development of a theory of hierarchical structure more effectively than demonstrations of how well it "works." In this way a gradual accumulation of principles and hypotheses may occur, so that expectations for the development of a theory of hierarchical structure with predictive power will not prove to be in vain.

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APPENDIX

FORTRAN PROGRAM FOR INTERTIDAL MODELS

```

C      ROCKY INTERTIDAL SIMULATION (RITS)
C      FOR NEW ENGLAND (RITSNE) CALL WAVE PRED MUSL BARN
C      FOR AUSTRALIA (RISTAT) CALL PRED LIMP BARN
C
      IMPLICIT REAL(M,L)
      DIMENSION BINCR(10,10),MINCR(10,10),BMORTC(10,10)
      COMMON/COVER/BCOV(1600),BADULT(1600),MCOV(1600)
      COMMON/SIZES/PRED(10,10),IYR,JSEAS,NDIM,NBYR,BR,MR
      COMMON/LIMPT/LIMP(10,10),LYR,LSL
      COMMON/SEAS/WDSEAS(24),PSEAS(24),BSEAS(24)
      COMMON/YARRAY/YP(12),YB(12),YM(12),YL(12)
      COMMON/ITER/ITERP,ITERB,ITERM,ITERL
      COMMON/TIMING/IBS,IGE,IMS,IPS
      COMMON/REQN/AO,A1,B0,B1
      COMMON/NSED/NSED1,NSED2,NSED3,NSED4,NSED5,NSED6,NSED7,
> NSED8,NSED9,NSED10,NSED11,NSED12,NSED13,NSED14
C
C
C *****
C
C..VARIABLE AND PARAMETER DEFINITIONS:
C
C..BINCR(II,JJ) -- BARNACLE RECRUITMENT INCREMENT FOR CELL II,JJ
C..MINCR(II,JJ) -- MUSSEL RECRUITMENT INCREMENT FOR CELL II,JJ
C..BMORTC(II,JJ)-- BARNACLE MORTALITY DUE TO MUSSEL COMPETITION
C
C  COMMON/COVER/
C..BCOV(IX) -- BARNACLE COVER FOR YEAR I, SEASON J, CELL II,JJ,
C....(FUNCTION DIMM(IX) IS USED TO CONVERT A
C....1-DIMENSIONAL SUBSCRIPT INTO A 4-DIMENSIONAL ARRAY
C..BADULT(II,JJ)--ADULT BARNACLE COVER FOR CELL II,JJ
C..MCOV(IX) -- MUSSEL COVER FOR YEAR I, SEASON J, CELL II,JJ,
C
C  COMMON/SIZES/
C..PRED(II,JJ) -- PREDATION LOSS FOR CELL II,JJ
C..IYR -- NUMBER OF YEARS SIMULATED
C..JSEAS -- NUMBER OF TIME STEPS WITHIN A YEAR
C..NDIM -- DIMENSION OF AREA SIMULATED, N=NDIM**2
C..NBYR -- IF BETWEEN YEAR VARIATION IS INCLUDED, NBYR=1,
C....OTHERWISE NBYR=0
C..BR -- BARNACLE GROWTH RATE
C..MR -- MUSSEL GROWTH RATE
C
C  COMMON/LIMPT/
C..LIMP(II,JJ) - CELLANA LEVEL IN CELL II,JJ
C..LYR -- LIMPET POPULATION LEVEL
C..LSL-- LIMPET POPULATION LEVEL STANDARD DEVIATION
C

```

```

C  COMMON/SEAS/
C..WDSEAS -- SEASONAL PATTERN OF WAVE DISTURBANCE PROBABILITY
C..PSEAS -- SEASONAL PATTERN OF PREDATION INTENSITY
C..BSEAS -- SEASONAL PATTERN OF BARNACLE RECRUITMENT
C
C  COMMON/YARRAY/
C..YP,YB,YM,YL -- ARRAYS WITH DIFFERENT LEVELS OF PREDATION,
C....BARNACLES, MUSSELS AND LIMPETS, RESPECTIVELY,
C....FOR WHICH MODEL IS RUN
C
C  COMMON/ITER/
C..ITERP,ITERB,ITERM,ITERL -- NUMBER OF DIFFERENT LEVELS OF
C....PREDATION, BARNACLES, MUSSELS AND LIMPETS FOR WHICH MODEL IS RUN
C
C  COMMON/TIMING/
C..IBS -- SEASONAL ITERATION WHEN BARNACLE RECRUITMENT BEGINS
C..IGE -- SEASONAL ITERATION WHEN BARNACLE GROWTH ENDS
C..IMS -- SEASONAL ITERATION WHEN MUSSEL RECRUITMENT BEGINS
C..IPS -- SEASONAL ITERATION WHEN PREDATION BEGINS
C
C  COMMON/REQN/
C..AO -- INTERCEPT FOR DETERMINATION OF LIMPET COMPETITIVE EFFECT
SLOPE
C..A1 -- SLOPE FOR DETERMINATION OF LIMPET COMPETITIVE EFFECT SLOPE
C..BO -- INTERCEPT FOR LIMPET NUMBER EQUATION
C..B1 -- SLOPE FOR LIMPET NUMBER EQUATION
C
C  COMMON/NSED/
C..NSED1-14 -- RANDOM NUMBER SEEDS
C
C..WDM -- WAVE DISTURBANCE PROBABILITY LEVEL MEAN
C..WDSO -- WAVE DISTURBANCE PROBABILITY STANDARD DEVIATION
C..PM -- PREDATION LOSS MEAN
C..PSD -- PREDATION LOSS STANDARD DEVIATION
C..MM -- MUSSEL RECRUITMENT MEAN
C..MSD -- MUSSEL RECRUITMENT STANDARD DEVIATION
C..BM -- BARNACLE RECRUITMENT MEAN
C..BSD -- BARNACLE RECRUITMENT STANDARD DEVIATION
C
C..WDYR,PYR,MYR,BYR -- WAVE, PREDATION, MUSSEL, AND BARNACLE LEVELS
C....WITH ANY YEARLY VARIATION ADDED
C
C..WPROB -- WAVE DISTURBANCE PROBABILITY WITH ANY YEARLY
C....SEASONAL VARIATION ADDED
C..PPROB -- PREDATION LOSS LEVEL WITH ANY YEARLY AND SEASONAL
C....VARIATION ADDED
C
C *****

```

```

C
C
CALL INPUT(WDM,WDSO)
C
I=1
J=1
C
C...ASSIGNS PRED, LIMPET, MUSSEL AND BARNACLE MEANS AND
C...STANDARD DEVIATIONS FOR EACH MODEL RUN
C
DO 980 KP=1,ITERP
PM=YP(KP)
PSD=YP(KP+6)
DO 960 KLL=1,ITERL
LM=YL(KLL)
LSD=YL(KLL+6)
DO 940 KM=1,ITERM
MM=YM(KM)
MLSD=YM(KM+6)
DO 920 KB=1,ITERB
BM=YB(KB)
BSD=YB(KB+6)
C
C...BEGINS A MODEL RUN FOR 1 COMBINATION OF PREDATION, LIMPETS,
C...MUSSELS AND BARNACLES (EITHER LIMPETS OR MUSSELS ARE 0)
C
CALL QINIT(BMORTC)
C
WRITE(6,1120)
WRITE(6,1130) YP(KP),YL(KLL),YM(KM),YB(KB)
WRITE(6,1120)
1120 FORMAT(/,'
*****
> *****',/)
1130 FORMAT(/,' ***** PRED= ',F6.2,' CELLANA= ',F6.2,' MUSL=
',
> F6.2,' BARN= ',F6.2,' *****',/)
C
DO 800 I=1,IYR
C
C...MAY CHOOSE TO INCLUDE AMONG YEAR COMPONENT OF RANDOM VARIATION
IF (NBYR.EQ.0) GO TO 20
C
C...ADDS AMONG YEAR COMPONENT TO VARIATION IN PARAMETERS
CALL RNORM(NSED1,NSED2,RNM1,RNM2)
CALL RNORM(NSED3,NSED4,RNM3,RNM4)
WDYR=RNM1*WDSO+WDM
PYR=RNM2*PSD+PM
MYR=RNM3*MLSD + MM
LYR=RNM3 * LSD + LM
BYR=RNM4*BSD+BM
GO TO 30

```

```

C
20 CONTINUE
   WDYR=WDM
   PYR=PM
   MYR=MM
   LYR=LM
   BYR=BM
30 CONTINUE
C
   WRITE(6,1150) I,PYR,LYR,MYR,BYR
1150 FORMAT(/,' ***** YEAR= ',I5,
> ' PYR=',F6.2,' LYR=',F6.2,' MYR=',F6.2,' BYR=',F6.2)

```

```

C
   DO 700 J=1,JSEAS
   WPROB = WDYR * WDSEAS(J)
   PPROB = PYR * PSEAS(J)
   WRITE(6,1160) J,WPROB,PPROB
1160 FORMAT(/,' ***** SEASON=',I5,
> ' 1X,' WPROB= ',F6.2,1X,' PPROB=',F6.2,/)

```

```

C
   IF (J.EQ.1.AND.I.EQ.1) GO TO 120
   CALL RESET(I,J,BMORTC)
   CALL LMPT(I,J)
   CALL WAVE(I,J,WPROB)
   CALL PREDR(I,J,PPROB,PSD)
120 CONTINUE
C
   CALL MUSL(I,J,BMORTC,MYR,MLSD,MINCR)
   CALL BARN(I,J,BMORTC,BYR,BSD,BINCR)
   CALL OUTPUT(I,J,KP,KB,KLL,KM)
700 CONTINUE
800 CONTINUE
920 CONTINUE
940 CONTINUE
960 CONTINUE
980 CONTINUE
   STOP
   END

```

```

C
C *****
C

```

```

SUBROUTINE INPUT(WDM,WDSO)
IMPLICIT REAL(M,L)
DIMENSION WDSEAS(24),BSEAS(24),PSEAS(24)
COMMON/SIZES/PRED(10,10),IYR,JSEAS,NDIM,NBYR,BR,MR
COMMON/LIMPT/LIMP(10,10),LYR,LSO
COMMON/SEAS/WDSEAS(24),PSEAS(24),BSEAS(24)
COMMON/YARRAY/YP(12),YB(12),YM(12),YL(12)
COMMON/ITER/ITERP,ITERB,ITERM,ITERL
COMMON/TIMING/IBS,IGE,IMS,IPS
COMMON/REQN/AO,A1,BO,B1
COMMON/NSED/NSED1,NSED2,NSED3,NSED4,NSED5,NSED6,NSED7,
> NSED8,NSED9,NSED10,NSED11,NSED12,NSED13,NSED14

```

C

```

READ(5,350) ITERP,ITERB,ITERM,ITERL
READ(5,350) IBS,IGE,IMS,IPS
READ(5,390) BR,MR,AO,A1,B0,B1
READ(5,400) JSEAS,IYR,NDIM,NBYR
READ(5,450) NSED1,NSED2,NSED3,NSED4,NSED5,NSED6,NSED7
READ(5,450) NSED8,NSED9,NSED10,NSED11,NSED12,NSED13,NSED14
READ(5,500) (YP(N),N=1,12)
READ(5,500) (YB(N),N=1,12)
READ(5,500) (YM(N),N=1,12)
READ(5,500) (YL(N),N=1,12)
READ(5,550) (WDSEAS(J),J=1,24)
READ(5,550) (PSEAS(J),J=1,24)
READ(5,550) (BSEAS(J),J=1,24)
350 FORMAT(/,4I5)
390 FORMAT(/,6F5.2)
400 FORMAT(/,4I5)
450 FORMAT(/,7I8)
500 FORMAT(/,12F5.2)
550 FORMAT(/,12F5.2,/,12F5.2)

```

C

```

WRITE(6,600) IBS,IGE,IMS,IPS
WRITE(6,650) BR,MR,AO,A1,B0,B1
WRITE(6,700) ITERP,ITERB,ITERM,ITERL
WRITE(6,750) JSEAS,IYR,NDIM,NBYR
WRITE(6,800) NSED1,NSED2,NSED3,NSED4,NSED5,NSED6,NSED7
WRITE(6,800) NSED8,NSED9,NSED10,NSED11,NSED12,NSED13,NSED14
WRITE(6,1980) (YP(N),N=1,12)
WRITE(6,1980) (YB(N),N=1,12)
WRITE(6,1980) (YM(N),N=1,12)
WRITE(6,1980) (YL(N),N=1,12)
WRITE(6,2000) WDM,WDSO
WRITE(6,2002) (WDSEAS(J),J=1,24)
WRITE(6,2004) (PSEAS(J),J=1,24)
WRITE(6,2006) (BSEAS(J),J=1,24)
600 FORMAT(/,' IBS= ',I5,' IGE= ',I5,' IMS= ',I5,' IPS= ',I5,/)
650 FORMAT(/,' BR= ',F5.2,' MR= ',F5.2,' AO= ',F5.2,' A1= ',F5.2,
> ' B0= ',F5.2,' B1= ',F5.2,/)
700 FORMAT(/,' ITES = P,B,M,L ',4I5)
750 FORMAT(/,' JSEAS= ',I5,' IYR= ',I5,' NDIM= ',I5,' NBYR= ',I5)
800 FORMAT(/,2X,7I8)
1980 FORMAT(/,2X,12F6.2)
2000 FORMAT(' WDM= ',F5.2,' WDSO= ',F5.2)
2002 FORMAT(' WDSEAS ',12F5.2,/,9X,12F5.2)
2004 FORMAT(' PSEAS ',12F5.2,/,9X,12F5.2)
2006 FORMAT(' BSEAS ',12F5.2,/,9X,12F5.2)
RETURN
END

```

C

C *****

```

C *****
C
  SUBROUTINE QINIT(BMORTC)
    IMPLICIT REAL(M,L)
    DIMENSION BMORTC(10,10)
    COMMON/COVER/BCOV(1600),BADULT(1600),MCOV(1600)
    COMMON/SIZES/PRED(10,10),IYR,JSEAS,NDIM,NBYR,BR,MR
    COMMON/LIMPT/LIMP(10,10),LYR,LSO
C
C    INITIALIZES ABUNDANCES
C    INITIALIZE BMORTC FOR WHEN I=1 AND J=1 SINCE CAN'T USE RESET
YET
C
    DO 60 II=1,NDIM
    DO 50 JJ=1,NDIM
      BMORTC(II,JJ)=0.0
      LIMP(II,JJ)=0.0
      PRED(II,JJ)=0.0
50  CONTINUE
60  CONTINUE
C
    IXTOT=IYR*JSEAS*NDIM**2
    DO 10 I=1,IXTOT
      MCOV(I)=0.0
      BCOV(I)=0.0
      BADULT(I)=0.0
10  CONTINUE
    RETURN
    END
C
C *****

```

C *****

C
 SUBROUTINE RESET(I,J,BMORTC)
 IMPLICIT REAL(M,L)
 DIMENSION BMORTC(10,10)
 COMMON/COVER/BCOV(1600),BADULT(1600),MCOV(1600)
 COMMON/SIZES/PRED(10,10),IYR,JSEAS,NDIM,NBYR,BR,MR
 COMMON/LIMPT/LIMP(10,10),LYR,LSO

C
 C THIS ROUTINE SETS COVS TO PREVIOUS VALUES
 C AND RESETS BMORTC, PRED, AND LIMP TO 0
 C

DO 60 II=1,NDIM
 DO 50 JJ=1,NDIM
 PRED(II,JJ)=0.0
 BMORTC(II,JJ)=0.0
 LIMP(II,JJ)=0.0

C
 C...IF THIS IS THE FIRST SEASON, SET VALUES EQUAL TO VALUES
 C...AT THE END OF LAST YEAR
 C

IX=DIMM(I,J,II,JJ)
 IF (J.EQ.1) GO TO 19
 GO TO 20
 19 IZ=DIMM(I-1,JSEAS,II,JJ)
 BCOV(IX)=BCOV(IZ)
 MCOV(IX)=MCOV(IZ)
 BADULT(IX)=BADULT(IZ)
 GO TO 50
 20 IY=DIMM(I,J-1,II,JJ)
 BCOV(IX)=BCOV(IY)
 MCOV(IX)=MCOV(IY)
 BADULT(IX)=BADULT(IY)
 IF (J.NE.4) GO TO 50
 IL=DIMM(I,J,II,JJ)
 BADULT(IL)=BCOV(IL)
 50 CONTINUE
 60 CONTINUE
 RETURN
 END

C
 C *****

```

C *****
C
  SUBROUTINE LMPT(I,J)
    IMPLICIT REAL(M,L)
    COMMON/COVER/BCOV(1600),BADULT(1600),MCOV(1600)
    COMMON/SIZES/PRED(10,10),IYR,JSEAS,NDIM,NBYR,BR,MR
    COMMON/LIMPT/LIMP(10,10),LYR,LSD
    COMMON/REQN/A0,A1,B0,B1
    COMMON/NSED/NSED1,NSED2,NSED3,NSED4,NSED5,NSED6,NSED7,
> NSED8,NSED9,NSED10,NSED11,NSED12,NSED13,NSED14
C
  DO 200 II=1,NDIM
    DO 100 JJ=1,NDIM
      IX=DIMM(I,J,II,JJ)
C...CALCULATES MAXIMUM CELLANA NO. DEPENDENT ON FREE SPACE
      LIMP(II,JJ) = B0 - (B1 * BCOV(IX))
C...ADDS RANDOM COMPONENT TO LIMPET POPULATION LEVEL THEN
C...REDUCES CELLANA LEVEL DUE TO POPULATION EFFECT
      CALL RNORM(NSED5,NSED6,RNM1,RNM2)
      LIMPR= RNM1* LSD + LYR
      IF (LIMPR.GT.1) LIMPR=1
      IF (LIMPR.LT.0) LIMPR=0
      LIMP(II,JJ)=LIMP(II,JJ) * LIMPR
      IF (LIMP(II,JJ).LT.0.0) LIMP(II,JJ)=0.0
      WRITE(6,1010) LIMP(II,JJ),LIMPR,LYR,LSD
1010 FORMAT(/,' LIMP= ',F6.2,' LIMPR= ',F6.2,' LYR= ',F6.2,
> ' LSD= ',F6.2,/)
      100 CONTINUE
      200 CONTINUE
      RETURN
      END
C
C *****

```


C *****

C

```

SUBROUTINE WAVE(I,J,WPROB)
  IMPLICIT REAL(M,L)
  COMMON/COVER/BCOV(1600),BADULT(1600),MCOV(1600)
  COMMON/SIZES/PRED(10,10),IYR,JSEAS,NDIM,NBYR,BR,MR
  COMMON/NSED/NSED1,NSED2,NSED3,NSED4,NSED5,NSED6,NSED7,
> NSED8,NSED9,NSED10,NSED11,NSED12,NSED13,NSED14

```

C

C...CHOOSSES A RANDOM NUMBER TO DETERMINE WHETHER

C...A WAVE DISTURBANCE OCCURS

C

```

DO 60 II=1,NDIM
DO 50 JJ=1,NDIM
WDIST=URAND(NSED7)
IF (WDIST.GT.WPROB) GO TO 50
IX=DIMM(I,J,II,JJ)
BCOV(IX)=0.0
MCOV(IX)=0.0
50 CONTINUE
60 CONTINUE
RETURN
END

```

C

C *****

C

```

SUBROUTINE PREDR(I,J,PPROB,PSD)
  IMPLICIT REAL(M,L)
  COMMON/COVER/BCOV(1600),BADULT(1600),MCOV(1600)
  COMMON/SIZES/PRED(10,10),IYR,JSEAS,NDIM,NBYR,BR,MR
  COMMON/TIMING/IBS,IGE,IMS,IPS
  COMMON/NSED/NSED1,NSED2,NSED3,NSED4,NSED5,NSED6,NSED7,
> NSED8,NSED9,NSED10,NSED11,NSED12,NSED13,NSED14

```

C

C...CHOOSSES PREDATION LEVELS FROM A TRUNCATED

C...RANDOM NORMAL DISTRIBUTION

```

DO 100 II=1,NDIM
DO 80 JJ=1,NDIM
IX=DIMM(I,J,II,JJ)
CALL RNORM(NSED8,NSED9,RNM1,RNM2)
PRED(II,JJ)=(RNM1*PSD + PPROB)
IF (J.LT.IPS) PRED(II,JJ)=0
IF (PRED(II,JJ).LE.0.) PRED(II,JJ)=0

```

C

```

WRITE(6,1010) PRED(II,JJ)
1010 FORMAT(' PRED(II,JJ)= ',F6.2)
80 CONTINUE
100 CONTINUE
RETURN
END

```

C

C *****

```

C *****
C
  SUBROUTINE MUSL(I,J,BMORTC,MYR,MIV,MINCR)
    IMPLICIT REAL(M,L)
    DIMENSION MINCR(10,10),BMORTC(10,10)
    COMMON/COVER/BCOV(1600),BADULT(1600),MCOV(1600)
    COMMON/SIZES/PRED(10,10),IYR,JSEAS,NDIM,NBYR,BR,MR
    COMMON/TIMING/IBS,IGE,IMS,IPS
    COMMON/REQN/AO,A1,B0,B1
    COMMON/NSED/NSED1,NSED2,NSED3,NSED4,NSED5,NSED6,NSED7,
> NSED8,NSED9,NSED10,NSED11,NSED12,NSED13,NSED14
C
  DO 680 II=1,NDIM
  DO 670 JJ=1,NDIM
    IX=DIMM(I,J,II,JJ)
    IF (J.LT.IMS) GO TO 670
    CALL RNORM(NSED10,NSED11,RNM1,RNM2)
C...DETERMINES MINCR, RECRUITMENT RATE
    MINCR(II,JJ)=(RNM1*MIV+ MYR)
    IF (MINCR(II,JJ).LT.0) MINCR(II,JJ)=0.
C
C...MINCA IS THE RECRUITMENT RATE ADJUSTED FOR FREE SPACE
C...AND RANDOM VARIATION IN TIME
    FREE=(100. - MCOV(IX)) /100.0
    MINCA=MINCR(II,JJ) * FREE
C
C...DECIDES IF THERE IS ENOUGH BARNACLE OR
C...MUSSEL COVER TO ALLOW MUSSEL RECRUITMENT
    IF (BCOV(IX).LT.10.0.AND.MCOV(IX).LT.10.0) MINCA=0.0
C
C...FREEB FOR BARNACLES - USED IN APPORTIONING MUSL OVERGROWTH
C...MUST BE BEFORE MCOV IS INCREMENTED
    FREEB= 100. - MCOV(IX) - BCOV(IX)
C
C...MGR IS INCREASE DUE TO MUSSEL GROWTH
C...MA IS ACTUAL NET CHANGE IN MUSSEL COVER
C
    MGR= MR * FREE * MCOV(IX)
    MA= MINCA + MGR - PRED(II,JJ)
    MCOV(IX) = MCOV(IX) + MA
    IF (MCOV(IX).GT.100) MCOV(IX)=100
C
C...CALCULATES BARNACLE MORTALITY DUE TO MUSSEL COMPETITION
C...ADDED .01 SO THAT WON'T HAVE DENOM.=0 WHEN MCOV=100
    BMORTC(II,JJ) = MA * (BCOV(IX) / (FREEB + BCOV(IX)
> + .01))
    IF (MA.LT.0) BMORTC(II,JJ)=0

```

```

C
  WRITE(6,2005) II,JJ
  WRITE(6,2020) MCOV(IX),BMORTC(II,JJ),MINCR(II,JJ),MINCA,
> MGR,MA
2005 FORMAT(2X,' II= ',I5,' JJ= ',I5)
2020 FORMAT(' MCOV=',F9.3,' BMORTC=',F9.3,' MINCR=',F9.3,
> ' MINCA= ',F9.3,' MGR= ',F9.3,' MA= ',F9.3,/)
  IF (MCOV(IX).LT.0.) MCOV(IX)=0.
670 CONTINUE
680 CONTINUE
  RETURN
  END

C
C *****
C
  SUBROUTINE BARN(I,J,BMORTC,BYR,BSD,BINCR)
  IMPLICIT REAL(M,L)
  DIMENSION BINCR(10,10),FUCUSE(10,10),BMORTC(10,10),BSEAS(24)
  COMMON/COVER/BCOV(1600),BADULT(1600),MCOV(1600)
  COMMON/SIZES/PRED(10,10),IYR,JSEAS,NDIM,NBYR,BR,MR
  COMMON/LIMPT/LIMP(10,10),LYR,LSO
  COMMON/SEAS/WDSEAS(24),PSEAS(24),BSEAS(24)
  COMMON/TIMING/IBS,IGE,IMS,IPS
  COMMON/REQN/AO,A1,B0,B1
  COMMON/NSED/NSED1,NSED2,NSED3,NSED4,NSED5,NSED6,NSED7,
> NSED8,NSED9,NSED10,NSED11,NSED12,NSED13,NSED14

C
  DO 780 II=1,NDIM
  DO 760 JJ=1,NDIM
    IX=DIMM(I,J,II,JJ)

C
C...LOSS DUE TO MUSSEL COMPETITION IS SUBTRACTED
C...WITH LOSS OF ADULTS PROPORTIONAL TO THEIR ABUNDANCE
C
    BADULT(IX)=BADULT(IX) - BMORTC(II,JJ) *
> BADULT(IX)/(BCOV(IX)+.01)
    BCOV(IX)=BCOV(IX)-BMORTC(II,JJ)

C
    IF (J.LT.IBS) GO TO 760
    CALL RNORM(NSED12,NSED13,RNM1,RNM2)
    BINCR(II,JJ)=(RNM2*BSD + BYR)
    IF (BINCR(II,JJ).LT.0) BINCR(II,JJ)=0

```

```

C
  FREE = (100 - BCOV(IX)) / 100.
C...ECD - EFFECTIVE CELLANA DENSITY
C...Y - LIMPET (CELLANA) DENSITY AT WHICH NO BARNACLES SETTLE;
C      DEPENDS ON BARNACLE RECRUITMENT RATE (BINCA)--
C      ALLOWS SWAMPING EFFECT OF INCREASED BARNACLE RECRUITMENT
  BINCA= BINCR(II,JJ) * BSEAS(J) * FREE
  IF (FREE.LT.0.1) ECD=0
  IF (FREE.GE.0.1) ECD=LIMP(II,JJ) / FREE
  Y= AO + A1 * BINCA * FREE
  CL=ECD/Y
  IF (ECD.GE.Y) CL=1
  BSET = FREE * (BINCA - CL*BINCA)
C...BADULT IS BCOV FROM PREVIOUS YEAR, ADJUSTS GROWTH
  BGR= FREE * BR * (BCOV(IX) - BADULT(IX))
  IF (J.GT.IGE) BGR=0
  BA= BSET + BGR - PRED(II,JJ)
  BCOV(IX) = BCOV(IX) + BA
  IF (BCOV(IX).GT.100.) BCOV(IX)=100.
C
  WRITE(6,2020) II,JJ,BINCA,BMORTC(II,JJ),ECD,Y,CL,
    > BGR,BA,BCOV(IX)
2020 FORMAT(/,' BARN ',2I3,' BINCA= ',F6.2,' BMORTC= ',F6.2,
    > 2X,F6.2,'/',F6.2,' PR LOSS= ',F6.2,' BGR= ',F6.2,' BA=
',F6.2,
    > ' BCOV= ',F6.2,/)
50 CONTINUE
  IF ((BCOV(IX)+MCOV(IX)).GT.100)
    > BCOV(IX)=100-MCOV(IX)
  IF (BCOV(IX).LT.0.) BCOV(IX)=0.
760 CONTINUE
780 CONTINUE
  RETURN
  END
C
C *****
C
  SUBROUTINE RNORM(NSEDA,NSEDB,RNM1,RNM2)
  DATA PI2/.62831853E01/
C
C...URAND IS THE SYSTEM'S RANDOM UNIFORM NUMBER GENERATOR
C...RNORM CHOOSES NUMBERS FROM A RANDOM NORMAL DISTRIBUTION
C
  A1=URAND(NSEDA)
  A2=URAND(NSEDB)
  RNM1=SQRT(-.2E01*ALOG(A1))*SIN(PI2*A2)
  RNM2=SQRT(-.2E01*ALOG(A1))*COS(PI2*A2)
  RETURN
  END
C
C *****

```

```

C *****
C
C      FUNCTION DIMM(I,J,K,L)
C      COMMON/SIZES/PRED(10,10),IYR,JSEAS,NDIM,NBYR,BR,MR
C
C...CONVERTS SINGLE DIMENSIONED ARRAY FOR USE WITH 4 SUBSCRIPTS
C
C      DIMM=(((L-1)* NDIM+K-1) * JSEAS+J-1) * IYR + I
C      RETURN
C      END
C
C *****
C
C      SUBROUTINE OUTPUT(I,J,KP,KB,KLL,KM)
C      IMPLICIT REAL(M,L)
C      COMMON/COVER/BCOV(1600),BADULT(1600),MCOV(1600)
C      COMMON/SIZES/PRED(10,10),IYR,JSEAS,NDIM,NBYR,BR,MR
C      COMMON/LIMPT/LIMP(10,10),LYR,LSO
C      COMMON/YARRAY/YP(12),YB(12),YM(12),YL(12)
C
C      300 CONTINUE
C      DO 500 II=1,NDIM
C      DO 400 JJ=1,NDIM
C      IX=DIMM(I,J,II,JJ)
C      WRITE(25,2400) I,J,II,JJ,MCOV(IX),BCOV(IX),LIMP(II,JJ),
C      > YP(KP),YP(KP+6),YB(KB),YB(KB+6),YM(KM),YM(KM+6),
C      > YL(KLL),YL(KLL+6)
C      2400 FORMAT(4I2,11F6.2)
C      400 CONTINUE
C      500 CONTINUE
C      RETURN
C      END
C
C      END OF DATA
C
C *****

```

VITA

Joyce Waterhouse was born in Pasadena, California and lived in that city until graduating from Pasadena High School in June 1976. She attended the University of California, Irvine until 1980, when she received a Bachelor of Science degree in Biological Sciences. From the fall of 1980 to December of 1985, she attended the University of Tennessee, Knoxville where she was awarded a Ph.D. in Ecology.

The author is a member of the Ecological Society and Phi Beta Kappa. She will be pursuing postdoctoral research after graduation.